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IMPACT AND MANAGEMENT OF THE JACK PINE BUDWORM IN THE UPPER PENINSULA OF MICHIGAN

By

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ABSTRACT

IMPACT AND MANAGEMENT OF THE JACK PINE BUDWORM IN THE UPPER PENINSULA OF MICHIGAN

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Stand-level top-kill and tree mortality resulting from the 1991-1993 jack pine budworm (*Choristoneura pinus pinus* Freeman) outbreak were quantified for 99 jack pine (*Pinus banksiana* Lamb.) stands in the Raco Plains area of the Hiawatha National Forest. Tree growth of 84 surviving, top-killed, and dead trees was measured, and merchantable volume and financial value losses were calculated. Top-kill and tree mortality peaked at 18 and 16%, two and four years after defoliation began, respectively. Trees that died following the outbreak had lower annual growth than top-killed and surviving trees after 1988. Growth of top-killed trees was less than growth of surviving trees in 1993-1995 and had not returned to pre-outbreak levels as of 1995. Merchantable volume and standing value loss totaled 19,500 m^3 and $289,800, respectively, for the 1,480 ha sample area. Current budworm management recommendations used in the Lake States were tested, and recommendations for management priorities were given.

To my grandpa,

Edward M. Conway

ACKNOWLEDGEMENTS

I would like to thank Dr. Deborah G. McCullough and Dr. Larry A. Leefers for their patience and guidance throughout this course of study. I would also like to thank my graduate committee members, Dr. Robert Haack and Dr. Donald Dickmann. Special thanks to Doug Heym, Hiawatha National Forest District Silviculturalist, for his enthusiastic help and support of this project. I am also grateful to Nathan Siegert, Dr. Raymond Miller, and everyone at the Upper Peninsula Tree Improvement Center for their help in the collection and measurement of the growth loss data. Funding for this study was provided by the Michigan Agricultural Experiment Station as part of its Status and Potential of Michigan's Natural Resources (SAPMINR) program.

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INTRODUCTION

Forest insect pests play an important role in determining forest stand composition and timber supply. Studies of the impact of forest insect pests are important because forest managers need information about pest impact to make efficient resource allocation decisions. Including impact of insect pests in forest planning is essential to accurately project future timber supply, develop management and silvicultural alternatives, and implement ecosystem management.

Sustaining the supply of timber is a primary goal of most forest management planning (MacLean 1990). Forest pest impact studies are necessary to help predict the effects that insect pests will have on future timber supply, harvest scheduling, and product quality. Without such studies, sustained timber yield may be overestimated (MacLean 1990).

Impact studies are also necessary to help develop management and silvicultural plans. By determining patterns of impact across different stand types, management and silvicultural plans can be implemented to reduce the future occurrence of insect outbreaks or to limit the severity of damage when outbreaks occur (MacLean and Porter 1996).

Forest managers of public lands are charged with managing forests for all benefits, including habitat for wildlife species, protection of watersheds, and recreational opportunities (National Environmental Policy Act of 1969 and National Forest Management Act of 1976). This ecosystem management approach requires a great deal of information. Understanding the impact of forest insect pests can help forest planners identify areas suitable for timber production and those suitable for wildlife habitat, recreation, or other uses.

The jack pine budworm, *Choristoneura pinus pinus* Freeman (Lepidoptera: Tortricidae), is a forest insect pest that can dramatically alter jack pine (*Pinus banksiana* Lamb.) forest composition and timber supply. The objective of this thesis is to provide information about the impact of the jack pine budworm and to examine and refine jack pine budworm management recommendations in the Lake States.

Jack Pine

Jack pine is an important tree species in the Lake States region of the United States (Minnesota, Wisconsin, and Michigan) and throughout much of Canada. Jack pine is the most widely distributed pine in Canada with a range that extends further north than any other North American pine (Cayford 1970; Rudolph and Laidly 1990). Geographically, jack pine is found from the Atlantic coast west to the Mackenzie River Valley in the Northwest Territories and south and east through the Prairie provinces, Lake States, and New England (Rudolph and Laidly 1990; Yeatman 1967).

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Jack Pine Timber

Jack pine is an important commercial timber species in the Lake States region of the United States because it often occupies dry sandy sites that are less productive and unsuitable for more site demanding tree species (Benzie 1977; Rudolph and Laidly 1990). Predominantly used in the production of pulp, jack pine accounted for 40% of all softwood pulp production in the Lake States in 1992 (Hackett and Piva 1994). On more productive sites, jack pine is also managed for the production of poles or saw logs (Benzie 1977). According to USDA Forest Service Timber Cut and Sold on National Forests under Sales and Land Exchanges reports (1977-1996), 303,000 m^3 (60 million board feet) of jack pine sawtimber was sold from the eight National Forests in the Lake States from 1977 to 1996.

Other Benefits from Jack Pine Forests

Jack pine forests provide habitat for many wildlife species. Game species such as white-tailed deer (*Odocoileus virginianus*), ruffed grouse (*Bonasa umbellus*), and black bear (*Ursus americanus*) are found in jack pine forests throughout the Lake States (Benzie 1977; Heym et al. 1993). Non-game species including pine marten (*Martes americana*), sandhill crane (*Grus canadensis*), coyote (*Canus latrans*), badger (*Taxidea taxus*), and eastern bluebird (*Sialia sialis*) can also be found in jack pine forests in the Lake States (Heym et al. 1993).

In northern lower Michigan, jack pine forests provide the only suitable habitat for the federally endangered Kirtland's warbler (*Dendroica kirtlandii*) (Benzie

1977). Due to the warblers' dependence on large tracts of young jack pine forest, special management efforts to encourage dense jack pine regeneration must be made in this area. Another federally endangered species, the Karner blue butterfly (*Lycaedis melissa samuelis* Nabokov), is found in pine and oak barrens in Wisconsin and southern Michigan (Haack 1993; Premo et al. 1994). Jack pine is the most common pine species in the pine barrens of the western part of the Karner blue's range (Haack 1993).

Recreational opportunities abound in jack pine forests in the Lake States. Numerous camping facilities and hiking trails exist on both state and federal jack pine forest lands. Hunting, fishing, and berry picking are also common recreation activities in jack pine forests. These activities are important for many rural economies in the Lake States, providing both subsistence for local residents and tourist dollars.

Jack Pine Management

In the Lake States, jack pine on public lands is managed to provide the biological, economic, and social benefits noted above. Jack pine is a short-lived, shade-intolerant, pioneer species, and seedlings require full sun and exposed mineral soil to regenerate (Benzie 1977; Rudolph and Laidly 1990). The recommended silvicultural system for jack pine is typically clearcutting, although seed tree and shelterwood methods may also be employed (Benzie 1977). Jack pine stands managed for pulpwood production typically do not receive intermediate treatments such as thinnings, in part due to cost and limited economic gain (Benzie 1977). Stands located on higher quality sites managed for pole

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for poles or saw logs may benefit from intermediate thinnings (Benzie 1977). Commercial rotation ages for jack pine in the Lake States range from 40 to 70 years depending on management objectives, site quality, markets for timber, and other factors (Benzie 1977).

Jack pine is a pyrophylic species. Although it is easily killed by fire, fire is an important component of the life-history of jack pine (Benzie 1977; Cayford 1970). Not only does the heat from fire release seeds from serotinous cones, but it also prepares seedbeds by eliminating tree and shrub competition and exposing mineral soil (Benzie 1977; Cayford 1970). Increasingly, managers are incorporating controlled burns into jack pine management regimes to encourage natural regeneration and to reduce the risk of catastrophic wildfire (Heym et al. 1993).

Jack Pine Budworm

The jack pine budworm (JPBW) is the most important insect pest of jack pine (Howse 1984). In the larval form, the JPBW is a small caterpillar that feeds almost exclusively on jack pine foliage and pollen cones. This univoltine insect is native to North America and is sympatrically distributed with the natural range of jack pine (Howse 1984).

Life Cycle

The JPBW overwinter as second instar larvae. After hatching in late July or early August, small first-instar larvae move to protected locations under the scales of tree bark or other protected locations on tree branches, spin hibernacula, and molt without feeding (Howse 1984). The following spring budwo

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budworm become active when jack pine trees are beginning to shed their pollen, usually in mid- to late May. At this time larvae move to the male (microsporangiate) strobili (i.e., pollen cones) to begin feeding.

The relationship between jack pine pollen cone availability and abundance and budworm survival is an important factor in the population dynamics of this insect (Batzer and Jennings 1980; Foltz et al. 1972; LeJeune 1950; LeJeune and Black 1950; Nealis and Loomic 1994). Jack pine pollen cones may provide both a more nutritious diet and a more favorable microclimate for developing larvae. This relationship figures prominently in studies of JPBW population dynamics and in JPBW management recommendations discussed in more detail below.

If suitable feeding sites are not found, larvae will disperse by exuding silk strands and dropping off branch terminals. If dispersing larvae do not land directly on a suitable host, their chance of survival is low (Batzer and Jennings 1980; Foltz et al. 1972; Graham 1935; Nealis and Lomic 1994). Thus, this dispersal phase is an important source of larval mortality (Batzer and Jennings 1980; Foltz et al. 1972). Foltz et al. (1972) observed an average of 12% survival for the egg to second instar age interval, and concluded that larval mortality observed during this age interval was the most important factor affecting population trends. Losses from spring dispersal can be the single most important source for larval mortality during this age interval (Batzer and Jennings 1980; Foltz et al. 1972).

Jack pine budworm larvae (fourth or fifth instars) migrate to newly expanded current-year foliage in mid- to late June (Graham 1935; Howse 1984). Feeding shelt

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shelters made of shoots and needles webbed together with silk are often constructed. Typically, the JPBW is a wasteful eater, clipping needles at the base and consuming only a portion of each needle (Howse 1984). Because of this wasteful feeding habit, JPBW defoliation tends to be disproportionate to the actual consumption requirements of the insect (Graham 1935). Larvae will consume previous years' foliage ("backfeeding") if current-year foliage is unavailable. Budworm will also feed on ovulate strobili and conelets, sometimes causing significant reductions in jack pine seed production (Graham 1935; Rauf et al. 1985).

Larval feeding usually lasts about six weeks during which time male larvae complete six and female larvae complete seven instars (Howse 1984; Lysyk and Nealis 1988). Larvae pupate near feeding sites in early to mid-July. Adults emerge in six to ten days and live for only a few days in mid- to late July. After mating, each adult female lays 20-60 eggs in clusters on individual jack pine needles (Howse 1984). In about ten days, eggs hatch, and first instars move to their overwintering sites.

Population Dynamics

Populations of JPBW can build rapidly both locally and over widespread areas, and substantial defoliation usually accompanies these increases (Howse 1984). Budworm population dynamics are characterized by bimodal stability. Bimodal stability is seen as follows: i) population stability at endemic levels, ii) rapid population release to outbreak levels, iii) population stability at outbreak levels, and iv) rapid population collapse to endemic levels.

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Outbreaks of JPBW occur periodically, occurring every six to ten years and lasting about two to four years (Clancy et al. 1980; Volney 1988; Volney and McCullough 1994). Factors that determine population release and collapse are still not well understood.

A number of studies have attempted to relate JPBW population trends to weather or to the presence or abundance of jack pine pollen cones. Foltz et al. (1972) performed a life-table study to examine JPBW population dynamics in Michigan. The authors concluded that egg to second instar survival, late larval survival, and realized fecundity were the most important factors affecting population fluctuations. These three factors explained 58 to 93% of the variation in population trends. The authors suggested that weather was a contributing factor in both population release and collapse and further, that defoliation (i.e., exhausting food resources) may also be responsible for outbreak collapse.

In one of the few attempts to predict the release phase of JPBW population trends, Clancy et al. (1980) developed mathematical models for predicting late larval and pupal density, and defoliation using data from an extensive long-term record of JPBW activity in northwestern Wisconsin. The independent variables used in this study were meteorological variables, specifically, deviations from normal temperature and precipitation in the years before an outbreak. While the models explained between 62% and 70% of the variation in late larval and pupal density and defoliation, few strong patterns were consistent in all three models. The authors found that favorable weather conditions when the previous generation was active (i.e., warm, dry previous spring and summer) were associated with high number of late-larvae and pupae in the current year. It was not clear, however, whether these factors were affecting the budworm directly or indirectly by affecting predators, parasites, pathogens, or host quality.

Batzer and Jennings (1980) examined possible relationships between JPBW population collapse and weather. They concluded that warm dry conditions favored the survival of late instars and that high humidity and below normal temperature during the third year of an infestation in northern Minnesota were at least partially responsible for its collapse. They further observed that stand density influenced pollen cone production, budworm dispersal, and early instar survival. While this points to a link between pollen cone production and JPBW larval survival, the authors suggested that both may be related to other variables.

Volney (1988) studied the JPBW outbreak history during a 50-year period in the Prairie provinces (Saskatchewan and Manitoba) of Canada and found that outbreaks tended to occur every ten years. He observed trends of increasing outbreak size over time and a strong relationship between JPBW outbreaks and the fire cycle in the Prairie provinces. Volney reported both a short outbreak time-lag following fire years (4 years) and a long outbreak time-lag following fire years (20-30 years). Volney speculated that the short time-lag may be due to weather and its effect on jack pine pollen cone production. He also suggested that while fire tended to be associated with drought years, water stress might also cause increased pollen cone production in jack pine which may increase JPBW survival. Volney speculated that the time-lag observed was the result of the time

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the time necessary for the trees to set pollen cones and for the JPBW population to build to outbreak levels.

In another long-term JPBW study, Volney and McCullough (1994) examined periodicity of JPBW outbreaks and relation of this periodicity to habitat types in northwestern Wisconsin. The authors observed three different outbreak periods (5, 6, and 10 years) on different sites, suggesting that population trends were site dependent. Another important finding from this study was that there was an important second-order (time-lagged), density-dependent factor influencing JPBW population at local sites. The authors suggested that this factor may be a complex of weather and jack pine pollen cone production or host quality.

While there appears to be a relationship between the abundance of jack pine pollen cones and JPBW populations, many studies of this relationship have been inconclusive or correlative. LeJeune and Black (1950) observed that budworm populations were higher on jack pine trees with more pollen cones. The authors suggested that pollen cones provide a nutritional advantage and a favorable habitat for vulnerable early instars. The biases evident in this study have been noted by Nealis and Lomic (1994). Other studies, however, have been inconclusive as to whether pollen cones provide a nutritional advantage (LeJeune 1950) or whether the presence of pollen cones increase JPBW survival (Nealis 1990).

Nealis and Lomic (1994) conducted a three part study to assess 1) early instar survival on jack pine branches with and without pollen cones in a laboratory assay, 2) relationships between larval density and pollen cone abundanc

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abundance in the field, and 3) relationships between dispersal loss and pollen cone abundance in the field. The laboratory experiment showed a strong relationship between budworm survival and pollen cones. Differences in the population density of JPBW on field-sampled jack pine branches were also observed to be directly related to the presence of pollen cones. The authors found that spring dispersal and presumably, larval mortality were higher in stands with trees that had a lower pollen cone density. Others have observed that defoliated jack pine subsequently produce few pollen cones (Batzer and Jennings 1980; Graham 1935; Kulman et al. 1963). Thus, reduced pollen cone production may be a driving factor in outbreak collapse. Further, the authors suggested that this was the second-order, density-dependent factor observed by Volney and McCullough (1994).

Impact

Defoliation can be severe both locally and over a large area during a JPBW outbreak. Needles clipped off by larvae dry, fade in color, and give the crowns of infested trees a distinctive reddish appearance. The direct impact of JPBW defoliation occurs in three forms – reduced tree growth, death of the terminal leader (top-kill) and tree mortality (Cerezke 1986; Graham 1935; Gross 1992; Gross and Meating 1994; Kulman et al. 1963; McCullough et al. 1996).

Growth Loss

When jack pine trees are defoliated by JPBW, one of the most subtle impacts is a reduction in growth. Defoliation stress reduces photosynthesis rate and alters allocation of resources within the tree. Height, diameter, and shoot growth are all parti

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are all particularly sensitive to defoliation, especially when current-year foliage is removed (O'Neil 1962). O'Neil (1962) found that new foliage is more important than old foliage for survival and growth of young jack pine and that marked reductions in height, diameter, and shoot growth were observed when current-year foliage was removed.

Kulman et al. (1963) observed dramatic reductions in the growth of jack pine defoliated by the JPBW in Minnesota. The authors observed that even lightly defoliated trees showed some reduction in growth. Heavily defoliated trees experienced nearly 100% latewood growth loss in the first year of defoliation and 100% earlywood and 73-91% latewood growth loss in the second year of defoliation relative to non-defoliated trees. The authors also observed that growth reduction was greatest in the upper stem, corresponding to the location of the most severe budworm defoliation.

Cerezke (1986) examined the growth of defoliated jack pine trees in Saskatchewan and compared it to the growth of trees from adjacent stands with less severe infestations. The author found significant reductions in radial growth in the third and fourth outbreak years. Reduced height and shoot growth were also observed.

Gross (1992) performed stem analysis on 84 JPBW-defoliated jack pine in Ontario and also noted significant growth loss. Compared to growth in the five years prior to the outbreak, the author estimated growth losses up to 75% for a single year. Both Cerezke (1986) and Gross (1992) found radial growth loss was greater in the upper portion of the stem.

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Mallett and Volney (1990) studied the growth of healthy, top-killed, and recently dead jack pine following a JPBW outbreak in Saskatchewan. The objectives of the study were to determine if there was a relationship among tree condition (i.e., healthy, top-killed, or dead), root condition, and root rotting organisms and if there was a relationship between tree growth prior to the JPBW outbreak and resultant tree condition. While the authors observed *Armillaria* root rot in all dead trees and in three of five top-killed trees, it was unclear as to whether root rot was primary or secondary to JPBW defoliation stress. The authors also found that growth of trees that eventually died had declined significantly before they died and that top-killed trees had grown faster before being damaged than trees that eventually died.

Top-kill

The tendency of JPBW to feed in the upper portion of the crown of the host tree where the foliage is more nutrient-rich, microclimate warmer, and foliar biomass greater frequently results in death of the terminal leader of the tree. The relationship between JPBW defoliation and top-kill has been well documented (Graham 1935; Kulman et al. 1963; Hall et al. 1993; McCullough et al. 1996), but the importance of the actual reduction in volume due to the dead wood in the top-killed portion of the tree has been debated. Hall et al. (1993) implied that the reduction in volume due to top-kill was an important component of JPBW impact and went on to develop and test a method of estimating this reduction in volume. On the other hand, Gross and Meating (1994) suggested that the reduction in volume due to top-kill was negligible because rarely did the dead woo

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dead wood extend into the merchantable portion of the tree. The effect of a loss in apical dominance in top-killed trees on subsequent years' growth is still unknown. Top-kill may also result in changes in crown shape by causing crooked or multiple leaders (Howse 1984; Kulman et al. 1963). In addition, there may be a relationship between reduced vigor caused by top-kill and incidence of root pathogens such as *Armillaria* root rot (Mallett 1995; Mallett and Volney 1990). Some investigators have suggested that top-kill is an important predetermining factor of tree mortality (Gross and Meating 1994; Kulman et al. 1963; Mallett and Volney).

