Relating jack pine budworm damage to stand inventory variables in northern Michigan

Deborah G. McCullough, Larry D. Marshall, Lyle J. Buss, and Jari Kouki

Abstract: Stand-level mortality and top kill from a 1991–1993 jack pine budworm (*Choristoneura pinus pinus* Freeman) outbreak were surveyed annually in the Raco Plains area of the Hiawatha National Forest in Michigan's Upper Peninsula from 1992 to 1994. Defoliation was visually estimated and percentage of trees killed or top killed was determined in 104 stands. In 1994, tree mortality attributable to the outbreak averaged 8% and 17% of trees had dead tops. Current stand inventory data, including age, site index, basal area, and size, were acquired from the Hiawatha Forest. Stands were grouped on the basis of inventory variables used for jack pine management in the Lake States region of the United States. Differences in tree mortality and top kill between groups, and associations between tree mortality and inventory variables, were evaluated. Tree mortality was greater in overmature stands and in overstocked stands, but stand size had little effect. Contrary to expectations, mortality was lower on poor sites with low site index values than on better sites with higher site index values. Mortality was not related to abundance of open-grown, full-canopied wolf trees or to abundance of trees infected with pine gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka (=*Peridermium harknessii* J.P. Moore)). Amount of top kill was related to defoliation severity and was higher in overmature and understocked stands. Top kill was not strongly associated with amount of tree mortality or with inventory variables.

Résumé : Les arbres morts et ceux dont la tête avait été tuée à cause de la tordeuse des bourgeons du pin gris (*Choristoneura pinus pinus* Freeman) ont été inventoriés annuellement à l'échelle du peuplement, de 1992 à 1994, suite à une épidémie survenue de 1991 à 1993 dans la zone de Raco Plains dans la Forêt Nationale Hiawatha située dans la partie septentrionale de la péninsule du Michigan. La défoliation a été estimée visuellement et le pourcentage d'arbres morts ou dont la tête seulement avait été tuée a été déterminé dans 104 peuplements. En 1994, 8% des arbres en moyenne ont été tués et 17% des arbres avaient la tête morte suite à l'épidémie. Les données courantes d'inventaire des peuplements, incluant l'âge, l'indice de site, la surface terrière et la dimension, furent obtenues de la Forêt Hiawatha. Les peuplements furent regroupés sur la base des variables inventoriées qui sont utilisées pour l'aménagement du pin gris dans la région des Grands Lacs aux États-Unis. Les différences entre les groupes de peuplements quant à la mortalité et à la mort de la tête des arbres ainsi que les relations entre la mortalité et les variables inventoriées ont été évaluées. Il y avait plus d'arbres morts dans les peuplements surannés et dans les peuplements dont la densité relative était excessive tandis que la dimension du peuplement avait peu d'influence. Contrairement à ce qu'on aurait pu supposer, la mortalité était plus faible sur les sites pauvres avec de faibles valeurs d'indice de site que sur les sites plus riches avec des valeurs d'indice de site plus élevées. La mortalité n'était pas reliée à l'abondance des arbres loups croissant à découvert avec une forte cime ni à l'abondance des arbres infectés par la rouille-tumeur du pin (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka (=*Peridermium harknessii* J.P. Moore)). La quantité d'arbres dont la tête avait été tuée était reliée à la sévérité de la défoliation et était plus élevée dans les peuplements surannés et dans les peuplements dont la densité relative était faible. La mort de la tête des arbres n'était pas étroitement associée à la quantité d'arbres morts ni aux variables inventoriées.

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Introduction

Jack pine (*Pinus banksiana* Lamb.) ecosystems are important both economically and ecologically in the Lake States region of the United States and across much of Canada. Jack pine is the primary softwood pulp source in the Lake States and is the most widely distributed pine in Canada (Hackett and Piva 1993; Moore 1984; Rudolph 1984). Jack pine is a fast-growing, shade-intolerant species and is largely restricted to sandy soils with low nutrient and moisture availability in the Lake States (Benzie 1977).

Because jack pine uses nutrients more efficiently than most other tree species, merchantable stands can be harvested from even poor sites (Alban et al. 1978; Bockheim and Leide 1991; Cayford 1970).

Jack pine budworm (*Choristoneura pinus pinus* Freeman) is a major pest of jack pine (Howse 1984) and is distributed sympatrically with its host. Extensive jack pine budworm (JPBW) outbreaks generally occur at intervals of 6 to 10 years and persist for 2 to 3 years (Volney 1988; Volney and McCullough 1994). Larvae mine pollen cones early in spring, then feed on current-year foliage as it expands (Kulman and Hodson 1961; LeJeune and Black 1950; Nealis and Lomic 1994). Severe defoliation, particularly in the upper canopy, and back-feeding on older foliage occur when populations are high. Effects of outbreaks can include reduced radial growth, top kill, tree mortality, and increased risk of wildfire (Cerezke 1986; Gross 1992; Gross and Meating 1994; Kulman et al. 1963).

Despite the important role that JPBW plays in jack pine ecosystems, few studies have quantified effects of JPBW defoliation at the stand level, the basic unit for forest management decision making. Hazard rating systems that are based on stand-level inventory data are frequently used by state, provincial, and federal resource management agencies to rank the relative vulnerability of stands to JPBW damage (e.g., Albers et al. 1995; Jones and Campbell 1986; Hall et al. 1995; Knowles and Marshall 1995; Weber 1986). Ideally, annual harvests can be allocated to high hazard stands that are most likely to sustain damage. High-hazard stands are generally assumed to include overmature stands, stands growing on poor sites, understocked or overstocked stands, or small stands with a high proportion of edge area (Jones and Campbell 1986; McCullough et al 1994; Weber 1986, 1995).

However, associations between JPBW damage and stand inventory variables have not been quantitatively evaluated and no hazard rating system has been tested or validated in the Lake States. Objectives of this study were to (*i*) quantify stand-level top kill and tree mortality resulting from a 1991–1993 JPBW outbreak in the eastern Upper Peninsula of Michigan and (*ii*) evaluate relationships among stand characteristics and the amount of mortality and top kill resulting from JPBW defoliation. We were interested primarily in stand-level inventory variables that are routinely collected and used operationally in forest management, rather than variables requiring additional sampling or intensive data collection (Hedden 1981; Marshall and McCullough 1995). Identification of consistent relationships between stand characteristics and JPBW-related damage could enable managers to prioritize stands for harvest or related activities and better incorporate impacts of JPBW in forest planning.

Methods

Study site

The study was conducted in the Raco Plains area of the eastern Hiawatha National Forest in Michigan's Chippewa County. The Raco Plains area is characterized by level to gently rolling terrain, sandy soils underlain by sand and gravel, and extensive tracts of jack pine forest (Heym 1993). All stands dominated by jack pine in four management compartments were surveyed annually from 1992 to 1994. Management compartments ranged in size from 6 to 14 km^2 and each included 20–30 stands. Stands ranged in size from 0.1 to 120 ha. Each stand in the four compartments was visited by Hiawatha National Forest personnel in 1991–1994, and boundaries and inventory data were updated. Selected inventory variables were acquired from the Hiawatha National Forest database. Stand variables included in this analysis were age, basal area per hectare (BA), area (in ha), and site index (SI). Basal area, a measure of stand density, is defined as the total cross-sectional area of dominant or codominant trees per unit of land area (Avery and Burkhart 1994; Husch et al. 1982). Site index is an indicator of site quality that is widely used in forest management in the Lake States. Site index is defined as the average total height of free-growing, uninjured, dominant or codominant trees in fully stocked, even-aged stands (Avery and Burkhart 1994; Carmean 1975; Haggland 1981; Husch et al. 1982).

JPBW damage survey

Circular, 0.01-ha fixed-radius survey plots were located in stands each year using randomly selected points from a grid overlaying compartment maps and aerial photos. At least two plots were located in each stand; an additional plot was allocated to stands larger than 32 ha, and two additional plots were allocated to stands larger than 48 ha. All stands within the four compartments were examined in 1992. Openings, recently harvested stands, or stands dominated by other species were not surveyed in 1993 and 1994. A total of 104 stands were surveyed in all 3 years. Surveys were conducted in late summer each year, after budworm larvae had completed feeding.

Defoliation was visually estimated in each plot in 1992–1994, using binoculars when needed. Defoliation was rated as severe when all or nearly all current-year foliage had been consumed in the upper crown and backfeeding on older foliage was observed. Moderate defoliation was recorded when most current-year foliage in the upper canopy was partially consumed, but little backfeeding had occurred. Defoliation was rated as low when most current-year foliage remained, even in the upper canopy, and little or no backfeeding was apparent. No ground surveys were conducted in 1991, the first year of the outbreak. Sketch maps produced by the USDA Forest Service during aerial surveys in 1991 were used to obtain a general estimate of defoliation in the four compartments in 1991.

Number of jack pine trees, dead trees, and top-killed trees were counted in each plot. Mortality and top kill were classified as "recent" (i.e., likely resulting from the 1991–1993 JPBW outbreak) or "previous" (i.e., occurring prior to the 1991–1993 outbreak). Although the designation was based on subjective criteria, it was not difficult to distinguish between recent and previous damage. Trees damaged before the 1991–1993 outbreak typically had exposed bleached wood due to bark sloughing off, and few small twigs remained in dead tops or on branches of dead trees. Stems often had evidence of decay and dead tops were frequently broken. In contrast, trees damaged during the 1991–1993 outbreak retained many small twigs even in the upper canopy of top-killed trees, evidenced little or no peeling bark, and tops were rarely broken. Percentages of recent and previous mortality and top kill were determined in each plot. Stand means were calculated and used in subsequent analyses.

Other hazard factors

Abundance of wolf trees (open-grown, full-canopied trees), suppressed or intermediate trees (i.e., crowns did not extend into the canopy with dominant and codominant trees), and trees infected with pine gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka (=*Peridermium harknessii* J.P. Moore)) were qualitatively ranked within each plot as none, few, or abundant each year. Median values of the estimated abundance of wolf trees, suppressed trees, and trees with gall rust were determined for each stand.

Statistical analysis

Stands were grouped for analysis using inventory variables including age, SI, BA, and area. Grouping was based on categories or threshold values used for jack pine management in the Lake States (Benzie 1977; Jones and Campbell 1986; McCullough et al. 1994; Weber 1995) and median values of the inventory variables. Stands were grouped by age (0–50 years old or >50 years), site quality (SI ≤ 15.2 or SI > 15.2), BA (understocked, BA < 16.1 m^2/ha; well stocked, 16.1 < BA < 25.2 m^2/ha; or overstocked, BA > 25.2 m^2/ha), and size (≤12 ha or >12 ha). Mortality and top kill measured in 1994 were used to assess cumulative damage resulting from the 1991–1993 outbreak, and data were log transformed to stabilize variance.

Associations among defoliation, mortality, top kill, and stand inventory data were analyzed using one-way and two-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA). Homogeneity of variance was evaluated using Levenes' test (Levene 1960). In a few cases when transformed variables did not meet assumptions of homogeneity of variance, the conservative Brown–Forsythe (Brown and Forsythe 1974) and Welch statistics (Dixon et al. 1990), with correspondingly reduced error degrees of freedom, were calculated to test significance of differences among groups. Pearson's correlation coefficient (r) was calculated to evaluate linear relationships among mortality, top kill, and inventory variables at the 0.05% level of significance (n = 104 stands). Associations between previous damage and recent damage were evaluated using Pearson's correlation coefficient (r) and ANCOVA.