Tree Mortality

Perhaps the most obvious impact of a JPBW outbreak is tree mortality. Studies of the artificial defoliation of jack pine indicate that complete defoliation or subsequent years of heavy defoliation will generally result in the death of the tree (Kulman et al. 1963; O'Neil 1962). Tree mortality can be particularly severe in stands with trees already stressed by suppression or previous insect attack (Graham 1935; Kulman et al. 1963). Kulman et al. (1963) observed 5 to 43% total tree mortality and up to 90% mortality in suppressed trees following a three-year outbreak in Minnesota. JPBW induced mortality may not always be as high as that observed in the above study, however. Two years after the collapse of a three-year JPBW outbreak in Ontario, Gross and Meating (1994) attributed only 0 to 10% tree mortality to JPBW defoliation. The authors noted that mortality higher than 5% was uncommon, even in stands that experienced severe defoliation.

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McCullough et al. (1996) studied the impact of the 1991-1993 JPBW outbreak in the Raco Plains area of Michigan's Upper Peninsula. The authors found that tree mortality in the year following the outbreak collapse averaged 8% and was as high as 40% in some stands. In one of the few attempts to empirically examine current JPBW management recommendations (see below), the authors found that mortality was significantly greater in stands 50 years old or older, in stands with site index greater than 15.2 m (50 ft), and in stands with basal area greater than 25.2 m^2/ha (110 ft^2/ac).

Merchantable Volume Loss

Most studies of JPBW impact have focused on quantification of growth loss, top-kill, and tree mortality (Gross 1992; Kulman et al. 1963; McCullough et al. 1996). Only a few studies have attempted to estimate the reduction in volume attributable to a JPBW outbreak (Cerezke 1986; Gross and Meating 1994).

Cerezke (1986) studied volume reduction resulting from a 1975-1978 outbreak in Saskatchewan. The volume of growth loss was estimated by comparing mean annual stem increment growth of the outbreak years with that of the five previous non-outbreak years. Significant annual volume reductions were observed for the last two outbreak years, 1977 and 1978, with a maximum reduction of 91% in 1978. This study was limited to examining volume reduction only in the final two years of the outbreak and did not look at possible post-outbreak volume loss.

Gross and Meating (1994) performed an extensive study of the JPBW outbreak in northeastern Ontario. The outbreak began in 1982 and peaked in

1986 when 1.9 million hectares were defoliated. The authors developed growth loss and tree mortality estimators based on defoliation histories. Using these estimators and aerial sketch-maps of defoliation, the authors determined that the impact of the four-year outbreak was 2.1 million m^3 of growth loss and 5.1 million m^3 of mortality loss. These are significant losses in light of the fact that annual jack pine harvests in Ontario at that time ranged from 5 to 5.7 million m^3 (Howse 1986).

Economic Loss

In general, little is known about the financial value of timber losses associated with JPBW outbreaks. A few previous studies have attempted to model the impact of a budworm outbreak on jack pine. Rose (1973) used a simulation model based on limited theoretical and biological data to evaluate the economic impact of jack pine budworm defoliation. The model combined initial stand conditions, stand growth, indices of defoliation probability, and defoliation damage to evaluate management policies in terms of present net worth. The study concluded that intensified management was necessary to reduce damages associated with budworm infestation. The author also suggested that chemical controls were more effective than silvicultural controls, but there was no indication of the economic feasibility of either. Finally, the study concluded that policies favoring shorter rotations and larger allowable cuts were economically preferable.

In a more recent study, a model of financial losses associated with jack pine budworm outbreaks in Michigan was constructed (Nyrop et al. 1983). Among the objectives

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objectives of this study was the determination of optimal rotation ages for jack pine factoring in potential defoliation, site index, and basal area. The authors also attempted to evaluate the cost-effectiveness of chemical control. They determined that shorter rotations would reduce financial loss attributable to JPBW defoliation and that pesticide use was not an economically viable option.

Management Recommendations

Management recommendations for JPBW in the Lake States are based on the use of silvicultural schemes, harvest scheduling, salvage, and cover-type conversion to minimize JPBW impact. For economic and environmental considerations, forest managers in the Lake States do not currently use insecticides to combat JPBW infestations or to limit timber losses (Benzie 1977; Heym et al. 1993; McCullough et al. 1994).

Silvicultural schemes, harvest scheduling, salvage, and cover-type conversion are used by forest managers to exploit observed patterns in JPBW impact. These patterns are based on JPBW impact studies (Batzer and Jennings 1980; Graham 1935; McCullough et al. 1996; Volney and McCullough 1994) and include disproportionately greater impact to suppressed trees, older stands, and higher density stands. These patterns may reflect preferential host selection by the insect, enhanced insect survival, host ability to recover from defoliation stress, or any number of other reasons or combinations. Other observations include the apparent tendency for open-grown "wolf" trees and trees located on stand edges to produce abundant pollen cones (Hodson and Zehngraff 1946; McCullough et al. 1994; Weber 1995).

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Minimizing Susceptibility

Managers attempt to minimize JPBW impact by reducing stand susceptibility and vulnerability by exploiting the patterns and observations noted above (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995). Susceptibility refers to the likelihood that the host will experience defoliation. Reducing susceptibility (i.e., increasing resistance) is accomplished by maintaining the host in its least desirable state for the insect. This involves minimizing the production of jack pine pollen cones and may be accomplished by reducing suppressed, wolf, and open-edge trees in the stand. Promoting age-class and species diversity may also decrease susceptibility (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

Many workers have observed that suppressed trees produce abundant pollen cones and enhance budworm survival by providing suitable hosts for dispersing larvae (Batzer and Jennings 1980; Hodson and Zehngraff 1946; McCullough et al. 1994; Weber 1995). Wolf trees may frequently produce abundant pollen cones throughout their large crowns (Hodson and Zehngraff 1946; McCullough et al. 1994; Weber 1995). To reduce the number of suppressed trees, even-aged stands are recommended. Reducing suppressed and wolf trees can also be accomplished by maintaining well stocked stands with basal area between 16.1 and 25.3 m^2/ha (70-110 ft^2/ac) (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

Decreasing the amount of open stand edge is also believed to reduce susceptibility. Edge trees are thought to produce more pollen cones than midstand trees

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stand trees (McCullough et al. 1994; Weber 1995). Avoiding strips, islands, and irregular cuts of jack pine has been recommended, but this so called "edge-effect" has not been empirically substantiated.

Though even-aged management is important, a diversity in age classes and species at the landscape level may also be important to minimize susceptibility (McCullough et al. 1994; Weber 1995). This suggestion is based on the belief that stands with different characteristics may be more favorable to budworm survival. By eliminating large contiguous areas of a particular stand type, overall JPBW impact may be reduced. However, no study to date has demonstrated this relationship empirically.

Minimizing Vulnerability

Vulnerability refers to the probability that the host will experience damage as a result of defoliation. Reducing vulnerability (i.e., increasing resilience) is accomplished by maintaining the host in its most vigorous state and therefore, increasing its ability to recover from the stress of defoliation. This is accomplished by shortening rotations and harvesting overmature stands, reducing competition by harvesting or thinning overstocked stands, and favoring high quality sites (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

The age at which jack pine trees become overmature may vary from site to site, depending on the quality of the site, presence of competitor species, climate, and other factors. In the Lake States, jack pine is generally considered mature to overmature at 40 to 55 years of age (MacAloney 1944; McCullough et al. 1994; Jo

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al. 1994; Jones and Campbell 1986; Weber 1986). Numerous studies have called for the rotation ages of jack pine to be reduced, particularly on low quality sites (MacAloney 1944; Nyrop et al. 1983; Rawat et al. 1987; Rose 1973; Rose 1974; Williams and Nautiyal 1992).

The disproportionate JPBW impact on suppressed trees has long been observed (Batzer and Jennings 1980; Graham 1935; Hodson and Zehngraff 1946; Kulman et al. 1963). Suppressed trees may be more vulnerable to JPBW impact because these trees are probably under considerable stress due to shade-intolerance and competition. A few authors have suggested that suppressed trees act as refugia for JPBW and should be removed from the stand in a non-commercial thinning (Batzer and Jennings 1980; Hodson and Zehngraff 1946). Maintaining stocking below 25.3 m^2/ha (110 ft^2/ac) is recommended to reduce both competition and the number of suppressed trees (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

Many studies of JPBW management have assumed jack pine trees on low quality sites were less vigorous and more vulnerable than trees on higher quality sites (Graham 1935; Nyrop et al. 1983; Rawat et al. 1987; Williams and Nautiyal 1992). It was often assumed that jack pine trees growing on low quality sites may experience more site-related stress and produce more pollen cones than those on higher quality sites (Graham 1935). However, recent studies in the Lake States indicate that the relationship between JPBW impact and site quality may be com

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A Jack Pine Budworm Outbreak in the Raco Plains Area

The Raco Plains area is a 18,200 ha (45,000 ac) area located in the eastern Hiawatha National Forest in the Upper Peninsula of Michigan. It is characterized by sandy glacial outwash soils (Rubicon, Croswell, and Kalkaska sands) and dominated by large areas of jack pine forest (Heym et al. 1993). The Raco Plains area is located between 46° 15" and 46° 25" north latitude and between 84° 43" and 84° 58" west longitude.

From 1991-1993, a JPBW outbreak occurred in the Raco Plains area. In 1991, aerial surveys indicated that an estimated 6560 ha (16,000 ac) were defoliated in the Raco Plains area (Heym et al. 1993). Defoliation increased in 1992, and roughly 75% of the jack pine stands in this area suffered moderate to severe defoliation (McCullough et al. 1996). By 1993, the JPBW population was in decline; however, noticeable defoliation was still observed in the area (McCullough et al. 1996). No defoliation was observed in 1994 when the JPBW population returned to endemic levels.

Thesis Objectives

The present research project addresses the impact of the 1991-1993 JPBW outbreak in the Raco Plains area. Impact studies are performed to quantify the impact of a particular outbreak, to evaluate patterns in impact across different stand types and in different areas, and to develop management recommendations and tools such as decision support systems to aid forest managers in

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managers in the decision making process. While this study joins many previous investigations of biological impact (i.e., growth loss, top-kill, and tree mortality) (Cerezke 1986; Gross 1992; Gross and Meating 1994; Kulman et al. 1963; McCullough et al. 1996), it is one of the first studies to quantify stand-level financial loss from a JPBW outbreak.

The overall objectives of this study were to:

1. Quantify the biological impact (i.e., growth loss, top-kill, and tree mortality) and financial loss from a single JPBW outbreak;
2. Examine how the patterns of biological impact and financial loss related to different stand types and to current management recommendations used in the Lake States.

Thesis Organization

This thesis is divided into three parts, each a discrete chapter. As such there may be some repetition in each chapter, particularly in the introduction and methods sections. In the first chapter, top-kill and tree mortality that occurred as a result of the 1991-1993 JPBW outbreak are quantified and examined in relation to stand characteristics and current management recommendations. Chapter two deals with the reduction in growth that occurred as a result of the 1991-1993 JPBW outbreak. The patterns of growth loss as they relate to tree status, stand characteristics, and management recommendations are discussed here. In the third chapter, merchantable volume and financial loss are quantified and examined with respect to stand characteristics and management recommendations. Finally, the major findings of this study and areas for future research of

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research of the impact and management of the JPBW in the Lake States are presented in a concluding chapter.

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CHAPTER 1

EMPIRICAL EVALUATION OF JACK PINE BUDWORM IMPACT AND MANAGEMENT RECOMMENDATIONS IN THE LAKE STATES

Introduction

Major forest insect pests such as the jack pine budworm (*Choristoneura pinus pinus* Freeman) play an important role in determining forest stand composition and timber supply. Impact studies of forest insect pests are needed to enable forest managers to make efficient resource allocation decisions, accurately predict future timber supply, develop management and silvicultural alternatives, and implement ecosystem management.

Jack pine (*Pinus banksiana* Lamb.) is an important economic and ecological forest resource in the Lake States. Jack pine is characterized by rapid juvenile growth and qualities desirable for commercial softwood pulp (Rudolph and Laidly 1990). Merchantable jack pine stands can be grown on marginally productive land that may be incapable of supporting other tree species (Benzie 1977; Cayford 1970). Jack pine is an important softwood pulp species in the Lake States, accounting for 40% of softwood pulp production in 1992 (Hackett and Piva 1994). Jack pine forests provide habitat for a number of wildlife species, including the federally endangered Kirtland's warbler (*Dendroica kirtlandii*) and Karner blue butterfly (*Lycaedis melissa samuelis* Nabokov) (Benzie 1977; Haack

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The jack pine budworm (JPBW) is the most important insect pest of jack pine (Howse 1984). Outbreaks of this foliage-feeding caterpillar occur regularly in the Lake States, about every six to ten years (Volney and McCullough 1994). During a JPBW outbreak, severe defoliation can occur locally and over a widespread area. Defoliation during a JPBW outbreak can result in reduced tree growth, mortality of the terminal leader of the tree (top-kill), and tree mortality (Graham 1935; Gross 1992; Kulman et al. 1963; McCullough et al. 1996). Significant losses in merchantable volume of jack pine can result from a single JPBW outbreak (Gross and Meating 1994).

For economic and environmental considerations, forest managers in the Lake States do not currently use insecticides to combat JPBW infestations or limit timber losses (Benzie 1977; Heym et al. 1993; McCullough et al. 1994). Instead, current management recommendations are based on the use of silvicultural guidelines, harvest scheduling, salvage, or cover-type conversion to minimize JPBW impact. Current management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area). These guidelines are designed to reduce competition and the number of suppressed trees in overstocked stands and to reduce the number of wolf trees in understocked stands (Albers et al.

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Previous studies have examined the relationship between JPBW survival and the abundance of pollen cones (LeJeune 1950; LeJeune and Black 1950; Nealis 1990; Nealis and Loomic 1994) and quantified the impact of individual JPBW outbreaks (Gross 1992; Gross and Meating 1994; Kulman et al. 1963). However, comparatively little work has been performed to validate current JPBW management recommendations in the Lake States (McCullough et al. 1996).

The purpose of this chapter was to examine the top-kill and tree mortality that resulted from the 1991-1993 JPBW outbreak in the Raco Plains area in the Upper Peninsula of Michigan and to validate current JPBW management recommendations in the Lake States.

The specific objectives of this chapter were to: (*i*) quantify the top-kill and tree mortality of the Raco Plains outbreak; (*ii*) examine the patterns of top-kill and tree mortality with respect to stand characteristics including age, site index, basal area, suppressed tree proportion, and wolf tree proportion; and (*iii*) evaluate current JPBW management recommendations used in the Lake States. I tested the following null hypotheses derived from current JPBW management recommendations:

H_0: There is no difference in top-kill and tree mortality between "young" stands (< 50 yrs) and "old" stands (≥ 50 yrs).

H_0: There is no difference in top-kill and tree mortality between low site index stands (< 15.2 m) and high site index stands (≥ 15.2 m).

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H_0: There is no difference in top-kill and tree mortality among poorly stocked (< 1,300 TPH, < 16.1 m^2/ha), well stocked (1,300-1,734 TPH, 16.1-25.3 m^2/ha), or overstocked stands (> 1,734 TPH, > 25.3 m^2/ha).

H_0: There is no difference in top-kill and tree mortality between stands with few suppressed trees (≤ 10%) and stands where suppressed trees were common (> 10%) (20-year-old or older stands, only).

H_0: There is no difference in top-kill and tree mortality between stands with wolf trees and stands without wolf trees (20-years-old or older stands, only).

Methods

Study Site

The Raco Plains is a 18,200 ha (45,000 ac) area located in the Hiawatha National Forest in the Upper Peninsula of Michigan (Figure 1-1). This area is characterized by level to gently rolling terrain, sandy glacial outwash soils of the Rubicon, Croswell, and Kalkaska types, and large tracts of even-aged jack pine forest (Heym et al. 1993).

In 1991, a JPBW outbreak was first observed in the Raco Plains area, and aerial surveys indicated that an estimated 6,560 ha (16,000 ac) were defoliated (Heym et al. 1993; McCullough et al. 1996). Defoliation increased the following year (1992), and roughly 75% of the jack pine stands in this area suffered moderate to severe defoliation (McCullough et al. 1996). By 1993, the JPBW population was in decline, although noticeable defoliation was still observed in the area (M

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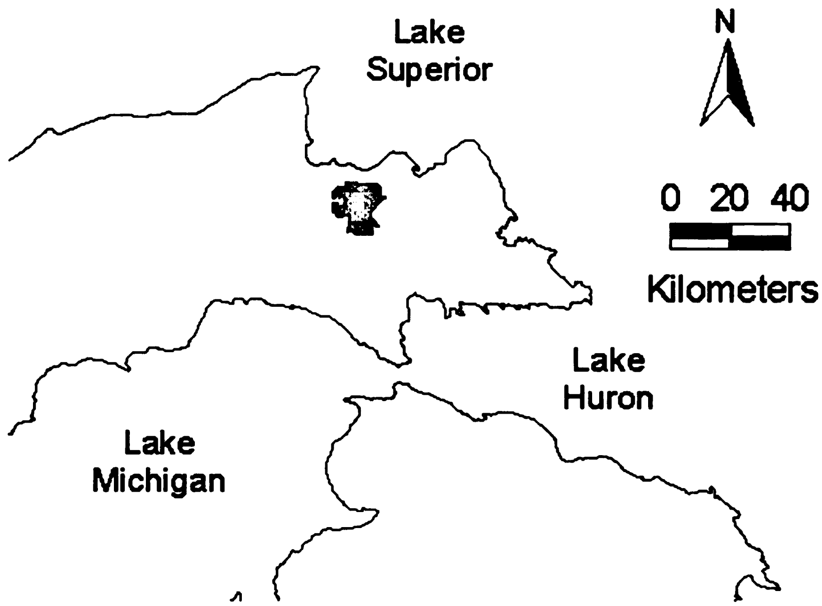

Figure 1-1 – The Raco Plains area of the Hiawatha National Forest located in the eastern Upper Peninsula of Michigan.

Sampling in the Raco Plains area has been performed annually since 1992 in four USDA Forest Service management compartments (compartment numbers 49, 58, 78, and 79) (Figure 1-2). The four compartments average 730 ha (1,800 ac) in size and contain a total of 240 stands. All survey compartments were visited by USDA Forest Service personnel from 1991-1994, and inventory characteristics (e.g., forest type, stand age, site index, etc.) and stand boundaries were updated. All stands with at least 50% of the basal area in jack pine were surveyed in each compartment.

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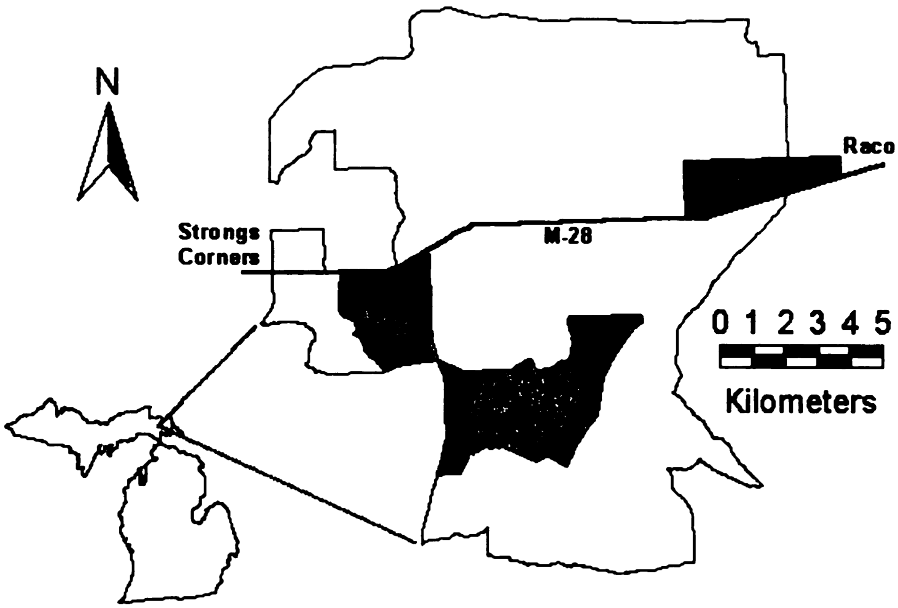

Figure 1-2 – USDA Forest Service management compartments in the Raco Plains area of the Hiawatha National Forest sampled from 1992 to 1996.