ANOVA was used to examine differences in mortality and top kill among stands grouped on the basis of abundance of wolf trees, suppressed or intermediate trees, and gall rust. Associations among these ranked variables, inventory data, and JPBW damage were evaluated using Spearman's nonparametric correlation coefficient (r_s) (Conover 1980) at the 0.05 level of significance (n = 104 stands). These variables would rarely be included in inventory databases or used operationally to predict stand vulnerability to JPBW damage and were therefore not included in subsequent analyses.

Nonlinear associations of mortality and inventory variables

Because of the potential impact of JPBW-related mortality on productivity, yield, or noncommodity objectives, additional analyses were conducted to evaluate associations between recent mortality and stand inventory variables. Results from multiple linear regression indicated that inventory variables explained little variance in recent mortality. For example, the best subset of predictors based on Mallows' C_p (Hocking 1972) explained less than 20% of variability in recent mortality (adjusted r^2 = 0.15; df = 3,100). Further, scatterplots indicated associations between recent mortality, and most inventory variables were not strongly linear. Therefore, proportion of recently killed trees in stands with nonzero values of mortality (p) was transformed into the log odds ratio λ, where $\lambda = \ln(p/1 - p)$. We then fit a smoothed additive regression model: $\lambda = s(\text{area}) + s(\text{BA}) + s(\text{SI}) + s(\text{age}) + e$, where $s(x)$ was a smoothed function of its argument. Each smoothed regression function was plotted against its argument to examine nonlinear associations between inventory variables and recent mortality. ANOVA was used to test significance of predictors; equations lacking each variable were compared to the smooth regression model with all predictors. Estimated mortality (calculated using the inverse logs odd ratio $p = (\exp \lambda)/(1 + \exp \lambda))$ was plotted against observed values to evaluate fit of the model.

Because smoothed regressions cannot be used to generate a predictive function or explicit expressions of smoothed functions, plots of smoothed regression functions were used to identify continuous broken straight lines to describe nonlinear associations (Seber and Wild 1989). Variables were transformed, and performance of the broken line regression (a submodel of smoothed regression) was tested against the smoothed regression. Results indicated that the broken line submodel did not differ significantly from the smoothed regression model (F = 1.02; df = 7,52; P = 0.440).

Nonlinear analyses were conducted using SPLUS statistical software (Statistical Sciences Inc. 1993); other analyses were conducted using BMDP386 statistical software (Dixon et al. 1990).

Results

Stands

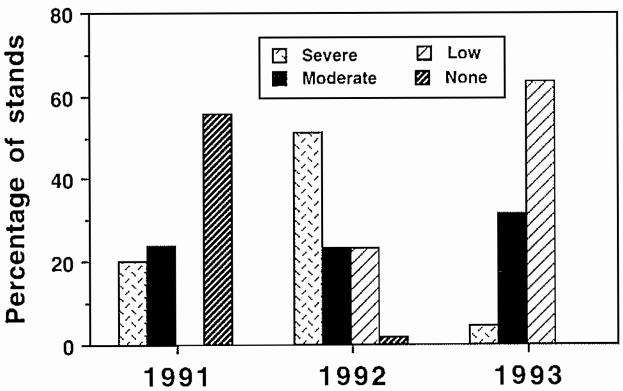
A total of 104 stands dominated by jack pine, accounting for 1497 ha, were surveyed annually. Stand age ranged from recently harvested areas with new seedlings up to 72 years old. Stand age averaged 49 years, with a median age of 55 years. In the Lake States, where jack pine is frequently harvested at 40–55 years of age, nearly two-thirds of the surveyed stands would be considered mature to overmature (Benzie 1977; Jones and Campbell 1986; Weber 1986, 1995). Site index of surveyed stands ranged from 11.3 to 18.3 m, fairly representative of sites typically occupied by jack pine in the Lake States (Jones and Campbell 1986; Schmidt and Carmean 1988; Weber 1995). Mean and median SI was 15.2 m. Basal area of surveyed stands ranged from 2.3 to 37.8 m^2/ha, with a mean BA of 16.3 m^2/ha. Approximately 50% of the surveyed stands were either saplings or would likely be considered understocked (<16.1 m^2/ha) by Lake States managers (Albers et al. 1995; Benzie 1977; McCullough et al. 1994; Weber 1986, 1995). Roughly 35% of stands would be considered well stocked (16.1 < BA < 25.2 m^2/ha) and 15% were overstocked (BA > 25.2 m^2/ha). Stand size ranged from 1 to 122 ha, with an average size of 15 ha. Almost 70% of stands were less than 16.2 ha in size, reflecting federal restrictions on clearcut size in northeastern national forests (D. Heym, District Silviculturist, Hiawatha National Forest, personal communication).

Stand age was significantly correlated with BA (r = 0.584), as expected. Correlations of age and SI were marginally significant (r = 0.241), and age was not related to stand size (r = −0.022). Basal area was significantly correlated with SI (r = 0.443), indicating that better quality sites supported higher stocking. Stand size was not significantly associated with other stand measurements.

Defoliation

Defoliation by JPBW was first observed on the Hiawatha National Forest in 1991 (Fig. 1). Estimates from sketch maps made during 1991 aerial defoliation surveys suggested that roughly 40% of stands in the four compartments were moderately to severely defoliated (USDA Forest Service, Northeastern Area State and Private Forestry, Forest Health Management, 1991 Hiawatha National Forest

Fig. 1. Percentage of stands with severe, moderate, light, or undetectable jack pine budworm defoliation from 1991 to 1993 (n = 104 stands).



sketch map). Defoliation in the Raco Plains area peaked in 1992, when 75% of the stands surveyed sustained moderate or high defoliation (Fig. 1). In 1993, moderate to severe defoliation was observed in only 20% of the stands and the outbreak largely collapsed. Although JPBW larvae were occasionally found in 1994, there was no noticeable defoliation in the study area. Less than 5% of the 104 stands sustained severe defoliation in more than 1 year. Most stands experienced 1 year of severe defoliation and 1 year of light or moderate defoliation.

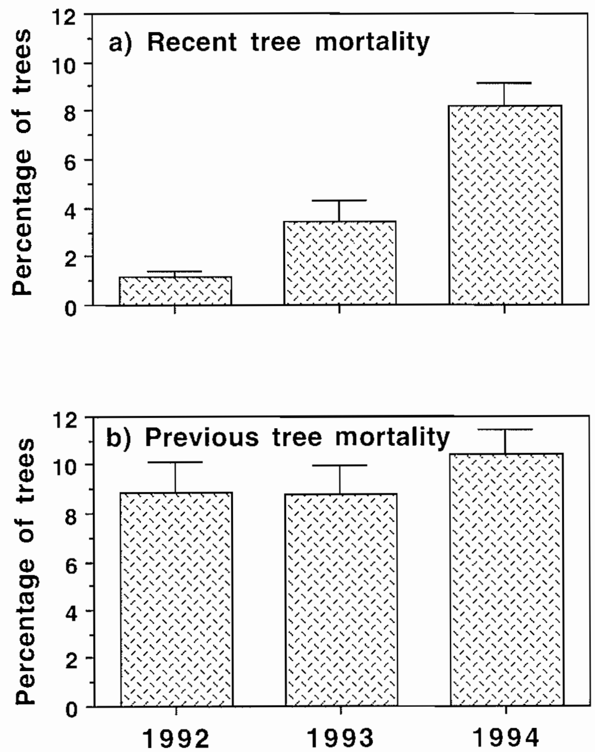
Mortality

Percentage of recently killed trees jumped dramatically from less than 2 percent in 1992 to roughly 8 percent in 1994 (Fig. 2a). Mortality in individual stands in 1994 ranged from 0 to almost 40%. Recent mortality was not significantly associated with estimated defoliation in 1991 (r_s = 0.120), 1992 (r_s = −0.117), 1993 (r_s = 0.007), the sum of 1992 and 1993 defoliation rankings (r_s = −0.087), or the sum of 1991–1993 defoliation rankings (r_s = 0.107).

ANOVA results indicated that recent mortality was significantly higher in 50-year-old or older stands than in stands less than 50 years old (F = 16.39; P < 0.001) (Table 1). Recent mortality in stands with SI greater than 15.2 m was three times higher than mortality in stands with low SI (Table 1), a result that was statistically significant (F = 4.88; P = 0.029), but contrary to expectations. Recent mortality differed significantly among stands considered to be understocked, well stocked, or overstocked (F = 5.23; P = 0.007) (Table 1). As expected, mortality was greatest in overstocked stands where competition for light, nutrients, or water would presumably be most intense. Stands less than 12 ha and larger stands had similar levels of recent mortality (Table 1), and differences were not significant (P = 0.978). Correlation analysis supported ANOVA results, with significant linear associations between recent mortality and stand age (r = 0.306), SI (r = 0.308), and BA (r = 0.306). Associations between recent mortality and stand size were not significant (r = 0.026).

Two-way ANOVA was used to further examine interactions of age, SI, and BA on recent mortality (Table 2). Both age (F = 8.13; P = 0.005) and SI (F = 14.97; P = 0.003)

Fig. 2. Mean percentage (and standard error of the mean) of (a) recent tree mortality and (b) previous tree mortality in 104 stands sampled annually from 1992 to 1994. Recent mortality was attributable to the 1991–1993 jack pine budworm outbreak; previous mortality occurred before the outbreak.



significantly affected recent mortality, but the interaction was not significant (P = 0.350). These results again indicated that mortality was greater in high SI stands than in low SI stands, for both younger and older stands. Two-way ANOVA with SI and BA indicated that recent mortality differed due to SI (F = 12.17; P < 0.001), but not due to stocking (P = 0.373), or the interaction (P = 0.389). Mortality in high SI stands was consistently greater than that in low SI stands in understocked, well-stocked, and overstocked stands (Table 2). For example, in stands on better sites, mortality ranged from 10% in understocked stands to 14% in overstocked stands, while 3–9% of trees on low SI stands died. Interactions of age and BA could not be determined using two-way ANOVA, because there were no young overstocked stands. Stands were grouped into five classes (Table 2), and a one-way ANOVA was used to test for significant differences among groups. Recent mortality differed significantly among the groups (F = 4.67; P = 0.032), with the lowest mortality occurring in young understocked stands and the greatest mortality occurring in older stands that were overstocked. Results of two-way ANOVA with stand age and size indicated significant differences between younger and older stands (F = 15.47; P < 0.001), but no significant differences due to size (P = 0.857) or the interaction (P = 0.113). When stand size was combined with either BA or SI in two-way ANOVA, both BA (F = 5.84; P = 0.004) and SI (F = 22.77; P = 0.001)

Table 1. Mean percentage of recently killed trees in 1994 in stands grouped by one inventory variable.

Inventory variable	% mortality*
Age (years)	
Younger (0–49; n=41)	4.5 (1.13)
Older (≥50; n=63)	10.7 (1.22)
Site index (m)	
Lower (0–15.2; n=54)	4.5 (0.94)
Higher (>15.2; n=50)	12.3 (1.39)
Basal area (m^2/ha)	
Understocked (0–16.0; n=50)	5.7 (1.27)
Well stocked (16.1–25.2; n=32)	9.0 (1.61)
Overstocked (>25.2; n=22)	12.9 (1.78)
Size (ha)	
Smaller (≤12; n=58)	8.2 (1.21)
Larger (>12; n=46)	8.3 (1.39)

*Standard error of the mean is in parentheses.

were significant, but stand size and the interaction terms were not (Table 2).