In 1996, 99 stands, covering 1,480 ha (3,600 ac), were surveyed in the Raco Plains area (Figure 1-3). Summary statistics for area, stand age, site index, basal area, and trees per hectare of the 99 sample stands are given in Table 1-1. Age of the 99 sample stands was positively correlated with site index (r = 0.21; P = 0.041) and basal area (r = 0.75; P < 0.0001). Site index of the 99 sample stands was positively correlated with basal area (r = 0.35; P < 0.0001) and trees per hectare (r = 0.25; P = 0.013).

Although some data from earlier sampling years were used in this chapter, most of the analysis in this chapter was performed on data collected in 1996. In all years, plot size and sampling technique were consistent to that reported by McCullough et al. (1995, 1996). However, sampling in 1996 was more intensive than in prev

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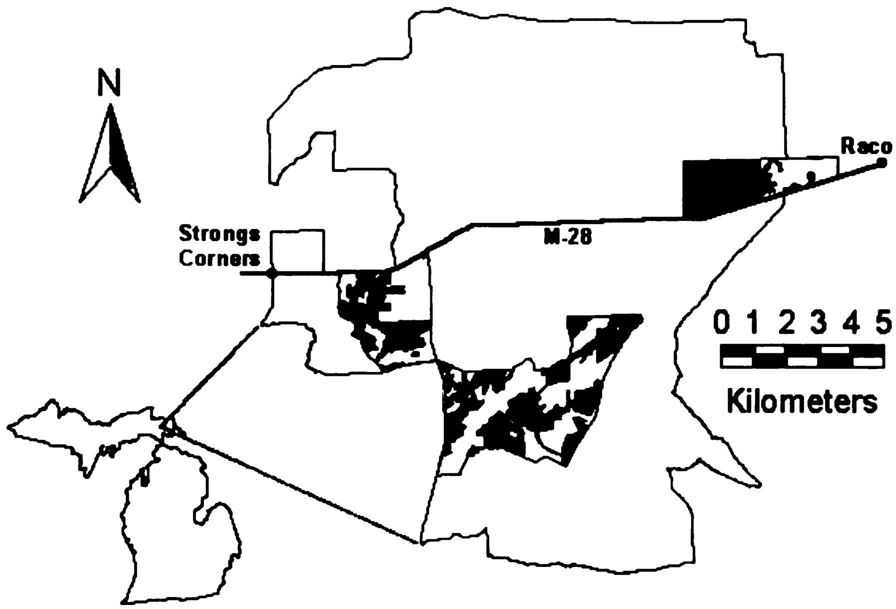

Figure 1-3 –Stands sampled in 1996 in the Raco Plains area of the Hiawatha National Forest.

Table 1-1 – Summary statistics for jack pine stands sampled in 1996 (n = 99).

	Mean[a]	Median	Minimum	Maximum
Area (ha)	14.9 (1.68)	10.9	0.8	101.7
Stand Age (years)	44 (2.1)	51	10	71
Site Index (m)	15.0 (0.15)	15.2	11.3	18.0
Basal Area (m^2/ha)	15.2 (0.87)	16.0	0.4	34.5
Number of Trees (per ha)	1353 (67.8)	1288	347	4293

[a] Standard error of the mean in parentheses

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Top-kill and Tree Mortality

To quantify top-kill and tree mortality resulting from the 1991-1993 JPBW outbreak, at least two fixed-radius, 0.01 ha (1/40 ac) circular plots were located in each of the 99 stands. Plots were randomly located each year. For the 1996 sampling, stands 8-19 ha (20-49 ac) in size were sampled with three plots. Those 20-39 ha (50-99 ac) in size received four sample plots. Stands 40-79 ha (100-199 ac) in size had five plots. Two stands had areas greater than 80 ha (200 ac), and they received six plots each. A total of 277 plots were sampled. The number of plots per stand represented a practical compromise between sampling effort and accuracy.

In all sample years, the total number of jack pine trees in each plot was tallied and the status of each tree (i.e., surviving, top-killed, or dead) was recorded. Each top-killed and dead jack pine tree was visually examined to determine if damage had occurred recently (i.e., as a result of the 1991-1993 JPBW outbreak) or before the 1991-1993 JPBW outbreak. We based this determination on the overall form of the tree, the presence of fine twigs, bark tightness, and other indicators of decay (McCullough et al. 1996).

In 1996, I also measured diameter at breast height (1.37 m) of all jack pine trees in each plot. In addition, I ranked all jack pine trees as dominant/ codominant, intermediate, suppressed, or wolf as defined by Smith (1986). Dominant/codominant trees were those with crowns extending above or forming the general level of the canopy. They received direct light from above and partial or little from the sides. Intermediate trees were shorter than the dominant/

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codominant trees, had crowns extending into the canopy, and received little light from above and none from the sides. Suppressed trees were those completely overtopped by surrounding trees. Wolf trees were branchy, open-grown trees with full crowns that received direct light from above and from the sides. Information on 2,899 trees was collected.

Analysis of Top-kill and Tree Mortality

Mean top-kill and tree mortality data from each of the five sample years (1992-1996) were plotted to examine cumulative top-kill and tree mortality in the Raco Plains area over time. I also examined top-kill and tree mortality among dominant/codominant, intermediate, suppressed classes of trees. Finally, percentages of surviving, top-killed, and dead trees for wolf trees and dominant/codominant trees not classified as wolf trees were calculated.

Analysis of Stand Characteristics

Associations between top-kill and tree mortality, and stand characteristics including age, site index, basal area, suppressed tree proportion, and wolf tree proportion were examined by calculating Pearson's product-moment correlation coefficient (*r*) and by dividing stand characteristics into four to six groups and plotting mean top-kill and tree mortality values for each group. This method of graphical analysis reduced variability in the top-kill and tree mortality data. Thus, overall association between top-kill and tree mortality and stand characteristics could be examined.

Because of the importance of tree mortality as a determinant of volume loss, I performed regression analysis on the tree mortality data. Step-wise multiple linear regre

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linear regression was performed with stand age, site index, and stand basal area as independent variables. Linear regression analysis was also performed on tree mortality data transformed to empirical logits in an attempt to investigate nonlinear relationships between tree mortality and stand characteristics.

Analysis of Management Recommendations

Divisions in stand characteristics for testing management recommendations were based on previous studies of JPBW impact (McCullough et al. 1996) and on current jack pine and JPBW management guidelines for the Lake States (Albers et al. 1995; Benzie 1977; McCullough et al. 1994; Weber 1995). One-way analysis of variance (ANOVA) was used to test for significant differences in top-kill and tree mortality between groups of stands differing in age, site index, density, suppressed tree proportion, and wolf tree proportion. When significant differences were observed among stand density groups, Hochberg's GT2-method of multiple comparison was used to determine which stand density pairs differed significantly (Sokal and Rohlf 1995). Levene's test was used to test for heteroscedasticity in the top-kill and tree mortality data (Levene 1960). Where necessary, top-kill data were transformed to stabilize the variance using the square root transformation (age test), and tree mortality data were transformed to stabilize the variance using the natural logarithm transformation (site index and stand density tests) (Sokal and Rohlf 1995).

The site index class test was interpreted as a test of site quality. Site index refers to the height of the dominant or dominant/codominant trees in a stand at the index year 50 (Carmean 1975; Carmean and Lenthall 1989; Wenger 1984).

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It is commonly considered an expression of site quality, as height growth of trees is assumed to be independent of stand density and strongly related to site quality (Carmean 1975; Wenger 1984). Although the shortcomings of using height growth as an indicator of site quality have been recognized (Carmean 1975; Carmean and Lenthall 1989), site index is commonly used by resource managers in the Lake States (Benzie 1977). Other indicators of site quality including ecological classification, land type association, and soil maps were examined. Because these site quality indicators are relatively homogenous for the Raco Plains area (Heym et al. 1993), they would be of limited value in assessing differences in JPBW impact and were not included in the analysis.

Two measures of stand density were used to test for differences in top-kill and tree mortality between stocking classes: trees per hectare (TPH) for stands in the "young" age class (i.e., less than 50 years old) and basal area (m^2/ha) for stands in the "old" age class (i.e., stands 50 years old or older). I chose TPH as a measure of stocking for "young" stands because these stands tend to have small average diameter at breast height, and their density is not accurately estimated by basal area.

The 10% criterion for the proportion of suppressed trees in the stand and the presence/absence criterion for wolf trees in the stand were based on thresholds that were assumed necessary to affect JPBW impact. Stands younger than 20 years old were not likely to have reached crown closure or to have developed stratified canopies. Therefore, few trees in these stands would be suppressed and all trees could be considered open-grown. For these reasons, only stands

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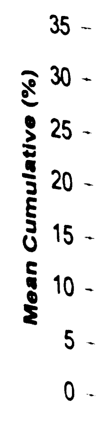

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20 years old or older were used in the analysis of suppressed and wolf tree proportion.

Results

Analysis of Top-kill and Tree Mortality

Since sampling for JPBW impact began in 1992, there has been a dramatic increase in the amount of top-kill and tree mortality in the Raco Plains area. In the first sampling year (1992), 5% of the trees in the Raco Plains area had top-kill (Figure 1-4). In 1993, top-kill increased to 19%. Rates of top-kill recorded in 1994 (17%) and 1996 (18%) were approximately equal to that of 1993. The notably high top-kill percentage recorded in 1995 (26%) may have been a result of random plot locations in high density top-kill areas or sampling error. One stand sampled in 1996 experienced 91% top-kill, but this was an extreme case. Fourteen of the 99 stands I sampled had no top-killed trees in 1996.

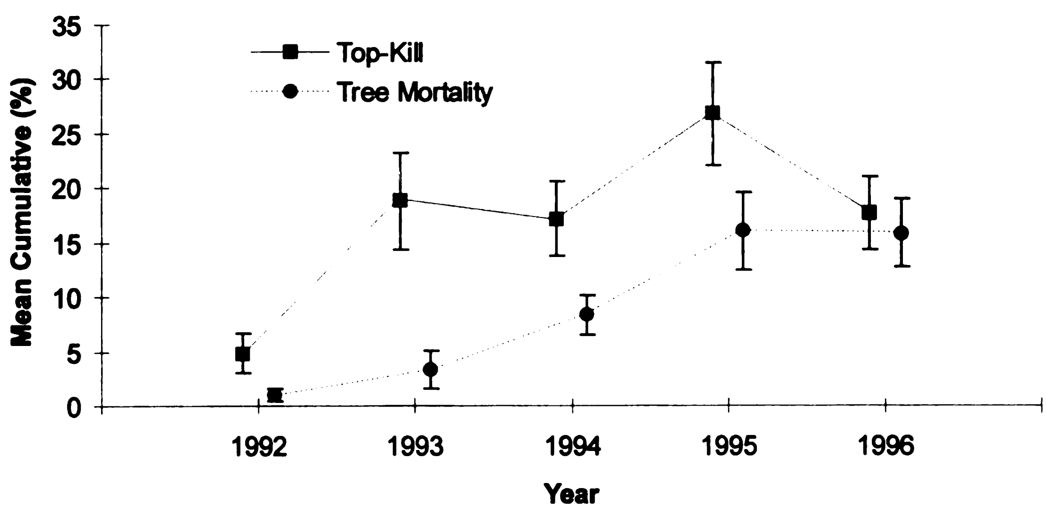

Figure 1-4 – Mean cumulative top-kill and tree mortality percentages attributable to the 1991-1993 JPBW outbreak (with 95% confidence intervals).

Tree mortality attributable to the 1991-1993 JPBW outbreak was observed to be only 1% in 1992 (Figure 1-4). During 1992-1995, cumulative tree mortality was 3%, 8%, and 16%, respectively. The 1996 level of tree mortality was approximately equal to that observed in 1995 (16%). A maximum mortality rate of 50% was observed in one stand. Nearly one-third (31) of the 99 sample stands had no tree mortality in 1996. It should be noted that among-year differences in both top-kill and tree mortality percentages could have been due to re-randomized plot location each year.

All trees in each sample plot were classified as suppressed, intermediate, or dominant/codominant based on their relative position within the canopy of the sample plot. Of the 2899 jack pine trees sampled, 73% of the trees in the sample stands were classified as dominant/codominant, while 16% were intermediate and 11% were suppressed (Table 1-2).

Table 1-2 – Mean percentage of surviving, top-killed, and dead trees in 1996 by crown class[a].

	Surviving	Top-Killed	Dead	Total
Suppressed	3.3 (1.16)	2.5 (0.91)	5.3 (1.47)	11.1 (2.00)
Intermediate	7.9 (2.26)	2.9 (0.81)	4.8 (1.35)	15.6 (2.41)
Dominant/Codominant	55.2 (4.48)	12.4 (3.18)	5.8 (1.57)	73.4 (2.99)
Total	66.4 (5.02)	17.7 (3.36)	15.9 (3.07)	100

[a] Standard error of the mean in parentheses

Most dominant/codominant (75%) and intermediate trees (50%) survived the 1991-1993 JPBW outbreak. Nearly half the suppressed trees (49%) and nearly one-third of the intermediate trees (30%) died following the outbreak. Only 8% of the dominant/codominant trees in the sample were dead in 1996.

The majority of surviving trees (85%) and top-killed trees (63%) were dominant/codominant trees. Suppressed trees accounted for only 5% and 15% of the surviving and top-killed groups, respectively. Dead trees were equally distributed among the three tree crown classes.

While more than three quarters of the dominant/codominant trees not classified as wolf trees survived the 1991-1993 JPBW outbreak, two-thirds of the wolf trees survived the 1991-1993 JPBW outbreak (Table 1-3). Wolf trees experienced 24% top-kill and 9% tree mortality compared to 15% top-kill and 8% tree mortality of other dominant/codominant trees.

Table 1-3 – Mean percentage of surviving, top-killed, and dead trees in 1996 for wolf and dominant/codominant (not wolf) trees[a].

	Surviving	Top-Killed	Dead	Total
Wolf	67.7 (4.70)	23.5 (4.05)	8.8 (3.23)	100
Dominant /Codominant (Not Wolf)	76.8 (2.62)	15.2 (2.29)	8.0 (1.05)	100

[a] Standard error of the mean in parentheses

Analysis of Stand Characteristics

Top-kill

Top-kill was positively correlated with stand age, stand basal area, and the proportion of suppressed trees in the stand (Table 1-4). Top-kill was negatively correlated with the proportion of wolf trees in the stand (Table 1-4).

Table 1-4 – Pearson's product-moment correlation coefficient (*r*) for top-kill, tree mortality, and stand characteristics.

	Top-Kill	Tree Mortality
Stand Age	0.54 **	0.57 **
Site Index	0.15	0.39 **
Stand Basal Area	0.48 **	0.68 **
Suppressed Tree Proportion	0.25 *	0.24 *
Wolf Tree Proportion	-0.20 *	-0.55 **

** Significant at the 0.01 level (2-tailed)
* Significant at the 0.05 level (2-tailed)

Graphical analysis indicated that top-kill remained fairly low and constant for the four youngest stand age groups, increasing slightly with age, but remaining nearly 10% until age reached 50 years (Figure 1-5). A sharp increase in top-kill was seen in stands that were 50 years old or older. Although top-kill increased slightly with site index, this trend was not strong (Table 1-4 and Figure 1-6). There was a strong positive association between top-kill and stand basal area (Table 1-4 and Figure 1-7). However, the slight reduction in top-kill in the 20.8-27.6 m^2/ha (91-120 ft^2/ac) group and the extreme variability in the over 27.6 m^2/ha (120 ft^2/ac) group obscured this pattern somewhat. Although the association between top-kill and the proportion of suppressed trees in the stand was positive, this was likely due to the low rate of top-kill observed in stands with no suppressed trees (Table 1-4 and Figure 1-8). No association was seen between top-kill and higher relative abundance of suppressed trees in the stand. There was a slight negative association between top-kill and the proportion of wolf trees in the stand (Table 1-4 and Figure 1-9), probably due to slightly lower amounts of top-kill in stands with the highest proportion of wolf trees.

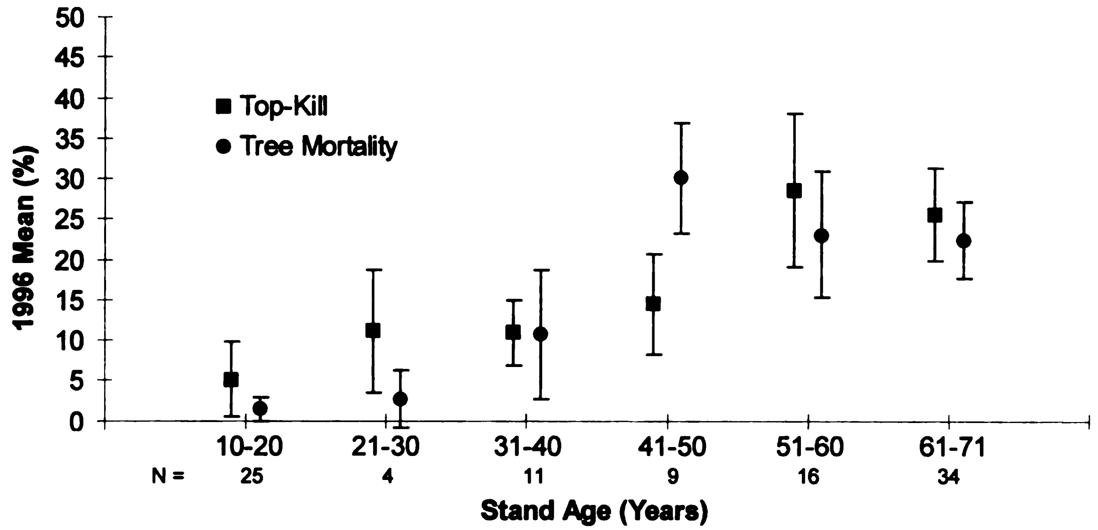

Figure 1-5 – Mean top-kill and tree mortality in 1996 by stand age (with 95% confidence intervals).

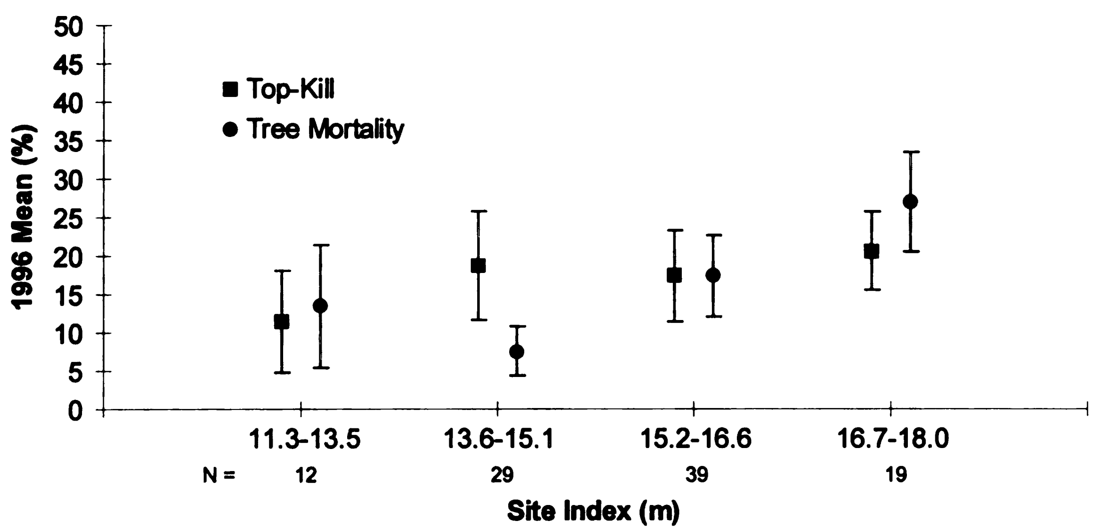

Figure 1-6 – Mean top-kill and tree mortality in 1996 by site index (with 95% confidence intervals).

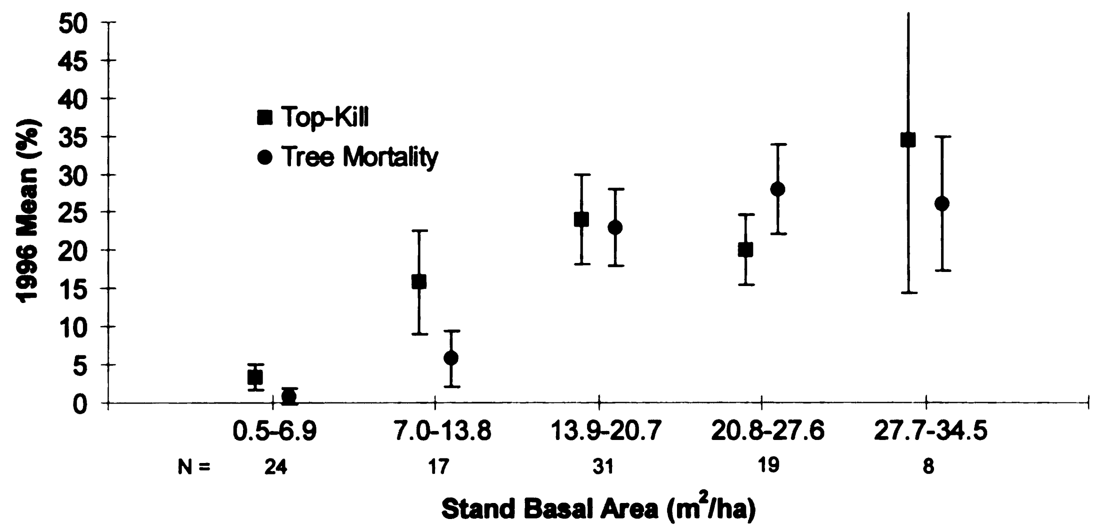

Figure 1-7 – Mean top-kill and tree mortality in 1996 by stand basal area (with 95% confidence intervals).

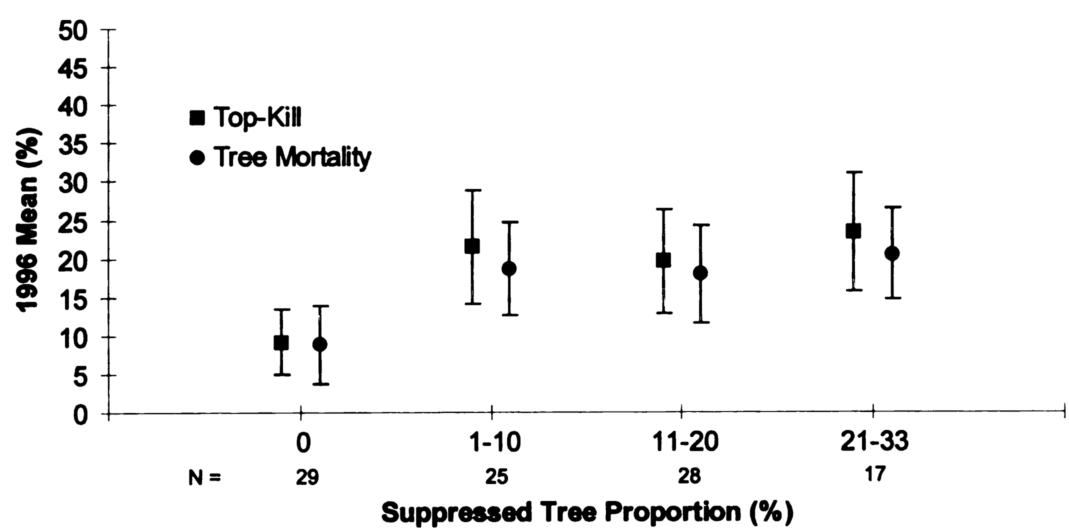

Figure 1-8 – Mean top-kill and tree mortality in 1996 by suppressed tree proportion (with 95% confidence intervals).

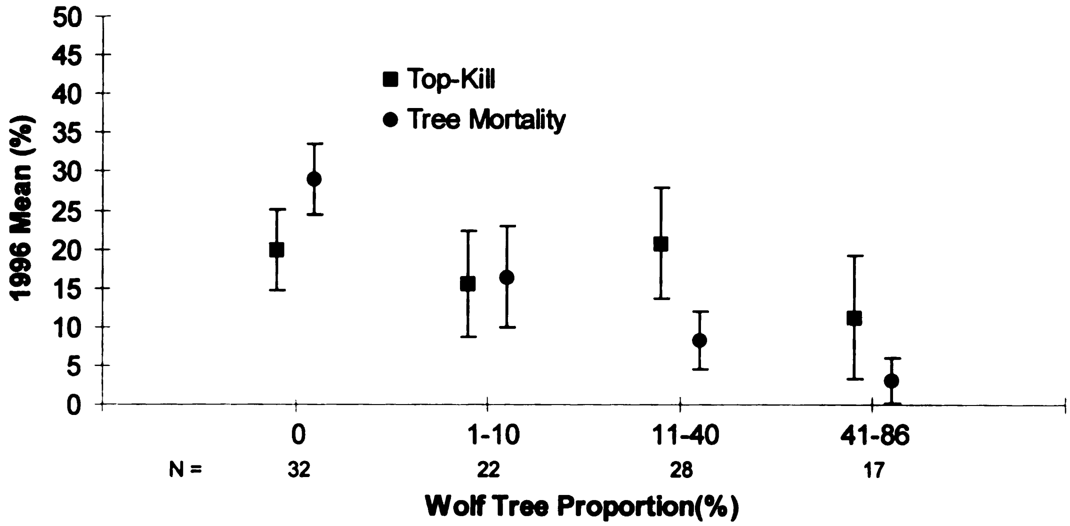

Figure 1-9 – Mean top-kill and tree mortality in 1996 by wolf tree proportion (with 95% confidence intervals).

Tree Mortality

Tree mortality was positively correlated with stand age, site index, stand basal area, and the proportion of suppressed trees in the stand (Table 1-4). Tree mortality was negatively correlated to the proportion of wolf trees in the stand (Table 1-4).

A strong positive association between tree mortality and stand age is apparent in Figure 1-5. Tree mortality was low in stands younger than 30 years old but increased sharply in stands over 40 years old. Tree mortality also showed a positive association with site index, despite relatively low tree mortality in the 13.6-15.1 m (45-49 ft) site index group (Table 1-4 and Figure 1-6). Perhaps the strongest association in the data was between tree mortality and stand basal area (Table 1-4 and Figure 1-7). There was a particularly large increase in mortality between the 7.0-13.8 m^2/ha (31-60 ft^2/ac) group and the 13.9-20.7 m^2/ha (61-90 ft^2/ac) group. As with top-kill, tree mortality was positively associated with the proportion of suppressed trees in the stand, but again, this was probably due to the low amount of tree mortality in stands with no suppressed trees (Table 1-4 and Figure 1-8). No association was seen between tree mortality and higher relative abundance of suppressed trees in the stand. Finally, tree mortality showed a sharp negative association with the proportion of wolf trees in the stand (Table 1-4 and Figure 1-9).

Step-wise multiple linear regression analysis yielded a significant model (F = 46.91; $P < 0.0001$; $n = 99$) that explained 49% of the variation in the mortality data (standard error in parentheses below coefficients):

$$M = \underset{(0.12)}{-0.29} + \underset{(0.0081)}{0.018}\, SI + \underset{(0.0014)}{0.011}\, BA \qquad [1]$$

where M is the tree mortality percentage in the stand, SI is the site index of the stand (m), and BA is stand basal area (m^2/ha). Stand age dropped out of the model due to its strong positive correlation with basal area ($r = 0.75$; $P < 0.0001$). Linear regression on mortality data that were transformed to empirical logits also yielded a significant model ($F = 125.74$; $P < 0.0001$; $n = 99$). This model explained 84% of the variation in the transformed mortality data and can be interpreted as the following equation (standard error in parentheses below coefficients):

$$M = \frac{e^x}{1 + e^x} \qquad [2]$$

where:

$$x = \underset{(3.3)}{-6.8} + \underset{(0.22)}{0.11}\, SI + \underset{(0.20)}{0.20}\, BA - \underset{(0.013)}{0.0021}\, SI\, BA \qquad [3]$$

Analysis of Management Recommendations

Current management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area).

Top-kill

Top-kill was significantly greater in stands 50 years old and older than in younger stands ($F = 55.71$; $P < 0.0001$; $df = 1$) (Table 1-5). Age class explained 37% of the variation in the transformed top-kill data. Top-kill did not differ significantly between low and high site index classes ($F = 0.29$; $P = 0.594$; $1 - \beta = 0.92$; $df = 1$), stocking class ($F = 1.67$; $P = 0.194$; $1 - \beta = 0.66$; $df = 2$), suppressed tree proportion ($F = 0.001$; $P = 0.980$; $1 - \beta = 0.95$; $df = 1$), or wolf tree proportion ($F = 0.28$; $P = 0.601$; $1 - \beta = 0.92$; $df = 1$) (Table 1-5).

Tree Mortality

Tree mortality was significantly greater in stands 50 years old and older than in younger stands ($F = 23.98$; $P < 0.0001$; $df = 1$) and greater in high site index stands than low site index stands ($F = 5.92$; $P = 0.017$; $df = 1$) (Table 1-5). Age class and site index class explained 20 and 5.7%, respectively, of the variation in tree mortality. Tree mortality was significantly different among stocking classes ($F = 4.93$; $P = 0.009$; $df = 2$). Hochberg's GT2-method indicated that tree mortality was lower in poorly stocked stands than in well stocked (*Mean Difference* = 1.16; *MSD* = 1.07; $P = 0.030$) or overstocked stands (*Mean Difference* = 1.40; *MSD* = 1.23; $P = 0.021$) (Table 1-5). There was no significant

Table 1-5 – Mean top-kill and tree mortality by management class[ab].

	N[c]	Top-kill (%)		Mortality (%)	
Age Class (years)					
Young (< 50)	49	8.7	(1.52)*a*	8.9	(1.93)*a*
Old (≥ 50)	50	26.6	(2.49)*b*	22.7	(2.05)*b*
Site Index Class (m)					
Low (< 15.2)	41	16.6	(2.75)*a*	9.3	(1.71)*a*
High (≥ 15.2)	58	18.5	(2.21)*a*	20.6	(2.19)*b*
Stocking Class[d] (TPH, m^2/ha)					
Poor (< 1,300, < 16.1)	34	13.4	(2.25)*a*	8.7	(2.14)*a*
Well (1,300-1,734, 16.1-25.3)	41	19.7	(2.68)*a*	18.9	(2.51)*b*
Over (> 1,734, > 25.3)	24	20.5	(4.28)*a*	21.1	(3.15)*b*
Suppressed Tree Class[e] (%)					
Few (≤ 10)	33	22.4	(2.95)*a*	20.9	(2.62)*a*
Abundant (> 10)	42	22.5	(2.65)*a*	20.5	(2.32)*a*
Wolf Tree Class[e] (%)					
Absent (0)	30	21.2	(2.68)*a*	31.0	(2.07)*a*
Present (> 0)	45	23.3	(2.75)*a*	13.8	(1.95)*b*
Total	99	17.7	(1.72)	15.9	(1.56)

[a] Standard error of the mean in parentheses
[b] Means within a management class followed by the same letter are not significantly different ($\alpha = 0.05$)
[c] Number of sample stands
[d] TPH - "young" stands, m^2/ha - "old" stands
[e] Stands 20 years old or older, only

difference in tree mortality between well stocked and overstocked stands (*Mean Difference* = 0.24; *MSD* = 1.19; *P* = 0.946) (Table 1-5). There were no significant differences in tree mortality between stands with few and abundant suppressed trees (F = 0.02; P = 0.897;1 - β = 0.95; *df* = 1) (Table 1-5). However, tree mortality was significantly greater in stands without wolf trees than in stands with wolf trees (F = 34.13; P < 0.0001; *df* = 1) (Table 1-5). The presence of wolf trees accounted for 32% of the variation in the tree mortality.

Discussion

Estimates of top-kill and tree mortality following the 1991-1993 JPBW outbreak were probably conservative. From 1992-1996, the USDA Forest Service harvested jack pine from 15 stands in the study management compartments (Heym et al. 1993). These stands were cut to limit timber losses associated with the outbreak, and the stands selected for harvest were those the Forest Service believed to be the most vulnerable to impact (Heym et al. 1993). If these harvested stands had suffered heavy top-kill or tree mortality, then the 1996 data likely underestimated the true impact of the 1991-1993 JPBW outbreak.

No attempt was made in this study to relate JPBW impact to defoliation. The relationship between impact from the 1991-1993 JPBW outbreak in the Raco Plains area and defoliation was examined in two previous studies (Kouki et al. 1997; McCullough et al. 1996). Both found that defoliation was positively associated with the amount of top-kill in the stand and that defoliation was not associated with the amount of tree mortality in the stand. I have not included defoliation in the present analysis because of the results presented in the two previous studies. In addition, the objectives of the present study focus on timber management. Quantifying defoliation is a time-consuming and often subjective process, and measured defoliation may not be available to the forest manager. Forest managers would benefit from relating JPBW impact to readily available stand characteristics.

Top-kill and Tree Mortality

Data on the cumulative top-kill and tree mortality percentages indicated that top-kill accumulated fairly rapidly following the onset of the outbreak. This was evident in the 5% top-kill rate observed in 1992, the second year of the outbreak. Although some studies of top-kill in jack pine have suggested an association between root pathogens and top-kill (Mallett 1995; Mallett and Volney 1990), we would expect an endemic top-kill rate to be lower that 5%. Mean top-kill in 1993, 1994, and 1996 was approximately equal suggesting that top-kill resulting from the 1991-1993 JPBW outbreak leveled off the third year after defoliation began.

Tree mortality accumulated more slowly than top-kill. In 1992, we observed a mortality rate of only 1%, which is similar to expected rates of endemic jack pine mortality (Buchman et al. 1983). In the next three years, tree mortality increased annually to a maximum of 16% and a maximum annual increase of 7.7% from 1994 to 1995. Tree mortality appears to have leveled off in 1996 at about 16%.

This suggests two trends in tree mortality in the Raco Plains area. First, there was a time lag between the onset of defoliation and the onset of tree mortality resulting from this defoliation. Previous studies of defoliation of jack pine have determined that one complete defoliation or successive years of heavy defoliation are necessary to cause mortality (Kulman 1971; O'Neil 1962). Complete defoliation or successive years of heavy defoliation most likely did not occur in the Raco Plains area until 1992, the second year of the outbreak, and increased mortality was not recorded until 1993. This suggests that forest managers should expect that tree mortality will generally not begin to accumulate until a few years after a JPBW outbreak begins, providing time for managers to plan and execute silvicultural or salvage operations.

The second trend was that of increasing tree mortality for only three years after the outbreak collapsed. Other workers have observed tree mortality for as many as five years (Gross and Meating 1994; Hopkin and Howse 1995). It should be cautioned that although similar tree mortality rates were recorded for two successive years in 1995 and 1996, this does not necessarily indicate that tree mortality attributable to the 1991-1993 JPBW outbreak is no longer accumulating. Sampling errors such as excluding fallen dead trees in plot surveys may have underestimated tree mortality in 1996. Additional data in subsequent years is necessary to validate this three-year effect.

It was apparent from the results of the crown class comparisons that suppressed trees suffered disproportionately high mortality. One-half of the suppressed trees in the Raco Plains area died as a result of the 1991-1993 JPBW outbreak. Other workers have also observed similar mortality rates in suppressed trees (Batzer and Jennings 1980; Graham 1935; Hodson and Zehngraff 1946; Kulman et al. 1963). Suppressed jack pine trees receive little direct sunlight, are undoubtedly low vigor trees that grow slowly, and are probably highly vulnerable to additional stress such as defoliation. Also, suppressed trees in the understory may collect dispersing budworm larvae from the dominant/codominant trees. They may also produce relatively more pollen cones than trees of other crown classes, leading to higher budworm survival and defoliation (Batzer and Jennings 1980; Nealis and Loomic 1994).

Whatever the underlying reason may be, the death of suppressed trees may be of little concern to forest managers. Typically, these trees are not merchantable, and their mortality may act as a natural thinning from below, regulating and, perhaps, increasing productivity of the stand (Mattson and Addy 1975).

Suppressed trees did not suffer disproportionate top-kill. Most top-killed trees (63%) in the Raco Plains area were in the dominant/codominant crown class. It is likely that many suppressed trees could not tolerate heavy defoliation of their terminal leaders without succumbing to mortality.

Stand Characteristics

Perhaps the most striking pattern in the relationship between JPBW impact and various stand characteristics was the positive association between top-kill and tree mortality and stand age. Although early workers have noted the positive relationship between JPBW impact and stand age (Graham 1935), many studies have been confined to sampling only from older, merchantable jack pine stands (Gross and Meating 1994; Kulman et al. 1963).

The underlying reason for the relationship between JPBW impact and stand age may be straightforward. Jack pine in the Lake States is a relatively short-lived, shade-intolerant species (Benzie 1977; Rudolph and Laidly 1990). Jack pine stands on poorer sites may begin to stagnate as young as age 40 due to declining vigor or an inability to withstand the stress of damaging agents (Benzie 1977). It is evident from the high rates of JPBW impact in the Raco Plains area that many of these stands are stagnating or "breaking up." Although perhaps not the only factor contributing to this break up, defoliation that occurred during the 1991-1993 JPBW outbreak was an important component of the stress leading to the decline in these stands.

Although top-kill was highly variable and fairly evenly distributed across different site index stands, tree mortality was positively associated with site index. This pattern of tree mortality is contradictory to the intuitive assumptions that JPBW impact is greater on low quality sites where trees are under more stress due to limited moisture and nutrients than trees on higher quality sites. When JPBW outbreaks occur, the additional stress of defoliation is thought to result in increased JPBW impact compared with stands on better sites (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994). Also, stress, particularly drought stress, has been suggested to increase production of jack pine pollen cones (Volney 1988), and the positive relationship between pollen cone production and JPBW larval survival has been well documented (Batzer and Jennings 1980; Graham 1935; Hodson and Zehngraff 1946; Nealis and Loomic 1994).