Smoothed regression plots were examined to evaluate nonlinear associations between amount of recent mortality and stand attributes (Fig. 3). Mortality was relatively low and unrelated to stand age in stands that were 41 to 50 years old (Fig. 3*a*). However, mortality increased sharply with age in stands that were 50 to 55 years old and older. There was a negative association between age and mortality in young stands less than 30 years old. This may represent competition and natural thinning, but should be interpreted cautiously since only a few young stands were included in our survey. In the few stands with SI less than 14.3 m, there was a negative association with recent mortality (Fig. 3*b*). However, there was a strong linear association between mortality and SI for stands with a SI of 14.3 to 16.8 m. The association was slightly positive in stands with SI of 16.8 to 17.4 m, but the slope was not as steep. Mortality increased linearly with BA up to a BA of 12.6 m^2/ha, and also increased linearly when BA exceeded 26.4 m^2/ha (Fig. 3*c*). Mortality in stands with a BA of 12.8 to 26.2 m^2/ha did not appear to be strongly influenced by stocking. Mortality increased with stand size up to 16.2 ha, then was negatively related to stand size in stands that were larger than 16.2 ha (Fig. 3*d*). A broken straight line regression was developed using smoothed regression functions. Transformed inventory variables predicted about 40% of the variation in proportion of recent mortality in stands with nonzero values of mortality (r^2 = 0.395; df = 6,52; F = 5.66; P < 0.0001).

Other hazard factors

Wolf trees, also known as orchard trees, may contribute to JPBW larval survival because of their heavy production of pollen cones that provide a refuge for larvae in spring before current-year foliage expands (Foltz et al. 1972; LeJeune 1950; Nealis and Lomic 1994). Wolf trees were ranked as abundant in 33 stands, occasional in 39 stands, and were not observed in remaining stands. Abundance of wolf trees in stands was significantly and negatively associated with recent mortality (r_s = −0.401), stand BA (r_s = −0.665), age (r_s = −0.400), and SI (r_s = −0.397). Recent tree mortality was greatest in stands with no wolf trees, and lowest in stands where wolf trees were abundant (F = 6.47; P = 0.002).

Suppressed or intermediate trees could also contribute to larval survival by intercepting larvae during dispersal or because of abundant pollen cone production, and are often severely defoliated during outbreaks (Batzer and Jennings 1980; Gross 1992; Kulman et al. 1963). Suppressed trees were abundant in only two stands, were occasionally present in 56 stands, and were not observed in 46 stands. Mortality was significantly greater when at least a few suppressed or intermediate trees were present in the stand than in stands with no suppressed or intermediate trees (F = 15.84; P < 0.001). This difference and the significant correlation between abundance of suppressed or intermediate trees and mortality (r_s = 0.318) may, however, be confounded with the influence of other stand attributes. Abundance of suppressed or intermediate trees was correlated with stand BA (r_s = 0.369), SI (r_s = 0.369), and age (r_s = 0.236).

Gall rust is a chronic and common pathogen in jack pine stands (Hiratsuka 1987), but increased vulnerability of infected trees to defoliation impact has not been previously evaluated. Gall rust was abundant in 53 stands, and a few infected trees were present in 40 other stands. There was no significant difference in recent mortality between stands where gall rust was abundant and stands with few or no infected trees (P = 0.131). The correlation between recent mortality and gall rust abundance was not significant (r_s = −0.055). Abundance of gall rust was negatively correlated with SI (r_s = −0.418), indicating that the pathogen may be more common on poor sites than on better sites. Gall rust and stand age were not significantly associated (r_s = −0.147); correlations between gall rust and BA were negative but marginally significant (r_s = −0.251).

Previous mortality

Amount of previous mortality was consistent among the 3 years of the survey, with means ranging from 9 to 10.5% (Fig. 2*b*). Associations between previous and recent mortality in stands were examined to determine whether some stands were likely to repeatedly sustain high mortality during JPBW outbreaks. Amount of previous mortality in stands was significantly associated with recent mortality (r = 0.293) and was a significant covariate (F = 5.19; P = 0.025) when ANCOVA was used to evaluate effects of stand traits on recent mortality. However, further analysis revealed that when stands with zero values were excluded, there was no significant relationship between recent and previous mortality. Results from linear regression analysis of previous mortality on recent mortality using only stands with nonzero values were not significant (P = 0.992) and explained little variation in percent recent morality (r = 0.020). This indicated that abundance of standing dead trees was not a good predictor of the amount of mortality from the recent outbreak.

Table 2. Mean percentage of recently killed trees in 1994 in stands grouped by two inventory variables.

	Age		Site index		Size	
	Younger	Older	Lower	Higher	Smaller	Larger
Basal area						
Understocked	3.9 (1.31) n=30	6.6 (2.39) n=10	3.2 (1.10) n=37	12.6 (3.07) n=13	7.8 (2.09) n=30	3.15 (1.11) n=23
Well stocked	10.1 (2.07) n=22	8.3 (2.42) n=20	6.6 (2.08) n=12	10.5 (2.23) n=20	7.3 (1.63) n=21	12.3 (3.41) n=11
Overstocked	— n=0	13.5 (1.76) n=21	8.8 (2.51) n=5	14.1 (2.13) n=17	11.1 (2.45) n=10	14.3 (2.58) n=12
Age						
Younger			2.9 (1.15) n=27	7.6 (2.27) n=14	5.9 (1.28) n=22	2.8 (1.24) n=19
Older			6.1 (1.43) n=27	14.1 (1.63) n=36	9.5 (1.59) n=36	12.1 (1.89) n=27
Site index						
Lower					5.3 (1.47) n=30	3.5 (1.04) n=24
Higher					11.3 (1.79) n=28	13.5 (2.20) n=22

Note: Standard error of the mean is in parentheses.