The higher mortality rates observed in the stands with higher site index values contradict some of the above assumptions. There are at least two possible explanations for this pattern. First, the lower site index jack pine stands tended to be some of the poorest quality sites in the Raco Plain area. These stands are generally located on edaphic extremes and are typically pure jack pine stands that do not support other tree species. High site index jack pine stands in this area often have higher proportions of hardwood competitors such as red maple (*Acer rubrum* L.), aspen (*Populus* spp.), or oaks (*Quercus* spp.). I speculate that particularly older jack pine on these sites may be under some stress related to the presence of hardwood competitors. This competition stress compounded with defoliation stress may have resulted in higher mortality in these stands.

Second, trees growing on low quality sites may be more frequently or more severely stressed because of deficient moisture or nutrients than trees on higher quality sites. However, reactions of trees to stress are complex and can include both immediate and long-lasting physiological responses (Johnson 1987). Plant growth regulators (PGRs) such as auxins, gibberellins, cytokinins, ethylene, and abscisic acid have been implicated in these physiological responses. Increased levels of PGRs following drought stress may enhance water uptake by increasing root membrane permeability (Johnson 1987). Nutrient deficiencies have been observed to alter carbon allocation, increasing root-to-shoot ratios in fast-growing trees (Ibrahim et al. 1997; Johnson 1987; Laurence et al. 1994). More importantly, there is evidence that these physiological responses modify the tree's subsequent response to different forms of stress, a phenomenon known as cross-adaptation (Johnson 1987). For example, low nitrogen treated cotton plants have more rapid responses to drought stress than high nitrogen treated plants (Johnson 1987).

The above discussion suggests that jack pine trees growing on low quality sites may be less vulnerable to JPBW impact than those on higher quality sites due to cross-adaptation from previous drought or nutrient stress events. Others have observed that tree mortality in oak species defoliated by a native looper complex in the central and southern Appalachians (Crow and Hicks 1990) and defoliated by gypsy moth (*Lymantria dispar* L.) in Pennsylvania (Quimby 1987) was higher on better quality sites than on poorer quality sites. Another study to predict susceptibility to gypsy moth defoliation found that while stands on dry ridges and sands sustained more frequent defoliation events (i.e., higher susceptibility), these stands were less likely to sustain high mortality than stands on mesic slopes and bottom sites (i.e., lower vulnerability) (Houston and Valentine 1977).

This is not the first study to observe a positive relationship between JPBW induced tree mortality and site quality. Trees on higher quality sites may have higher foliar nitrogen levels that have been shown to increase JPBW larval survival on young jack pine (McCullough and Kulman 1991a; McCullough and Kulman 1991b). Also, higher soil nitrogen levels have been shown to stimulate pollen cone production (McCullough and Kulman 1991b) which in turn may increase JPBW survival (Nealis and Loomic 1994).

As with stand age, both top-kill and tree mortality were positively associated with stand basal area. Jack pine trees in higher density stands may experience competition for nutrients, moisture, light, or space resulting in smaller crowns and lower leaf area. Because foliage serves as the main carbon store in conifers, jack pine trees with smaller crowns may have few reserves to allocate to recovery from defoliation stress, or they may lose proportionally more reserves through defoliation than larger crowned trees (Clancy et al. 1995). Also, JPBW larval dispersal occurs when first instar JPBW move to overwintering sites, when overwintering second instars emerge from their hibernacula to seek out feeding sites, and possibly, again when larvae move from pollen cones to newly expanded foliage. Dispersal losses are an important factor in larval mortality because few larvae survive if they do not land directly on suitable hosts (Batzer and Jennings 1980; Foltz et al. 1972; Nealis and Loomic 1994). The physical spacing of trees in higher density stands means that dispersing larvae have to travel shorter distances to suitable hosts and would likely have a higher probability of successful dispersal in these stands.

While no association between top-kill and suppressed tree proportion was present, tree mortality was positively associated with the proportion of suppressed trees in the stand. However, this positive association may have been the result of stand age rather than stand structure. Most stands with no suppressed trees were less than 20 years old. These stands have not reached crown closure, so overtopped trees were relatively rare. In stands where suppressed trees were present, there were no strong patterns in top-kill or tree mortality relative to the abundance of suppressed trees. Abundance of suppressed trees in a stand may, therefore, be a poor predictor of top-kill or tree mortality resulting from JPBW defoliation.

While there was no pattern in the highly variable relationship between top-kill and the proportion of wolf trees in the stand, tree mortality was negatively associated with the proportion of wolf trees in the stand. As with suppressed trees, this could be explained in part by stand age. Also, stands with high proportions of wolf trees generally were poorly stocked with few suppressed or intermediate trees. While wolf trees experienced mortality rates similar to other dominant/codominant trees, suppressed and intermediate trees accounted for two-thirds of the total tree mortality I observed. Stands with low numbers of suppressed and intermediate trees and a high proportion of wolf trees typically sustained low levels of mortality. This negative association also suggests that reducing abundance of wolf trees in a stand may have little effect on stand vulnerability during JPBW outbreaks.

The linear regression equation accounts for less than 50% of the variation in the tree mortality data which suggests that either tree mortality is dependent on variables other than site index and basal area (i.e., defoliation intensity, pollen cone abundance, etc.) or that the relationship between tree mortality and these factors is nonlinear. Analysis of a nonlinear relationship explained more variation in the tree mortality data than did linear analysis. However, I would caution that this function may not be the "best" function in terms of explaining the variability in tree mortality. Nonlinear functional form is difficult to determine with no underlying theory on the relationships between JPBW-induced tree mortality and the characteristics of the stand. Validation in other area and JPBW outbreaks and perhaps, modification is in order before this function is used for prediction.

Management Recommendations

Results of the tests for significant differences in top-kill and tree mortality between "young" and "old" stands and associations between impact and stand age, indicate that the management recommendation to shorten rotation lengths and eliminate overmature stands is valid. Further, if minimizing top-kill and tree mortality is the primary management goal, then the oldest stands should be given the highest management priority for harvest scheduling, salvage, or cover-type conversion. I believe that stand age is the most important factor to be considered in the management of JPBW impact because operationally, forest managers have more control over rotation lengths than over site quality or stand density.

In addition, this study joins the litany of others who call for the reduction of jack pine rotation length in the Lake States (Albers et al. 1995; Benzie 1977; Jones and Campbell 1986; McCullough et al. 1994; Nyrop et al. 1983; Rose 1973; Rose 1974; Weber 1995; Weber 1986; Williams and Nautiyal 1992). The present results indicated that by allowing stands to age past 40 years, managers may expect tree mortality to double with the next JPBW outbreak. If this is not reason enough, managers might also consider the stand-replacing disturbance cycles characteristic of jack pine ecosystems in the Lake States before the modern era of fire suppression. These cycles may well have been shorter than 50 years (Van Wagner 1978; Whelan 1995; Wright and Bailey 1982).

Although no differences were observed in top-kill, tree mortality was significantly greater in high site index stands than in low site index stands. Although this relationship must be validated in other Lake States forests, the present results suggest that management priorities may have to be adjusted to reduce JPBW impact. Higher quality sites may need to be prioritized for harvest, salvage operations, or cover-type conversion.

While the positive relationships between top-kill and tree mortality and stand basal area could be explained in part by the positive relationship between basal area and stand age, the finding of significantly less tree mortality in poorly stocked stands suggests that current management recommendations may overstate the need to eliminate poorly stocked stands to minimize JPBW impact. Management recommendations to eliminate poorly stocked stands come from the belief that wolf trees in understocked stands are favorable host for JPBW (Hodson and Zehngraff 1946; McCullough et al. 1994; Weber 1995). However, my results indicate that wolf tree abundance was generally negatively associated with tree mortality following a JPBW outbreak.

Although neither top-kill nor tree mortality was significantly greater in overstocked stands than in well stocked stands, I believe that the management recommendation to eliminate stands over 25.3 m^2/ha (110 ft^2/ac) is valid for two reasons. First, I saw a strong positive association between JPBW impact and stand basal area. Second, absolute top-kill and tree mortality (i.e., top-kill and tree mortality per hectare) will be greater in overstocked stands than in well stocked stands with similar proportional impact. Therefore, absolute timber losses are likely to be higher in overstocked stands than in well stocked stands. In addition to eliminating overstocked stands (i.e., harvest or thinning), I suggest that stands with the highest density be prioritized for harvest scheduling, salvage, or cover-type conversion.

My analysis indicated that suppressed trees sustained disproportionately higher mortality. However, there was no significant difference in either top-kill or tree mortality between stands with few suppressed trees and stands where suppressed trees were common. While suppressed trees may act as refugia for dispersing larvae (Batzer and Jennings 1980), their abundance in the stand did not adversely affect overall impact in the stand. From a management perspective, the loss of suppressed trees may be relatively unimportant. I suggest that management practices designed to reduce or eliminate the abundance of suppressed trees in the stand (e.g., non-commercial thinnings from below) be given low priority. In addition, unevenly-spaced planting or seeding that results in a mature stand with dense clusters of trees and high proportions of suppressed trees, will probably not increase stand vulnerability to JPBW damage.

My result of significantly lower tree mortality in stands with wolf trees than in stands without wolf trees was unexpected. Wolf trees have long been considered important to budworm survival (Hodson and Zehngraff 1946; McCullough et al. 1994; Weber 1995). However, their presence in the stand did not adversely affect top-kill and was associated with lower tree mortality. I recommend that stands containing a high proportion of wolf trees be given low priority for management operations.

Conclusions

The 1991-1993 JPBW outbreak resulted in widespread top-kill and tree mortality of jack pine in the Raco Plains area. By 1996, an average of 18% of the jack pine trees in the Raco Plains area were top-killed and an additional 16% had died as a result of the 1991-1993 JPBW outbreak. Stand age was clearly an important factor affecting JPBW impact. I observed dramatic increases in JPBW impact in older stands. Shortening rotation lengths and harvesting overmature jack pine is, perhaps, the single most important objective for forest managers. The oldest stands should be given the highest priority for management such as harvest or salvage.

While the relationship between top-kill and site quality was somewhat inconclusive, tree mortality was greater on higher quality sites. There are some compelling physiological reasons to reconsidering the management recommendation to favor high quality sites for jack pine. However, this relationship must be validated with data from other areas.

Poorly stocked stands sustained lower JPBW impact than did well or overstocked stands, probably due to higher competition between smaller crowned trees or increased JPBW larval survival. Though the exact relationship may not be clear, the management recommendation to eliminate overstocked stands seems valid, and the highest density stands should be prioritized for management.

Although suppressed trees suffered disproportionate rates of mortality, there was no clear association between the relative abundance of suppressed trees and overall impact in the stand. Practices designed to reduce the abundance of suppressed trees will probably have little effect on reducing the vulnerability of stands to JPBW impact.

Tree mortality was negatively associated with the abundance of wolf trees, and poorly stocked stands sustained relatively low top-kill and tree mortality. Due to the low volume and low JPBW impact, I suggest that poorly stocked stands be given low management priority.

CHAPTER 2

GROWTH OF JACK PINE TREES DEFOLIATED BY JACK PINE BUDWORM

Introduction

Understanding patterns of tree growth and the effect of forest insect pests on tree growth is important for a number of reasons. Tree growth determines the productivity of a stand and is an important component affecting long-term timber supply. Overestimation of future timber supply may result if negative effects of forest insect pests on tree growth are not considered in yield projections.

Tree growth can also be used as an indicator of tree vigor. Studying growth of trees that have been attacked by forest insect pests such as the jack pine budworm (*Choristoneura pinus pinus* Freeman) may lead to a more complete understanding of why trees die following defoliation. It may also lead to the identification of factors that pre-dispose trees to higher probabilities of mortality.

Jack pine (*Pinus banksiana* Lamb.) is an important economic and ecological forest resource in the Lake States. Jack pine is characterized by rapid juvenile growth and qualities desirable for commercial softwood pulp (Rudolph and Laidly 1990). Merchantable jack pine stands can be grown on marginally productive land that may be incapable of supporting other tree species (Benzie 1977; Cayford 1970). Jack pine is an important softwood pulp species in the Lake

States, accounting for 40% of softwood pulp production in 1992 (Hackett and Piva 1994). Jack pine forests provide habitat for a number of wildlife species, including the federally endangered Kirtland's warbler (*Dendroica kirtlandii*) and Karner blue butterfly (*Lycaedis melissa samuelis* Nabokov) (Benzie 1977; Haack 1993). Jack pine forests also provide settings for recreational activities such as bird watching, hunting, and berry picking.

Jack pine budworm (JPBW) is the most important insect pest of jack pine (Howse 1984). Outbreaks of this foliage-feeding caterpillar occur regularly in the Lake States, about every six to ten years (Volney and McCullough 1994). During a JPBW outbreak, severe defoliation can occur locally and over a widespread area, resulting in reduced tree growth, mortality of the terminal leader of the tree (top-kill), and tree mortality (Graham 1935; Gross 1992; Kulman et al. 1963; McCullough et al. 1996). Significant losses in merchantable volume of jack pine can result from a single JPBW outbreak (Gross and Meating 1994).

For economic and environmental considerations, forest managers in the Lake States do not currently use insecticides to combat JPBW infestations or limit timber losses (Benzie 1977; Heym et al. 1993; McCullough et al. 1994). Instead, current management recommendations are based on the use of silvicultural guidelines, harvest scheduling, salvage, or cover-type conversion to minimize JPBW impact. Current management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area). These guidelines are designed to reduce competition and the number of suppressed trees in overstocked stands and to reduce the number of wolf trees in understocked stands (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

A number of studies have examined the biology of the JPBW (Batzer and Jennings 1980; Foltz et al. 1972; LeJeune 1950; LeJeune and Black 1950; Nealis 1990; Nealis and Loomic 1994) and quantified the impact of individual JPBW outbreaks (Gross 1992; Gross and Meating 1994; Kulman et al. 1963). Nonetheless, questions remain regarding the vulnerability of jack pine trees to top-kill and tree mortality, the subsequent growth of trees following collapse of the outbreak, and the validity of the management recommendations in the Lake States.

The purpose of this chapter was to examine the growth of jack pine trees defoliated during the 1991-1993 JPBW outbreak in the Raco Plains area in the Upper Peninsula of Michigan.

The specific objectives of this chapter were to: (*i*) quantify the effect of the Raco Plains outbreak on jack pine growth and (*ii*) examine the patterns of tree growth with respect to trees status, stand characteristics, and current JPBW management recommendations used in the Lake States. I tested the following null hypotheses derived from current JPBW management recommendations:

H_0: There is no difference in tree growth during the outbreak between "young" stands (< 50 yrs) and "old" stands (≥ 50 yrs).

H_0: There is no difference in tree growth during the outbreak between low site index stands (< 15.2 m) and high site index stands (≥ 15.2 m).

H_0: There is no difference in tree growth during the outbreak among poorly stocked (< 1,300 TPH, < 16.1 m^2/ha), well stocked (1,300-1,734 TPH, 16.1-25.3 m^2/ha), or overstocked stands (> 1,734 TPH, > 25.3 m^2/ha).

H_0: There is no difference in tree growth during the outbreak between stands with few suppressed trees (≤ 10%) and stands where suppressed trees were common (> 10%) (20-year-old or older stands, only).

H_0: There is no difference in tree growth during the outbreak between stands with wolf trees and stands without wolf trees (20-years-old or older stands, only).

Methods

Study Site

The Raco Plains is a 18,200 ha (45,000 ac) area located in the Hiawatha National Forest in the Upper Peninsula of Michigan (Figure 2-1). This area is characterized by level to gently rolling terrain, sandy glacial outwash soils of the Rubicon, Croswell, and Kalkaska types, and large tracts of even-aged jack pine forest (Heym et al. 1993).

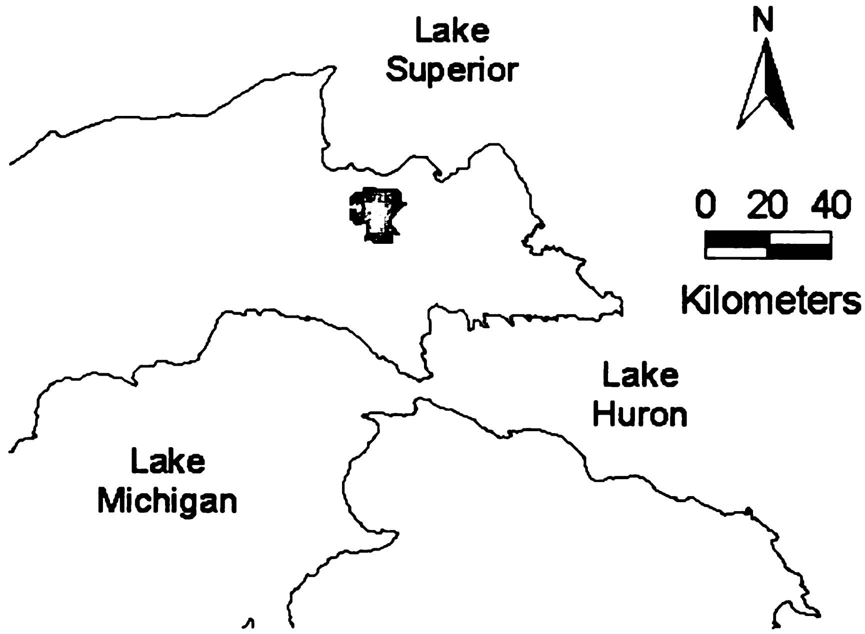

Figure 2-1 – The Raco Plains area of the Hiawatha National Forest located in the eastern Upper Peninsula of Michigan.

In 1991, a JPBW outbreak was first observed in the Raco Plains area, and aerial surveys indicated that an estimated 6,560 ha (16,000 ac) were defoliated (Heym et al. 1993; McCullough et al. 1996). Defoliation increased the following year (1992), and roughly 75% of the jack pine stands in this area suffered moderate to severe defoliation (McCullough et al. 1996). By 1993, the JPBW population was in decline, although noticeable defoliation was still observed in the area (McCullough et al. 1996). No defoliation was observed in 1994 when the JPBW population returned to endemic levels.

Sampling in the Raco Plains area has been performed annually since 1992 in four USDA Forest Service management compartments (compartment numbers 49, 58, 78, and 79) (Figure 2-2). The four compartments average 730 ha (1,800 ac) in size and contain a total of 240 stands. All survey compartments were visited by USDA Forest Service personnel from 1991-1994, and inventory characteristics (e.g., forest type, stand age, site index, etc.) and stand boundaries were updated. All stands with at least 50% of the basal area in jack pine were surveyed in each compartment.

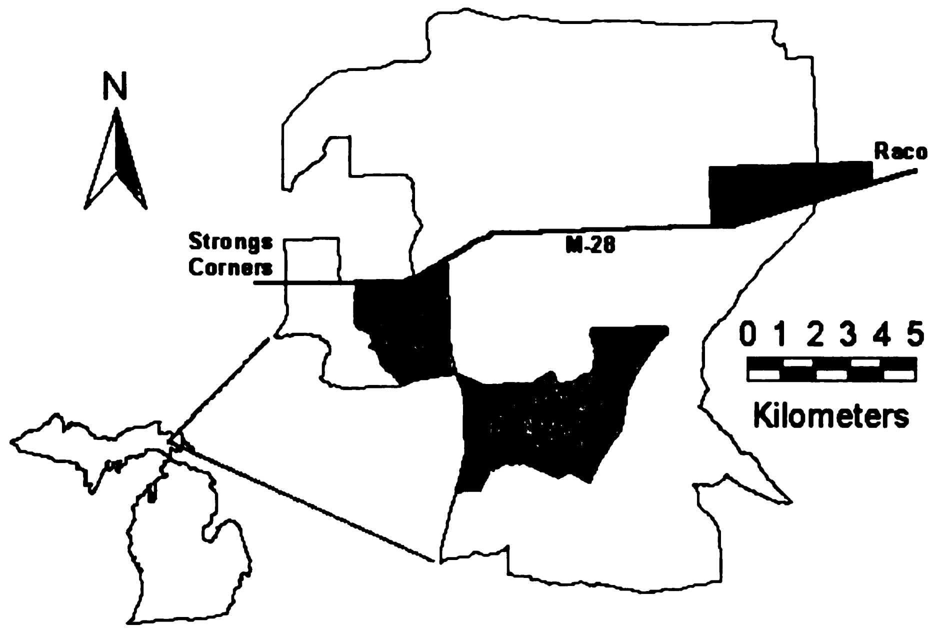

Figure 2-2 – USDA Forest Service management compartments in the Raco Plains area of the Hiawatha National Forest sampled from 1992 to 1996.

A total of 99 stands, covering 1,480 ha (3,600 ac), in the Raco Plains area met the 50% jack pine basal area criterion (Figure 2-3). Summary statistics for area, stand age, site index, basal area, and trees per hectare of the 99 sample stands are given in Table 2-1. Age of the 99 sample stands was positively correlated with site index ($r = 0.21$; $P = 0.041$) and basal area ($r = 0.75$; $P < 0.0001$). Site index of the 99 sample stands was positively correlated with basal area ($r = 0.35$; $P < 0.0001$) and trees per hectare ($r = 0.25$; $P = 0.013$).

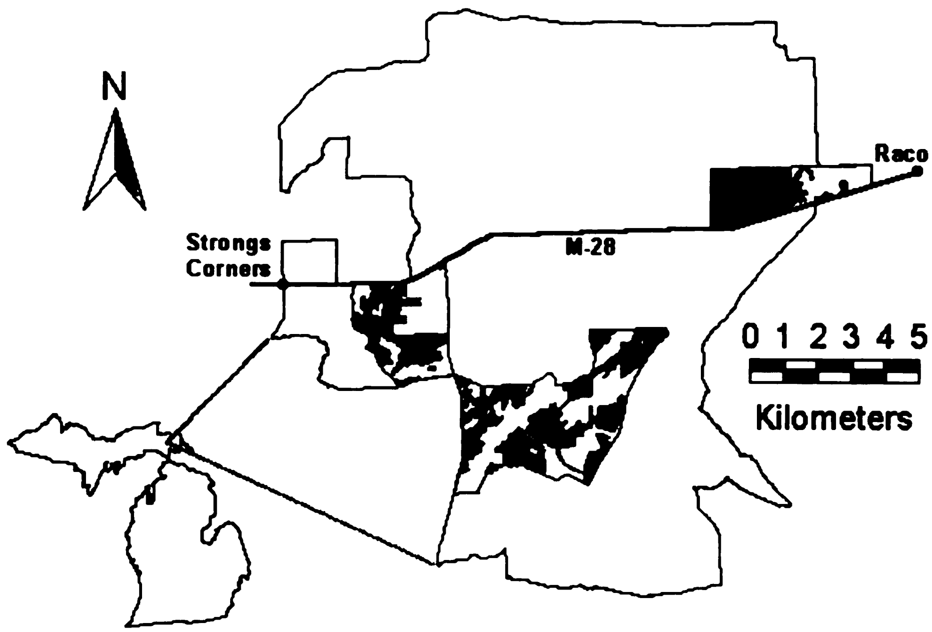

Figure 2-3 – Stands sampled in 1996 in the Raco Plains area of the Hiawatha National Forest.

Table 2-1 – Summary statistics for jack pine stands sampled in 1996 (n = 99).

	Mean[a]	Median	Minimum	Maximum
Area (ha)	14.9 (1.68)	10.9	0.8	101.7
Stand Age (years)	44 (2.1)	51	10	71
Site Index (m)	15.0 (0.15)	15.2	11.3	18.0
Basal Area (m^2/ha)	15.2 (0.87)	16.0	0.4	34.5
Number of Trees (per ha)	1353 (67.8)	1288	347	4293

[a] Standard error of the mean in parentheses

Tree Growth

To evaluate tree growth, all 99 jack pine-dominated stands were divided into 12 strata based on stand age, site index, and stand density (Table 2-2). Stratification was performed because it was not feasible to sample the growth of trees in each stand due to time constraints and stand destruction considerations. Stratification, as opposed to a purely random selection of trees, ensured that samples were taken from stands representative of the entire range of stand types.

Table 2-2 – Stand characteristics of each stratum.

Stratum	N[a]	Age	Site Index[b]	Stocking
young, low, poor	15	< 50 years	< 15.2	< 1,300 TPH[c]
young, low, well	4	< 50 years	< 15.2	1,300 ≤ TPH ≤ 1,734
young, low, over	5	< 50 years	< 15.2	> 1,734 TPH
young, high, poor	7	< 50 years	≥ 15.2	< 1,300 TPH
young, high, well	11	< 50 years	≥ 15.2	1,300 ≤ TPH ≤ 1,734
young, high, over	7	< 50 years	≥ 15.2	> 1,734 TPH
old, low, poor	8	≥ 50 years	< 15.2	< 16.1 m^2/ha[d]
old, low, well	6	≥ 50 years	< 15.2	16.1 ≤ m^2/ha ≤ 25.3
old, low, over	3	≥ 50 years	< 15.2	> 25.3 m^2/ha
old, high, poor	4	≥ 50 years	≥ 15.2	< 16.1 m^2/ha
old, high, well	20	≥ 50 years	≥ 15.2	16.1 ≤ m^2/ha ≤ 25.3
old, high, over	9	≥ 50 years	≥ 15.2	> 25.3 m^2/ha

[a] Number of stands
[b] Meters at 50 years
[c] Trees per hectare
[d] Basal area

Stands were stratified based on previous studies of JPBW impact in the Raco Plains area (McCullough et al. 1996) and on current jack pine and JPBW management guidelines for the Lake States (Albers et al. 1995; Benzie 1977; McCullough et al. 1994; Weber 1995). Two measures of stand density were used in the stratification scheme: trees per hectare (TPH) for "young" stands (i.e., less than 50 years of age) and basal area (BA) for "old" stands (i.e., 50 years of age or older). I chose TPH as a measure of stocking for "young" stands because some stands had small average DBH, and as a result, BA did not give an accurate estimate of stand density.

I randomly selected seven jack pine trees from each stratum, yielding a total of 84 sample trees. To locate a sample tree from a given stratum, a stand was selected at random with replacement from a list of all stands in that stratum. A random location within that stand was then chosen and the nearest dominant/ codominant jack pine tree was selected for sampling. To ensure that growth of top-killed and dead trees was measured, two of the seven sample trees in each stratum were recently top-killed and two were trees that had recently died. A total of 36 surviving trees, 24 top-killed trees, and 24 trees that had recently died were sample for growth. As often as possible the status of the tree to be selected was determined before choosing the location within the stand. However, at times a tree of another status had to be selected if, for example, there were no top-killed trees in that location of the stand.

Each sample tree was felled with a chainsaw, and total tree height, height to the base of the live crown (if applicable), height to merchantable top (10 cm diameter) (if applicable), and height to top-kill margin (if applicable) were measured.

I evaluated tree growth with stem analysis performed on sample tree discs to avoid problems with light or incomplete rings and variable ring growth throughout the entire stem (Gross 1992; MacLean 1990; O'Neil 1963; Thomson and Van Sickle 1980; Volney and Mallett 1992). I collected two- to four-centimeter thick discs at several locations along the bole of each sample tree. Discs were cut at stump height (0.30 m), breast height (1.37 m), and every 2 meters above breast height, without corresponding to branch nodes. At least three discs were taken from each tree. I took one additional disc, located at the margin of the dead leader, from each top-killed tree. Evaluating tree growth with this limited number of discs represented a practical compromise between accuracy and limited resources available for sampling and measurement.

To measure annual ring width, I kiln-dried, sanded one face, and located two average radii on each disc. I measured and cross-dated annual ring widths along these radii to the nearest 0.01 mm using an optical digitizing scanner and WinDENDRO image analysis software (Regent Instruments, Inc., Quebec, Quebec) to analyze the digitized image of the disc surface (Guay et al. 1992). WinDENDRO marks each ring using changes in the luminance or brightness of the pixels that make up a specified path or radius on the disc surface and measures the distance between each mark based on the calibration of the scanner. While WinDENDRO was very accurate in determining ring location, adding false rings and missing light or absent rings were common errors. Also, some problems were encountered occasionally when rings on some sample discs did not extend all the way around or were completely absent. This was particularly true for the dead trees in the sample. These trees often had many of the most recent years' growth-rings compressed into a very small area of the disc, making measurement difficult. Therefore, I used a binocular dissecting microscope to validate WinDENDRO's ring placement.

Growth Loss Estimation

To quantify radial growth loss that resulted from the 1991-1993 JPBW outbreak, I first had to determine a reference by which to gauge this loss.

MacLean (1990) suggested several methods of determining this reference. First, insecticide-protected, non-defoliated control tree growth could be compared to defoliated tree growth. The lack of such a control group in this study precluded the use of this method. Second, the growth of naturally occurring, lightly defoliated trees could be compared to that of heavily defoliated trees in the same area. Again, lack of such a situation in the present study area prohibited the use of this method. Third, non-host trees within defoliated jack pine stands could be examined for growth trends. This method was not practical for this study because jack pine trees in this area grow in relatively pure stands and because any non-host trees that were present in defoliated stands might have experienced release (i.e., increased growth) during the outbreak. Fourth, a growth model could be used to predict growth in the absence of the damaging agent. A potential problem with this method is that a slight growth reduction resulting from defoliation might be swamped by the prediction error of the model. Fifth, potential growth could be estimated by extrapolating pre-outbreak growth rates.

In the absence of other practical, valid methods, I used non-outbreak growth as the reference to measure growth loss from the 1991-1993 JPBW outbreak. Similar studies of jack pine growth in Saskatchewan and Ontario, Canada following JPBW defoliation (Cerezke 1986; Gross 1992) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth in British Columbia, Canada following western spruce budworm (*Choristoneura occidentalis* Freeman) defoliation (Alfaro et al. 1982; Thomson and Van Sickle 1980) also used this approach.

I chose to use growth of the five non-outbreak years (1982, 1987-1990) before the 1991-1993 JPBW outbreak as a reference to evaluate outbreak growth loss. The years 1983 to 1986 were not included because a JPBW outbreak and recovery occurred in the study area at that time (Heym et al. 1993). The measure of growth used in this study was specific volume increment (SVI). SVI is the annual volume of wood produced relative to total stem cambial area (Duff and Nolan 1957; Shea and Armson 1972). It is recognized as a sensitive measure of growth responses (MacLean 1990) and is conveniently equal numerically to the width of the annual ring (Duff and Nolan 1957).

A reference SVI was calculated for all discs that were alive in 1990 (i.e., had a 1990 growth ring). Discs having fewer than seven growth rings in 1996 (i.e., did not have a 1990 growth ring) were not included in the analysis. To determine the reference SVI for each tree as a whole, I averaged annual SVI for each of the five reference years for each disc in the sample tree. The reference SVI was set to the mean of these five SVI values.

Annual SVI for the years 1987-1995 for each sample tree was calculated by averaging the annual SVI of all discs in the tree. Annual growth for each tree was converted to proportions by dividing annual SVI by reference SVI. Converting the growth data into proportions helped to reduce the differences in secondary growth attributable to tree age or size (Gross 1992). From here on, whole-tree reference SVI, annual whole-tree proportional SVI, and mean whole-tree proportional SVI for the years 1991-1994 will be referred to simply as reference growth, annual growth, and outbreak growth, respectively.

Analysis of Growth Loss

To determine if growth of sampled trees was significantly reduced during the 1991-1993 JPBW outbreak, I compared annual SVI from 1991-1994 with average SVI over the reference period. In this test and all subsequent tests, only data from surviving and top-killed trees were used. Growth data from dead trees were not used because many of these trees had very little growth during the outbreak. Inclusion of the growth of trees that died would have likely underestimated average tree growth during the outbreak.

Due to the heteroscedasticity of the data as indicated by Levene's test (Levene 1960), the nonparametric Kruskal-Wallis test was used to analyze effects of the outbreak on annual SVI (Lehmann 1975; Sokal and Rohlf 1995). Significance of the Kruskal-Wallis test statistic (H) is assessed by the univariate χ^2. Although the Kruskal-Wallis test is based on a ranking of the data and does not test differences in means (Lehmann 1975; Sokal and Rohlf 1995), mean values were presented for comparison purposes.

Analysis of Tree Status

To analyze differences in growth among surviving, top-killed, and dead trees, I plotted annual growth from 1987-1995 for each group. One-way analysis of variance (ANOVA) was used to evaluate differences in annual growth from 1989-1995 of surviving, top-killed, and dead trees.

Analysis of Stand Characteristics

Associations between tree growth during the outbreak and stand characteristics including age, site index, basal area, suppressed tree proportion, and wolf tree proportion were examined using Pearson's product-moment correlation coefficient (*r*). I divided stand characteristics into four to six groups and plotted mean outbreak-affected growth for each group. This method of graphical analysis reduced variability in the growth data, and thus, allowed evaluation of the associations between outbreak growth and stand characteristics.

Analysis of Management Recommendations

Management recommendations were tested by grouping stands into classes based on previous studies of JPBW impact (McCullough et al. 1996) and on current jack pine and JPBW management guidelines for the Lake States (Albers et al. 1995; Benzie 1977; McCullough et al. 1994; Weber 1995). One way ANOVA was used to test for significant differences in outbreak-affected growth between stands grouped by age, site index, density, suppressed tree proportion, and wolf tree proportion. Levene's test was used to test for heteroscedasticity in the growth data (Levene 1960). Where necessary, growth data were transformed to stabilize the variance using the natural logarithm transformation (stand age, site index, and stand density tests) (Sokal and Rohlf 1995). In addition, mean annual growth for each management class was plotted for the years 1987-1995.

The site index class test was interpreted as a test for site quality. Site index refers to the height of the dominant or dominant/codominant trees in a stand at the index year 50 (Carmean 1975; Carmean and Lenthall 1989; Wenger 1984). It is commonly considered an expression of site quality, as height growth of trees is assumed to be independent of stand density and strongly related to site quality (Carmean 1975; Wenger 1984). Although the shortcomings of using height growth as an indicator of site quality have been recognized (Carmean 1975; Carmean and Lenthall 1989), site index is commonly used by resource managers in the Lake States (Benzie 1977). Other indicators of site quality including ecological classification, land type association, and soil maps were examined. Because these site quality indicators are relatively homogenous for the Raco Plains area (Heym et al. 1993), they would be of limited value in assessing differences in JPBW impact and were not included in the analysis.

The 10% criterion for the proportion of suppressed trees in the stand and the presence/absence criterion for wolf trees in the stand were based on thresholds that I assumed necessary to affect JPBW impact. Young stands were not likely to have reached crown closure or to have developed stratified canopies. Therefore, all trees in these stands could be considered open-grown and few trees would be suppressed. For these reasons, only stands 20 years old or older were used in the analysis of suppressed and wolf tree proportion.

Results

Analysis of Growth Loss

Annual growth of all trees and of surviving and top-killed trees was slightly reduced in 1988 and 1989 compared to reference growth (Figure 2-4). These years corresponded to a severe regional drought (Temperature-Precipitation-Drought Data, National Climatic Data Center, National Oceanic and Atmospheric Administration) that occurred in the summer of 1988. A more dramatic decrease in the mean growth of all trees (*n* = 84) resulted from the 1991-1993 JPBW outbreak. Growth of all trees in 1992, 1993, and 1994 was 68%, 62%, and 76% of the reference growth, respectively (Figure 2-4). Growth of surviving and top-killed trees (*n* = 60) was 80% of reference growth in 1992 and 76% of reference growth in 1993 (Figure 2-4).

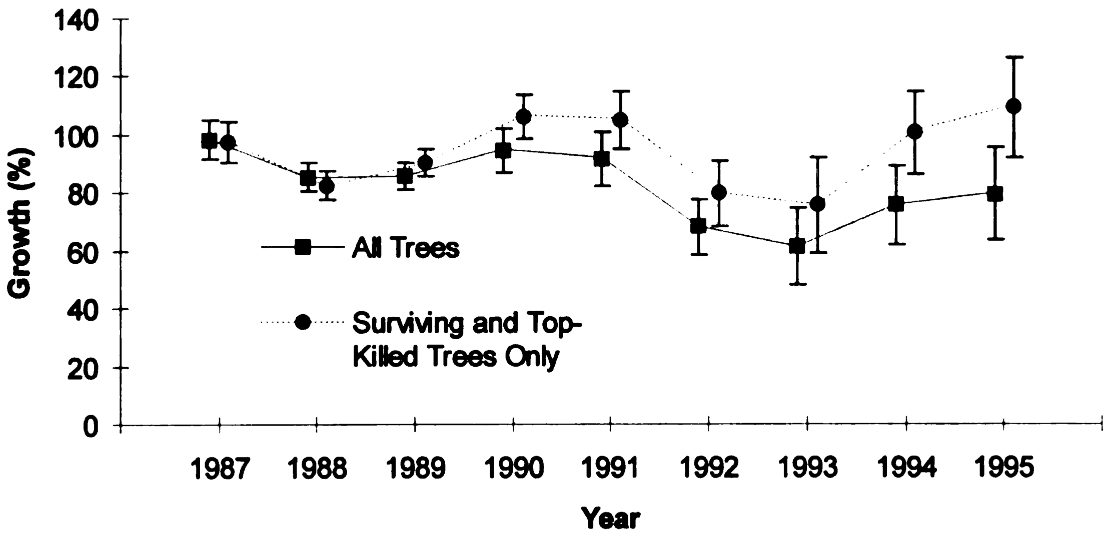

Figure 2-4 – Mean annual growth as percentages of reference growth (with 95% confidence intervals).

Results of Kruskal-Wallis tests indicated that there was a significant difference between the reference SVI and annual SVI in 1992 (H = 5.06; P = 0.025; df = 1) and 1993 (H = 6.74; P = 0.009; df = 1). Annual SVI in 1991 (H = 0.26; P = 0.611; df = 1) and 1994 (H = 0.21; P = 0.644; df = 1) did not differ significantly from reference SVI.