Top kill

Percentage of trees that were top killed as a result of JPBW defoliation during the 1991–1993 outbreak increased substantially from 1992 to 1993 (Fig. 4*a*). Recent top kill ranged from 0 to 76% of trees in individual stands surveyed in 1994.

Percentage of recently top-killed trees from the 1994 survey was significantly correlated with defoliation rankings obtained during our ground surveys in 1992 (r_s = 0.359) and 1993 (r_s = 0.326), and with the sum of 1992 and 1993 defoliation ratings (r_s = 0.360). The association between recent top kill and 1991 defoliation estimates from sketch maps was negative, but only marginally significant (r_s = −0.210), and recent top kill was not associated with the sum of 1991–1993 defoliation rankings (r_s = 0.038). Amount of recent top kill and recent mortality was not significantly related (r_s = 0.045), indicating that stand susceptibility to top kill may be quite different from susceptibility to mortality. Percentage of trees recently top killed was not significantly associated with stand BA (r = −0.088), SI (r = −0.084), or size (r = −0.158). Top kill was somewhat higher in older stands than in younger stands (Table 3), but differences were insignificant (P = 0.069). When stands were grouped on the basis of age and BA (Table 4), top kill was highest in understocked stands that were at least 50 years old (F = 5.14; P < 0.001). Other variables tested in two-way ANOVAs did not significantly affect recent top kill (Table 4). Amount of recent top kill was correlated with estimated abundance of gall rust (r_s = 0.243), but not with abundance of wolf trees (r_s = 0.161) or suppressed and intermediate trees (r_s = −0.082).

Previous top kill

Percentage of trees top killed before the 1991–1993 JPBW outbreak ranged from 6 to 8% in 1992 and 1993, but dropped in 1994 to an average of 1–2% (Fig. 4*b*). Reasons for the low amount of previous top kill recorded in 1994 were not clear but could have included mortality of previously top killed trees. Because values were so low in 1994, previous top kill measured during 1993 was also used to examine associations with other variables. Percentage of previously occurring top kill, measured in 1993, was not significantly associated with recent mortality (r = −0.095), recent top kill (r = 0.029), or previous mortality (r = −0.038).

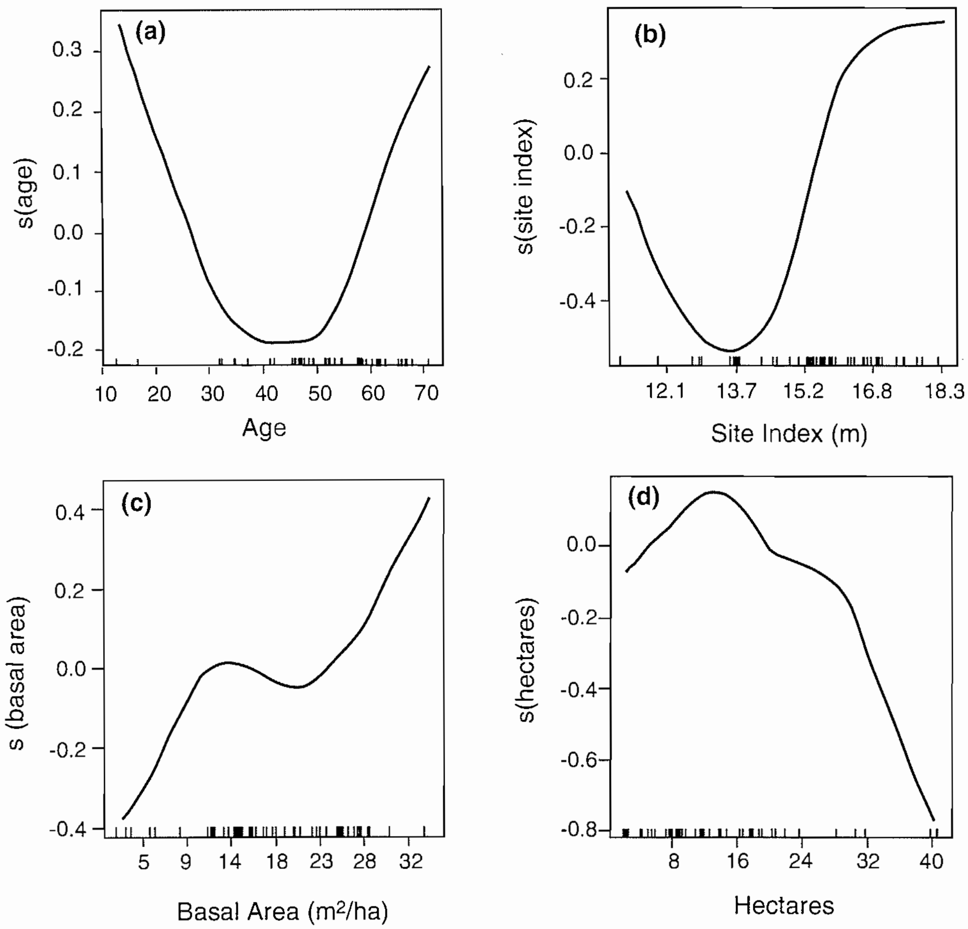
Discussion

During the 1991–1993 JPBW outbreak, few stands experienced more than 1 year of heavy defoliation, consistent with observations by Gross and Meating (1994) in Ontario. Weber (1995) speculated that severe defoliation does not occur in consecutive years because of delayed bud break, low pollen cone production, or female moth emigration from defoliated stands.

Stand-level estimates of the amount of mortality resulting from a JPBW outbreak are needed for forest planning and yield estimates. Tree mortality averaged 8% in 1994, although up to 40% of trees within individual stands were killed.