Analysis of Tree Status

A trend toward increasing disparity among surviving, top-killed, and dead trees appeared to occur during and immediately following the JPBW outbreak (Figure 2-5). Surviving trees in the sample appeared to have recovered in 1994 and 1995, growing at 120% and 133% of reference growth, respectively. Annual growth of top-killed trees was close to that of surviving trees until 1993, when growth fell off to only 56% of reference growth. Growth of top-killed trees in 1994 (73%) and 1995 (75%) suggested that these trees have not yet recovered their pre-outbreak growth rate (Figure 2-5). Results from one-way ANOVA indicated that annual growth of surviving trees was not significantly different from annual growth in top-killed trees in 1991 (F = 0.89; P = 0.350; $1 - \beta$ = .85; df = 1) or 1992 (F = 0.75; P = 0.391; $1 - \beta$ = .86; df = 1). However, annual growth of surviving trees was significantly greater than that of top-killed trees in 1993 (F = 4.05; P = 0.049; df = 1), 1994 (F = 11.59; P = 0.001; df = 1), and 1995 (F = 12.59; P = 0.001; df = 1). Average growth of trees that died following the 1991-1993 outbreak dropped steadily after 1988. Trees that died following the outbreak had lower annual growth than both surviving and top-killed trees in each year from 1989-1995 (Figure 2-5).

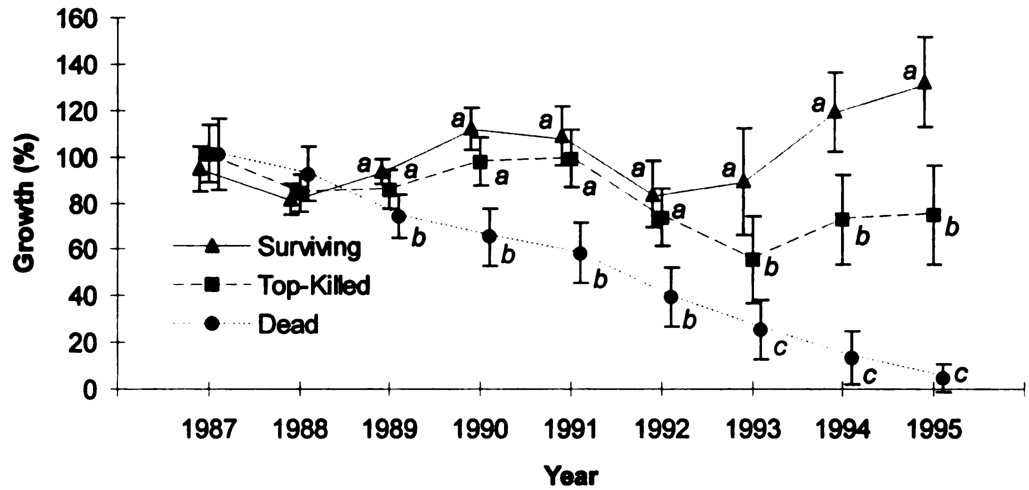

Figure 2-5 – Mean annual growth of surviving, top-killed, and trees that died as percentages of reference growth [with 95% confidence intervals, same letter indicates no significant difference (α = 0.05)].

Analysis of Stand Characteristics

Tree growth during the outbreak was negatively correlated with stand age, stand basal area, and proportion of suppressed trees in the stand, and positively correlated with proportion of wolf trees in the stand (Table 2-3).

Table 2-3 – Pearson's product-moment correlation coefficient (*r*) for outbreak growth of surviving and top-killed trees and stand characteristics.

	Outbreak Growth
Stand Age	-0.60 **
Site Index	-0.06
Stand Basal Area	-0.50 **
Suppressed Tree Proportion	-0.27 **
Wolf Tree Proportion	0.34 **

** Significant at the 0.01 level (2-tailed)

The relationship between stand age and outbreak growth is presented in Figure 2-6. This figure indicates that there was a slight pattern of decreased growth with increasing tree age. There was a particularly large difference in growth between the 10-20 year age group and the 21-30 year age group. Although outbreak growth was similar across different site indexes (Figure 2-7), there was a clear tend toward decreasing outbreak growth with increasing stand basal area (Figure 2-8). The positive correlation between outbreak growth and the proportion of suppressed trees in the stand is the result of relatively high outbreak growth in stands with no suppressed trees (Figure 2-9). There was no association between outbreak growth and abundance of suppressed trees in stands where suppressed trees were present (Figure 2-9). A similar, but reversed pattern is seen in the association between outbreak growth and wolf tree proportion (Figure 2-10). Stands with relatively high proportions of wolf trees had high relative outbreak growth, while no association was seen between outbreak growth and lower relative abundance of wolf trees in the stand (Figure 2-10).

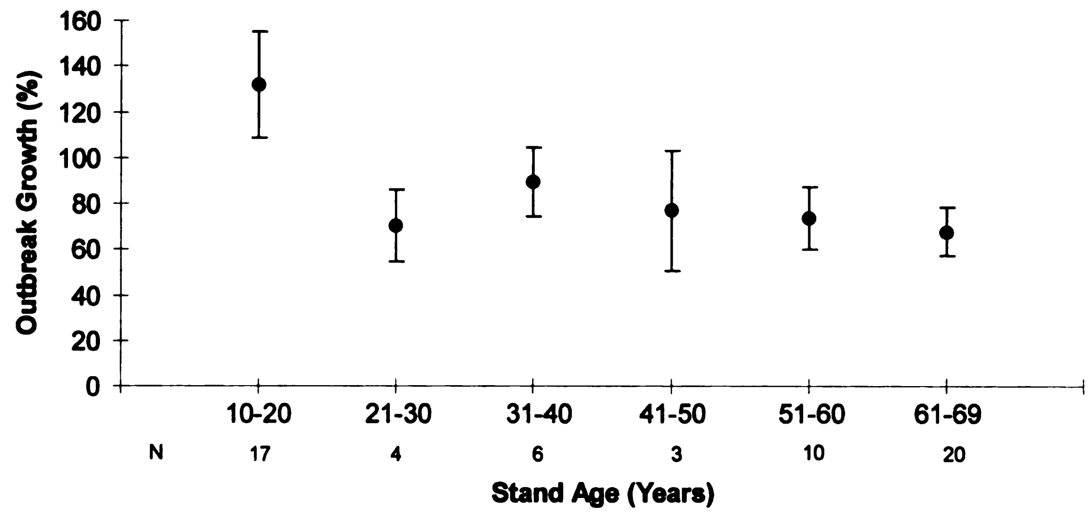

Figure 2-6 – Mean outbreak growth by stand age (with 95% confidence intervals, surviving and top-killed trees, only).

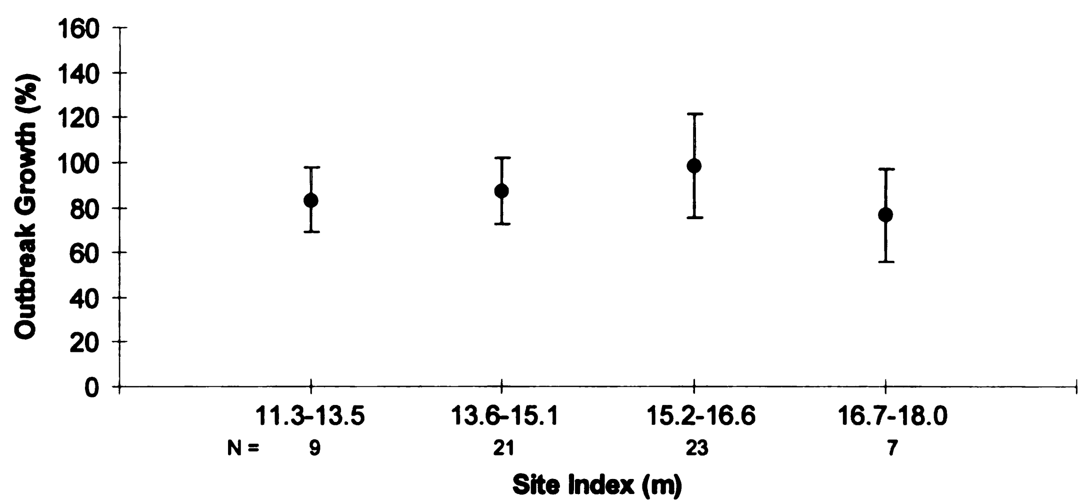

Figure 2-7 – Mean outbreak growth by site index (with 95% confidence intervals, surviving and top-killed trees, only).

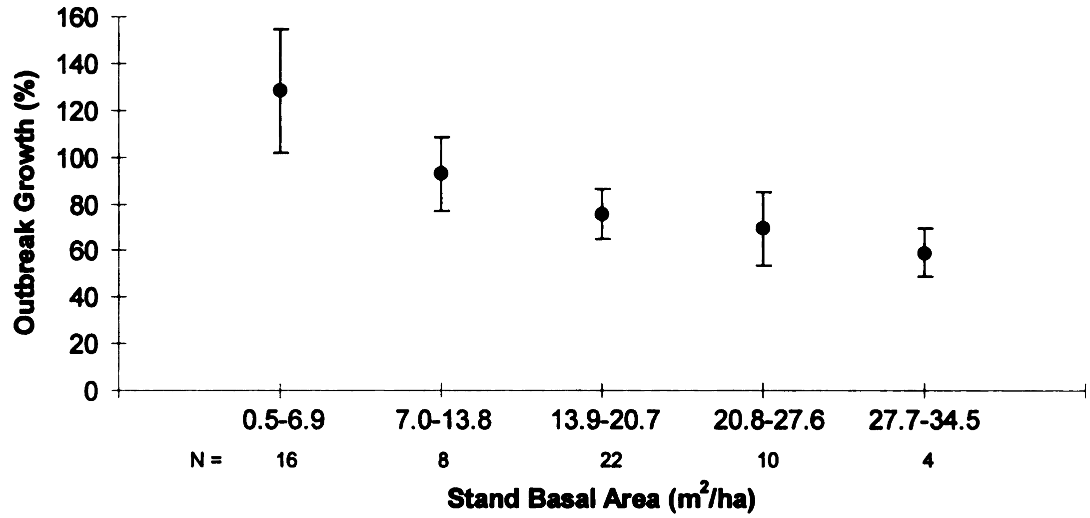

Figure 2-8 – Mean outbreak growth by stand basal area (with 95% confidence intervals, surviving and top-killed trees, only).

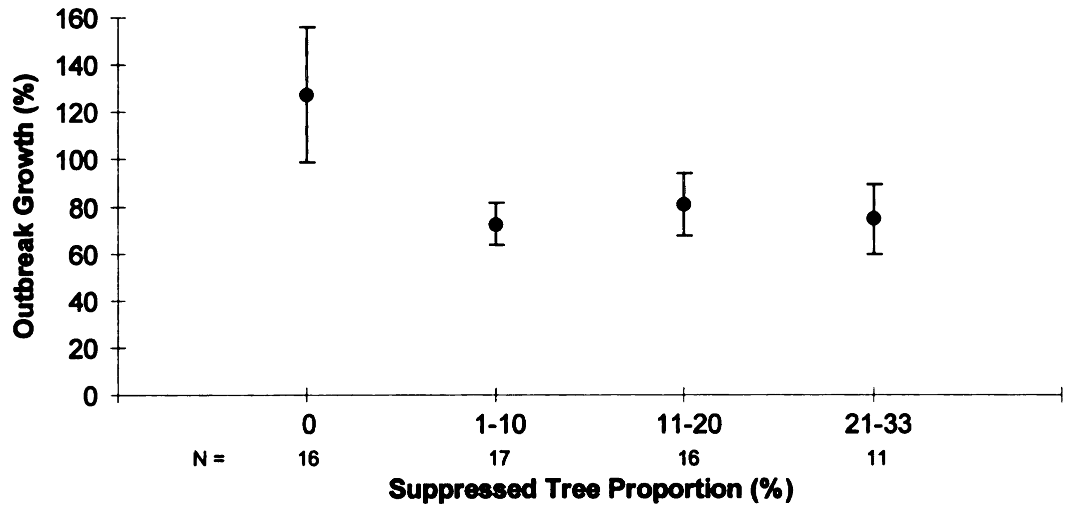

Figure 2-9 – Mean outbreak growth by suppressed tree proportion (with 95% confidence intervals, surviving and top-killed trees, only).

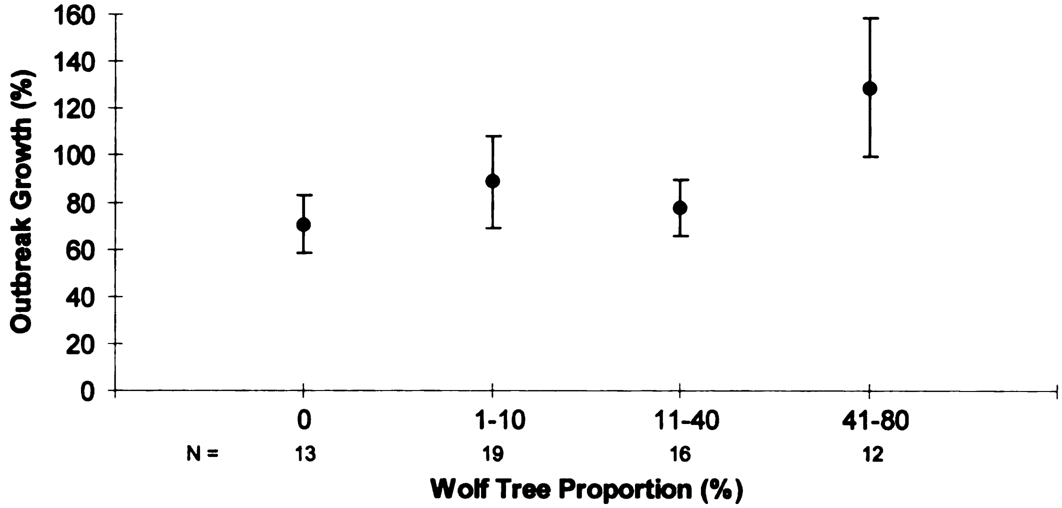

Figure 2-10 – Mean outbreak growth by wolf tree proportion (with 95% confidence intervals, surviving and top-killed trees, only).

Analysis of Management Recommendations

Current management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area).

Outbreak growth was significantly lower in trees from stands 50 years old or older than in trees from younger stands ($F = 18.49$; $P < 0.0001$; $df = 1$) (Table 2-4). Age class differentiation explained 24% of the variation in the transformed outbreak growth data. There were no significant differences in outbreak growth between site index classes ($F = 0.001$; $P = 0.976$; $1 - \beta = .95$; $df = 1$), stocking classes ($F = 1.71$; $P = 0.191$; $1 - \beta = .66$; $df = 2$), suppressed tree proportion ($F = 0.12$; $P = 0.735$; $1 - \beta = 0.94$; $df = 1$), or wolf tree proportion ($F = 0.47$; $P = .495$; $1 - \beta = 0.90$; $df = 1$) (Table 2-4).

Table 2-4 – Mean outbreak growth by management class[abc].

	N[d]	Outbreak Growth (%)	
Age Class (years)			
Young (< 50)	30	111.7	(9.50)*a*
Old (≥ 50)	30	69.2	(4.58)*b*
Site Index Class (m)			
Low (< 15.2)	30	87.9	(6.73)*a*
High (≥ 15.2)	30	93.1	(9.82)*a*
Stocking Class[e] (TPH, m^2/ha)			
Poor (< 1,300, < 16.1)	20	104.0	(12.95)*a*
Well (1,300-1,734, 16.1-25.3)	20	94.2	(10.25)*a*
Over (> 1,734, > 25.3)	20	73.2	(5.20)*a*
Suppressed Tree Class[f] (%)			
Few (≤ 10)	19	71.2	(5.60)*a*
Abundant (> 10)	24	73.7	(4.87)*a*
Wolf Tree Class[f] (%)			
Absent (0)	12	68.6	(6.45)*a*
Present (> 0)	31	74.2	(4.42)*a*
Total	60	90.5	(5.91)

[a] Standard error of the mean in parentheses
[b] Means within a management class followed by the same letter are not significantly different (α = 0.05)
[c] Surviving and top-killed trees, only
[d] Number of sample trees
[e] TPH - "young" stands, m^2/ha - "old" stands
[f] Stands 20 years old or older, only

Trees from "young" stands clearly showed greater growth than trees from "old" stands each year from 1991-1995 (Figure 2-11). In fact, mean annual growth of trees from "young" stands was never below reference growth (100%) in any of the years from 1991-1995. Mean annual growth of trees from "old" stands was less than reference growth (100%) in every year from 1991-1995 and less than growth of tree from "young" stands before the 1991-1993 outbreak began. By 1995, trees from "old" stands had yet to recover to pre-outbreak growth levels. Mean annual growth of trees was similar for each site index (Figure 2-12), suppressed tree (Figure 2-14), and wolf tree (Figure 2-15) class. Mean annual growth of trees in poor and well stocked stands were similar for all years. These trees appear to have recovered to pre-outbreak growth levels by 1994. Mean annual growth of trees in overstocked stands, however, was less than that of trees from both poor and well stocked stands in 1994 and 1995. Trees from overstocked stands had not recovered to pre-outbreak growth levels as of 1995.

Discussion

Growth Loss

Growth losses observed in this study were not as severe as those observed in other studies of JPBW impact (Gross 1992; Gross and Meating 1994). The reduction in 1993 growth to 62% of pre-outbreak levels was only a fraction of that observed by Gross (1992). During the 1984-1986 JPBW outbreak in Ontario, Gross (1992) observed tree growth in four sample stands reduced to a maximum of 29% of pre-outbreak levels. In addition, I observed only two years (1992 and 1993) of significant growth reduction. Other workers have found tree growth to

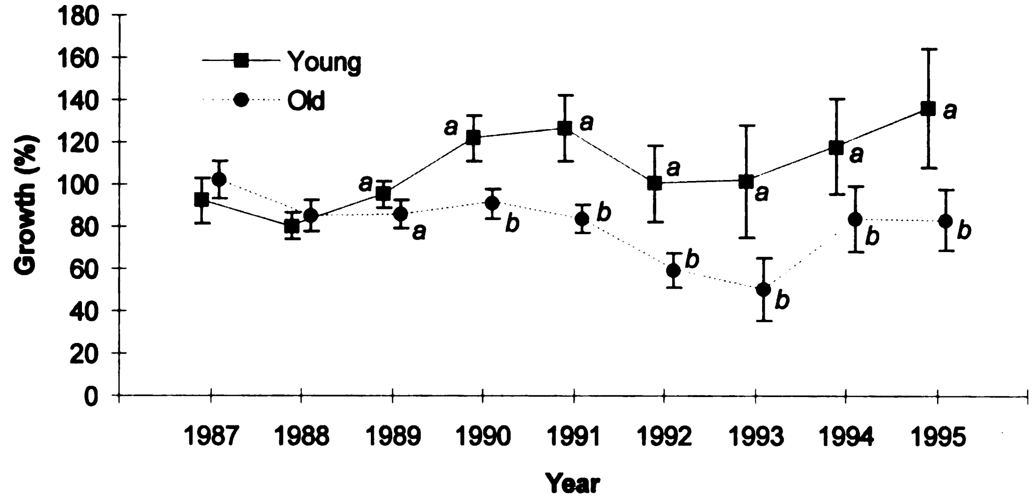

Figure 2-11 – Mean annual growth for trees in "young" (< 50 years) and "old" (≥ 50 years) stands [with 95% confidence intervals; surviving and top-killed trees, only; same letter indicates no significant difference ($\alpha = 0.05$)].