Our mean mortality values were somewhat higher than levels reported previously, but were probably conservative. Kulman et al. (1963) reported 2–6% mortality of

Fig. 3. Plots of smoothed regression functions illustrating associations between recent tree mortality and stand inventory variables, including (*a*) age, (*b*) site index, (*c*) basal area, and (*d*) size, in stands with nonzero mortality. Small vertical lines on the horizontal axis denote individual stands ($n = 59$).



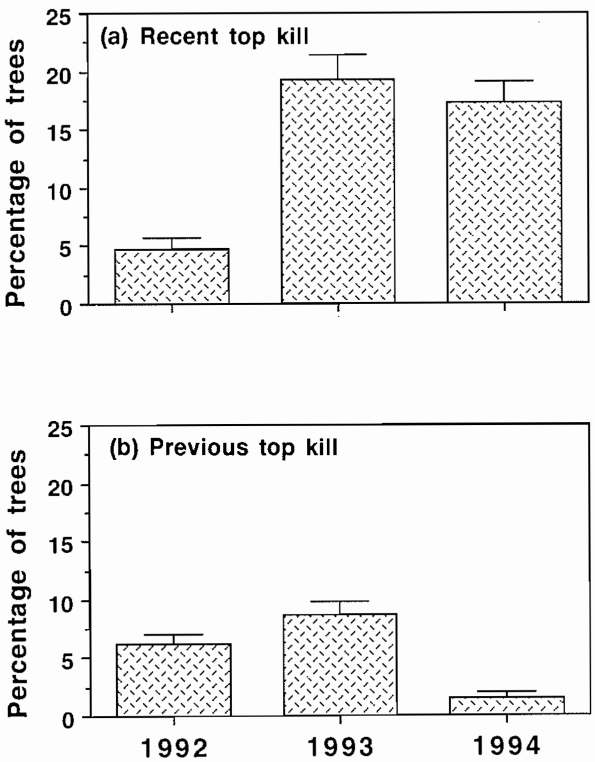
dominant or codominant trees 2 years after an outbreak in Minnesota. Mortality attributed to JPBW defoliation in northeastern Ontario ranged from 0 to 6%, but averaged only 2% across all stands (Gross 1992; Gross and Meating 1994). Surveys in other Ontario locations indicated that cumulative mortality resulting from the JPBW outbreak averaged 14% (Constable et al. 1988; Hopkin and Howse 1995). Mean mortality values in the stands we surveyed were likely reduced by salvage harvests in six mature to overmature stands during the 1993–1994 winter. In addition, we surveyed all stands dominated by jack pine, including young stands. The studies cited above were largely confined to older stands with trees of merchantable size, where defoliation effects would presumably be more severe (Gross and Meating 1994; Kulman et al. 1963). Mortality could continue to accumulate in the stands we surveyed, especially if secondary pests such as *Ips pini* (Say) become abundant.

Understanding the stand factors associated with high levels of JPBW-related mortality could enhance our ability to predict impacts of future outbreaks and to rate relative vulnerability of stands in management units. Managers should be wary, however, of overly simplistic hazard rating systems based on untested assumptions. We found that relationships between tree mortality and stand factors were often not linear, as evidenced by low correlation coefficients, and some associations (e.g., SI and mortality) were unexpected.

Our results did support current JPBW management guidelines that recommend maintaining stocking at 16.1–25.2 m^2/ha in the Lake States (e.g., McCullough et al. 1994). The significant association between BA and mortality was largely attributable to stands with BA less than 12.6 m^2/ha or exceeding 26.4 m^2/ha. Although stands with BA of 12.6–16.1 m^2/ha would not be considered well stocked, they did not appear to be at increased risk of JPBW-related mortality. Overstocked stands were more likely to sustain mortality than other stands.

Nonlinear relationships between stand age and recent mortality indicated that mortality in pole-sized or mature stands up to 48 years old tended to be fairly stable and was not strongly associated with age. However, once stands reached a threshold age of 50–55 years, vulnerability to JPBW-related mortality increased rapidly with stand age.

Fig. 4. Mean percentage (and standard error of the mean) of (*a*) recent top kill and (*b*) previous top kill in 104 stands sampled annually from 1992 to 1994. Recent top kill was attributable to the 1991–1993 jack pine budworm outbreak; previous top kill occurred before the outbreak.



Mortality in younger, sapling-sized stands was negatively related to stand age and may reflect natural thinning in stands with dense regeneration.

The strong positive association between recent mortality and SI was notable, because it was unexpected and contradicted previous assumptions about JPBW impact and site quality. The negative association between SI and mortality that we expected occurred only in stands on the poorest sites, with SI of less than 13.7–14.3 m. Stands with SI of 14.3–16.8 m exhibited a strong positive linear association between SI and mortality. This pattern was consistent regardless of stocking or stand age. Site index is routinely included in most resource management databases in the Lake States and is often the basis for management guidelines (e.g., Benzie 1977), although its limitations as a descriptor of site quality have previously been recognized (Carmean and Lenthall 1989; Gale and Grigal 1988; Monserud 1984). Other variables could likely be used to further evaluate associations between JPBW-related mortality and site quality. In the Raco Plains area, however, ecological landforms and general soil characteristics were relatively homogenous (Heym 1993) and would not have been useful in differentiating among our stands.

One hypothesis to explain the unexpectedly high mortality in high SI stands involves the allocation of biomass in response to environmental stress and the ability of trees to tolerate defoliation. For example, oak mortality resulting from gypsy moth (*Lymantria dispar* L.) defoliation

Table 3. Mean percentage of trees with recently killed tops in 1994 in stands grouped by one inventory variable.

Inventory variable	% Top kill*
Age (years)	
Younger (0–49; *n*=41)	13.4 (2.16)
Older (≥50; *n*=63)	19.4 (2.47)
Site index (m)	
Lower (0–15.2; *n*=54)	16.6 (2.34)
Higher (>15.2; *n*=50)	17.4 (2.60)
Basal area (m^2/ha)	
Understocked (0–16.0; *n*=50)	18.7 (2.81)
Well stocked (16.1–25.2; *n*=32)	17.7 (3.30)
Overstocked (>25.2; *n*=22)	12.1 (2.50)
Size (ha)	
Smaller (≤12; *n*=58)	19.6 (2.38)
Larger (>12; *n*=46)	13.8 (2.49)

*Standard error of the mean is in parentheses.

was positively associated with site index or fertile soil conditions in Maryland and West Virginia (Hicks 1984) and Pennsylvania (Quimby 1987). Quimby (1987) speculated that trees in more favorable growing conditions may have had lower root:shoot ratios and were perhaps less tolerant of defoliation than trees growing in more stressful sites. Studies with other forest species have demonstrated that root:shoot ratios and allocation to root biomass can be affected by site characteristics or growing conditions (e.g., Grier et al. 1981; Nadelhoffer et al. 1985). Little is known about biomass allocation in jack pine or how it may be altered by environmental conditions, defoliation, or stress.

However, previous research has indicated that site-related variables can influence vulnerability of jack pine trees to JPBW. For example, foliar nitrogen levels were positively associated with larval survival on young jack pine trees (McCullough and Kulman 1991*a*, 1991*b*). Nitrogen fertilization stimulated pollen cone production in young jack pine (McCullough and Kulman 1991*b*), which could subsequently affect larval survival (Nealis and Lomic 1994). Analysis of long-term JPBW survey data from Wisconsin indicated that JPBW population dynamics varied among ecological habitat types (Volney and McCullough 1994).

The link between SI and JPBW-related mortality needs further evaluation across a larger area, particularly in stands with SI of 18.3 m or higher, which were not common in our survey. If the pattern is consistent, however, it suggests that recommendations for JPBW management may need to emphasize presalvage of mature to overmature trees on relatively good sites.

Stand size did not consistently affect mortality in our stands, although size may be linked to JPBW defoliation or population dynamics, as suggested by Weber (1995). Influence of stand size on vulnerability to JPBW damage needs to be evaluated on a larger spatial scale, however, as most of our stands were less than 20 ha.

Table 4. Mean percentage of trees with recently killed tops in 1994 in stands grouped by two inventory variables.

	Age		Site index		Size	
	Younger	Older	Lower	Higher	Smaller	Larger
Basal area						
Understocked	13.6 (2.78) *n*=30	26.4 (5.31) *n*=10	16.7 (2.90) *n*=37	24.4 (6.97) *n*=13	19.4 (3.83) *n*=27	17.9 (4.24) *n*=23
Well stocked	13.9 (2.92) *n*=22	19.5 (4.20) *n*=20	20.6 (5.28) *n*=12	16.0 (3.73) *n*=20	22.6 (3.84) *n*=21	8.4 (3.64) *n*=11
Overstocked	— *n*=0	12.7 (2.65) *n*=21	6.6 (1.75) *n*=5	13.7 (3.24) *n*=17	13.5 (4.25) *n*=10	10.9 (3.31) *n*=12
Age						
Younger			12.6 (2.54) *n*=27	14.8 (4.13) *n*=14	15.0 (2.77) *n*=22	11.5 (3.42) *n*=19
Older			20.7 (3.83) *n*=27	18.4 (3.26) *n*=36	22.4 (3.38) *n*=36	15.4 (3.50) *n*=27
Site index						
Lower					20.3 (3.59) *n*=30	12.1 (2.55) *n*=24
Higher					18.8 (3.14) *n*=28	15.6 (4.43) *n*=22

Note: Standard error of the mean is in parentheses.

We hypothesized that other factors, including abundant wolf trees, gall rust, or suppressed and intermediate trees, could contribute to increased stand damage during JPBW outbreaks as a result of higher larval survival or more severe defoliation (Batzer and Jennings 1980; Foltz et al. 1972; Kulman et al. 1963; LeJeune 1950; Nealis and Lomic 1994; Weber 1995). However, there was no strong evidence that abundant gall rust or wolf trees increased stand vulnerability to mortality. Much of the Raco Plains forest was established as even-aged plantations (Heym 1993), and suppressed or intermediate trees were ranked as abundant in only two stands that we surveyed. Further research may be needed to more accurately quantify the distribution and importance of suppressed and intermediate trees in stands with varying attributes.

Amount of top kill averaged 17–19% and was roughly twice the amount of mortality in our stands in 1994. In Ontario, top kill averaged 6% in severely defoliated stands and was three times greater than tree mortality (Gross and Meating 1994). Top kill was greatest in understocked, mature to overmature stands, where JPBW larvae and defoliation may have been concentrated on relatively few stems. Top kill was not strongly related to other inventory variables, and ground surveys of defoliation severity may be necessary to accurately predict amount or location of defoliation.

The importance of top kill is debatable and may vary depending on tree age, management objectives, and other factors. Top kill resulting from severe defoliation can cause crooked or multiple leaders, flattened tree canopies and poor form, or increased susceptibility to *Armillaria* root disease (Cerezke 1986; Howse 1984; Kulman et al. 1963; Mallet and Volney 1990). Dead tops may act as ladder fuels, contributing to explosive wildfires. Top-killed trees would likely be subject to increased competition as a result of loss of dominance, perhaps increasing their long-term risk of mortality. On the other hand, in young or overstocked stands, particularly in dense post-wildfire regeneration, some mortality may represent natural thinning and stocking adjustment (Mattson and Addy 1975). Moreover, Gross (1992) concluded that in four stands aged 33 to 61 years old, top kill of 5 to 15% of trees resulted in negligible loss of merchantable volume.

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