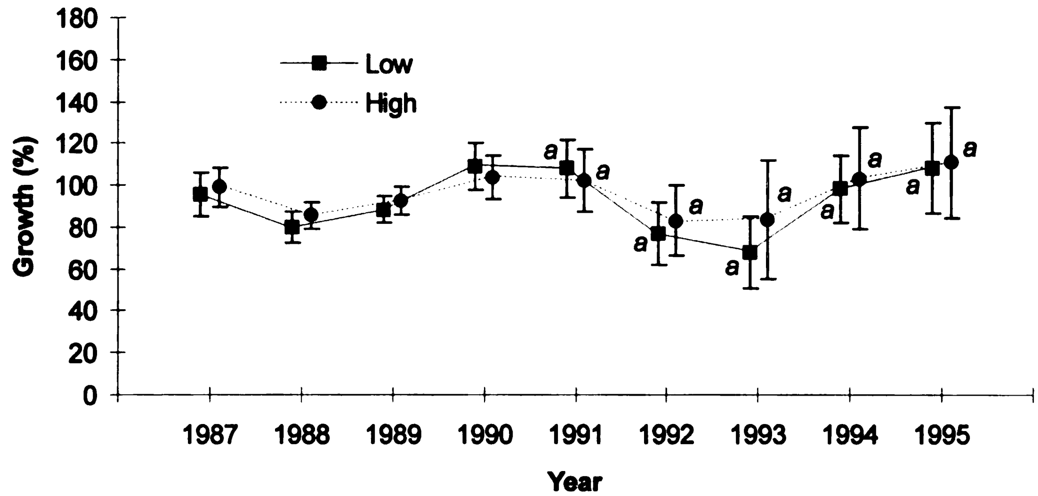

Figure 2-12 – Mean annual growth for trees in low (< 15.2 m) and high (≥15.2 m) site index stands [with 95% confidence intervals; surviving and top-killed trees, only; same letter indicates no significant difference ($\alpha = 0.05$)].

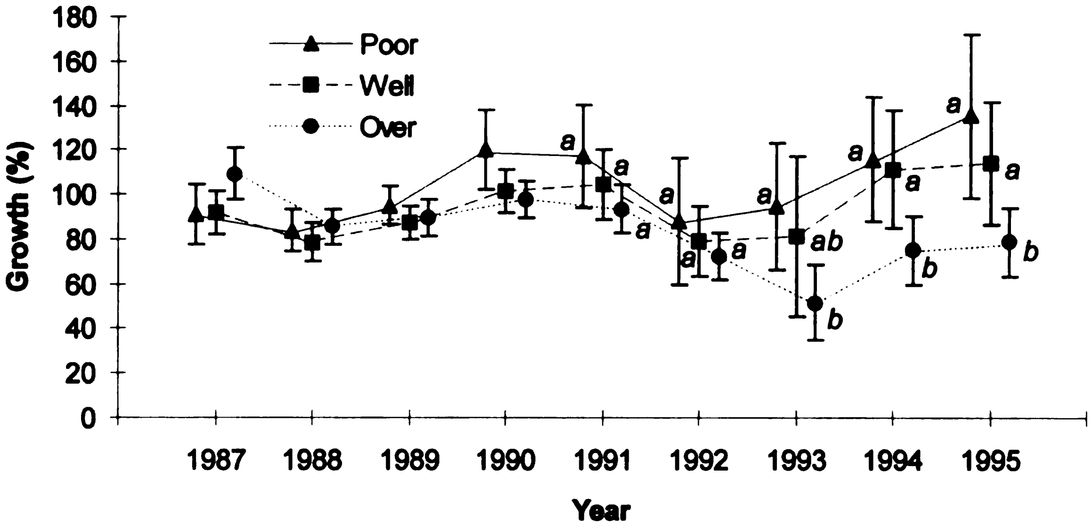

Figure 2-13 – Mean annual growth for trees in poor (< 1,300 TPH, < 16.1 m^2/ha), well 1,300-1,734 TPH, 16.1-25.3 m^2/ha), and overstocked (> 1,734 TPH, > 25.3 m^2/ha) stands [with 95% confidence intervals; surviving and top-killed trees, only; same letter indicates no significant difference (α = 0.05)].

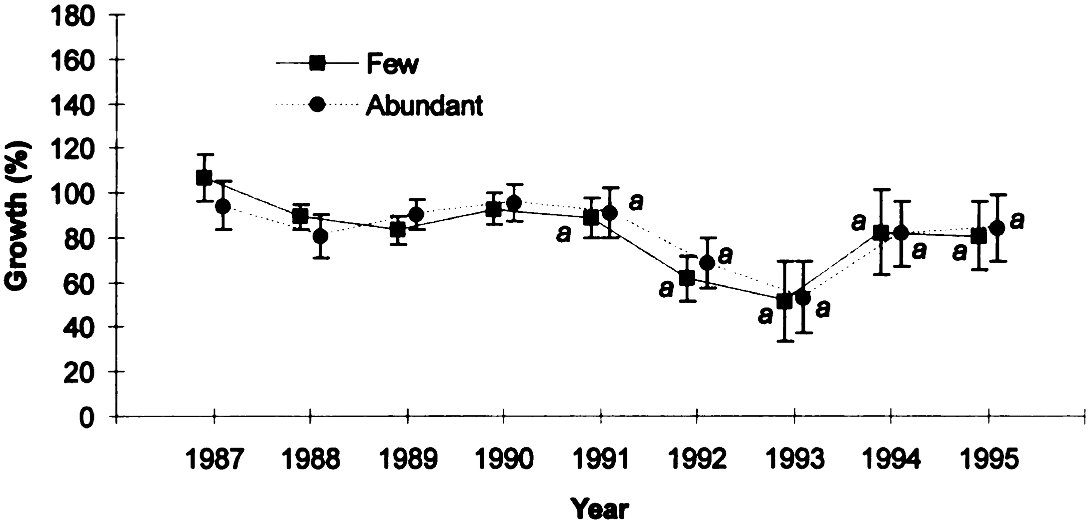

Figure 2-14 – Mean annual growth for trees in stands with few (≤ 10%) and abundant (> 10%) suppressed trees [with 95% confidence intervals; surviving and top-killed trees, only; same letter indicates no significant difference (α = 0.05)].

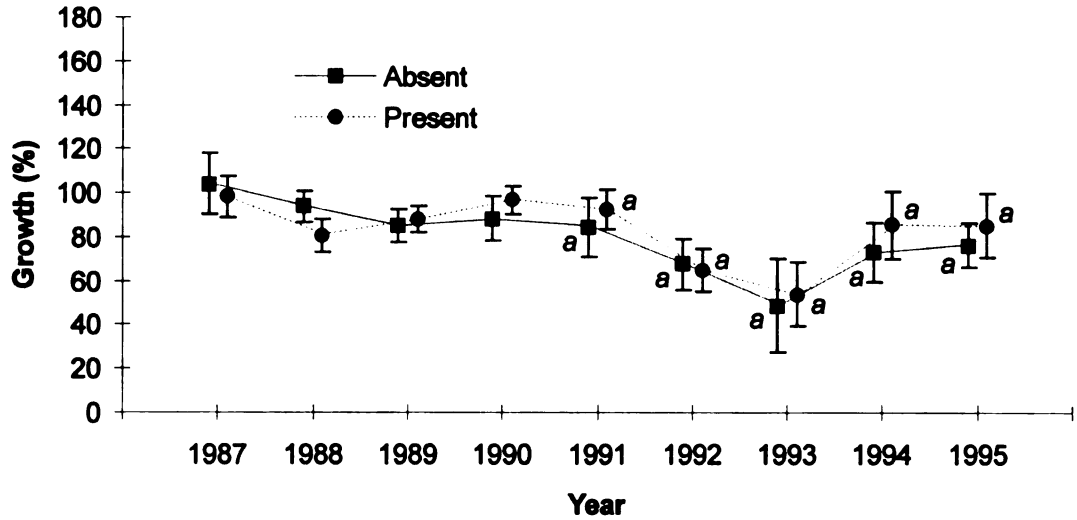

Figure 2-15 – Mean annual growth for trees in stands with wolf trees absent (0%) and present (> 0%) [with 95% confidence intervals; surviving and top-killed trees, only; same letter indicates no significant difference (α = 0.05)].

be reduced for three or four years (Cerezke 1986; Gross 1992; Gross and Meating 1994).One possible reason for these discrepancies may be that the stands sampled by other workers included only older trees of merchantable size. My sample included a wide range of tree ages, with 25% of the sample trees (21 trees) taken from stands 25 years old or younger. It is also possible that the relatively small growth reduction I observed was due to a relatively low rate of reference growth. Trees sampled in the Raco Plains area experienced a JPBW outbreak (1983-1985) and a severe regional drought (1988) in the decade before the 1991-1993 JPBW outbreak. Repeated stress over this time period may have depressed tree growth that was used as the reference to measure growth during the 1991-1993 JPBW outbreak.

Estimates of tree growth during and following the 1991-1993 JPBW outbreak are probably conservative. From 1992-1996, the USDA Forest Service harvested jack pine from 15 stands in the study management compartments (Heym et al. 1993). These stands were cut to limit timber losses associated with the 1991-1993 JPBW outbreak, and the stands selected for harvest were those the Forest Service believed to be the most vulnerable to impact (Heym et al. 1993). If these stands had suffered heavy impact, then the 1996 data would likely have underestimated the true impact of the 1991-1993 JPBW outbreak.

The largest reduction in growth occurred in 1993, the year after the most extensive defoliation of the outbreak. This is consistent with a trend observed by other workers (Cerezke 1986; Gross 1992; Gross and Meating 1994; Kulman et al. 1963). This observation may be explained by the relationship between radial growth and foliage in conifers. Earlywood growth in conifers is mainly controlled by photosynthate produced in previous years' foliage whereas latewood growth is primarily controlled by photosynthate produced in current-year foliage (Clancy et al. 1995; Kulman et al. 1963; Little and Savidge 1987; Savidge 1988). That is, in the spring of 1992, carbohydrate stores found primarily in the foliage of conifers (Clancy et al. 1995) were probably sufficient to initiate earlywood growth. However, by mid-summer, severe defoliation of the current-year needles limited latewood production in most trees. In 1993, both early- and latewood growth were minimal due to low carbohydrate reserves that resulted from defoliation of previous years' foliage and continued defoliation of current-year foliage.

The comparison of tree growth among surviving, top-killed, and dead trees supports the hypothesis that jack pine trees in the Raco Plains area were repeatedly stressed in the 1980's. The downward trend in the growth of trees that died after 1988 attests to the waning vigor of these trees before the 1991-1993 JPBW outbreak. It could be argued that the trees that eventually died as a result of defoliation during the 1991-1993 JPBW outbreak were pre-disposed to this fate due to prior stress events. Similarly, Mallett and Volney (1990) observed that growth of jack pine trees that eventually died following a JPBW outbreak in Saskatchewan had declined significantly long before they died. Although it has been suggested that top-kill may lead to tree death (Gross and Meating 1994; Kulman et al. 1963; Mallett and Volney 1990), it was difficult to determine if the dead trees in this sample were previously top-killed.

While other studies have shown dramatic reductions in growth of trees that eventually die as a result of defoliation (Mallett and Volney 1990; O'Neil 1962), comparatively little is known about how top-kill affects subsequent tree growth. Interestingly, my results indicate that top-kill seems to affect tree growth even after the collapse of the outbreak. Although top-killed trees were sampled at the margin of the dead top, the timing of the death of the leader of these trees was difficult to estimate due to the limited number of annual rings available for cross dating. However, my results clearly demonstrate that top-killed trees did not recover following the outbreak collapse as well as or as rapidly as did surviving trees. It is not clear how loss of apical dominance affects subsequent tree growth and survival, and whether top-killed trees will be able to recover to pre-outbreak growth levels or continue to die basipetally. Long-term studies are needed to track the growth and eventual fate of top-killed trees.

Stand Characteristics

The clear and consistent pattern of a positive association between JPBW impact and stand age was evident in the tree growth data. Older jack pine stands in the Raco Plains area contain overmature, non-vigorous trees that are highly vulnerable to JPBW impact. Overmature trees may offer a more suitable habitat for feeding budworm (i.e., produce more pollen cones) or may be unable to tolerate defoliation stress.

While reduction of tree growth due to JPBW defoliation seemed to be relatively unrelated to site index, tree growth during the outbreak was negatively associated to stand basal area. This observation may be partially explained by the JPBW impact-age relationship noted above, because age was positively correlated with basal area.

There are at least two other possible explanations for this observation. First, jack pine trees growing in stands with high basal area tend to have smaller crowns and less leaf area due to competition for light and growing space. Because foliage serves as the main carbon store in conifers, smaller crowned jack pine may have few reserves to allocate to recovery from defoliation stress, or they may lose proportionally more reserves through defoliation than larger crowned trees (Clancy et al. 1995).

Second, JPBW larval dispersal occurs when first instar JPBW move to overwintering sites, when overwintering second instars emerge from their hibernacula to seek out feeding sites, and possibly, again when larvae move from pollen cones to newly expanded foliage. Dispersal losses are an important factor in larval mortality because few larvae survive if they do not land directly on suitable hosts (Batzer and Jennings 1980; Foltz et al. 1972; Nealis and Loomic 1994). The physical spacing of trees in higher density stands means that dispersing larvae have to travel shorter distances to suitable hosts and would likely have a higher probability of successful dispersal in these stands.

Outbreak growth was negatively associated with the proportion of suppressed trees in the stands. However, this could be the result of age. Young stands that have reached not crown closure or developed stratified canopies are likely to have few suppressed trees. There was no association between outbreak growth and higher abundance of suppressed trees in the stand. I did not sample the growth of suppressed trees so it is possible that these trees are suffering greater reductions in growth as a result of JPBW defoliation. However, the growth of dominant/codominant trees during the JPBW outbreak does appear to be adversely affected when suppressed trees were abundant in the stand.

Overall outbreak growth was positively associated with the proportion of wolf trees in the stand. As with suppressed trees, this could be explained in part by stand age. It may also be related to stand density. Stands with high proportions of wolf trees are likely to be poorly stocked stands with low basal area, and basal area was negatively associated with outbreak growth.

Management Recommendations

The only significant relationship observed in this study between tree growth during a JPBW outbreak and management recommendations was that tree growth was significantly less in trees growing in "old" stands than in trees growing in “young” stands. Most striking about this relationship is that mean annual growth of trees in “young” stands was consistently greater than pre-outbreak growth levels despite JPBW defoliation. In addition, mean annual growth of trees in “old” stands had not recovered to pre-outbreak growth levels as of 1995.

This suggests that vigor of trees in older stands can deteriorate rapidly following a stress event such as a JPBW outbreak and further, and thus, rotation ages should be lowered to less than 50 years in the Lake States. Others have reached a similar conclusion regarding rotation ages (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Nyrop et al. 1983; Rose 1973; Rose 1974; Weber 1995; Weber 1986; Williams and Nautiyal 1992). Harvesting before stands become overmature may be the single most important management practice that reduces overall JPBW impact. In addition, I suggest that the highest management priority for harvest scheduling, salvage, or conversion be given to the oldest jack pine stands.

The results indicate that site quality had very little effect on tree growth during and following a JPBW outbreak. Therefore, it is difficult to come to any conclusions about the validity of the management recommendation to favor high quality sites for jack pine stands based on the tree growth data.

Although I observed no significant differences in overall growth during and immediately following the JPBW outbreak, two results lead me to believe that the recommendation to eliminate overstocked stands is valid. First, tree growth during the outbreak was negatively associated with stand basal area. Second, tree growth in overstocked stands was significantly less than tree growth in poor or well stocked stands in 1994 and 1995 and had not recovered to pre-outbreak levels as of 1995.

For these reasons, eliminating overstocked stands may reduce growth loss attributable to JPBW defoliation. Further, I suggest that overstocked stands be given priority for management operations such as harvest scheduling, salvage, or cover-type conversion.

The abundance of suppressed trees in the stand did not adversely affect tree growth during the 1991-1993 JPBW outbreak. While the abundance of suppressed trees in the stand may increase susceptibility of the stand by providing suitable favorable habitat for JPBW (Batzer and Jennings 1980), their abundance did not increase vulnerability of the stands in terms of greater reduction in tree growth. For forest managers, this suggests that the presence of suppressed trees may not be a great concern. In addition, I suggest that management activities designed to reduce or eliminate suppressed trees (e.g., non-commercial thinnings from below, planting or seeding activities that ensure even spacing, etc.) be given low priority due to the limited effect they would have on reducing stand vulnerability.

Finally, I observed no significant difference in tree growth during the outbreak between stands with and without wolf trees. Wolf trees may provide favorable JPBW habitat by producing abundant pollen cones throughout their full crowns (Hodson and Zehngraff 1946). However, this did not translate into higher impact in the form of increased reduction in growth. This observation combined with the negative association between tree growth during the outbreak and stand basal area and relatively low merchantable volume typically found in poorly stocked stands suggests that poorly stocked stands should be given low management priority.

Conclusions

The 1991-1993 JPBW outbreak resulted in significant reduction in growth of jack pine trees in the Raco Plains area, although this reduction was not as great as growth loss observed following other JPBW outbreaks (Kulman et al. 1963; Gross 1992; Gross and Meating 1994). The reason for this discrepancy may be that my sample included many young trees or that pre-outbreak growth that was used as a reference was depressed due to stress events in the 1980's. The pattern of growth of trees that died as a result of the outbreak also suggests that the jack pine trees in this area may have been weakened by a series of stress events before the 1991-1993 JPBW outbreak.

Top-killed trees and trees from "old" stands (≥ 50 years) had yet to recover to pre-outbreak growth levels in 1995. Whether top-killed trees will be able to recover or whether these trees will die before or during the next JPBW outbreak is unknown.

Stand age is clearly an important factor in the determination of growth loss due to JPBW defoliation. I observed dramatic decreases in tree growth in older stands. The management recommendation to shorten rotation lengths and harvest overmature jack pine is a good one and perhaps, the single most important objective for the forest manager.

There was no clear association between the relative abundance of suppressed trees and overall impact in the stand. Nonetheless, tree growth in overstocked stands was lower than tree growth in poor or well stocked stands in 1994 and 1995. This suggests that some factor other than the abundance of suppressed trees was responsible for decreased growth. Higher competition between smaller crowned trees or increased JPBW larval survival are two suggestions. Whatever the reason may be, the management recommendation to eliminate overstocked stands seems to be valid.

The presence of wolf trees in the stand was not related to reduced tree growth. Tree growth during the outbreak was negatively associated with stand basal area. Due to these observations and the low volume often found in poorly stocked stands, I suggest that these stands be given low management priority.

CHAPTER 3

FINANCIAL EVALUATION OF A JACK PINE BUDWORM OUTBREAK AND IMPLICATIONS FOR MANAGEMENT

Introduction

Jack pine (*Pinus banksiana* Lamb.) is one of the most widely distributed and economically important tree species in the Lakes States region of the United States (Minnesota, Wisconsin, and Michigan) and in Canada (Hackett and Piva 1994; Yeatman 1967). It is characterized by rapid juvenile growth and qualities desirable for commercial softwood pulp (Rudolph and Laidly 1990). Merchantable stands can be grown on marginally productive land that may be incapable of supporting other tree species (Benzie 1977; Cayford 1970). In the Lake States, jack pine accounted for 40% of softwood pulp production in 1992 (Hackett and Piva 1994).

Jack pine budworm (*Choristoneura pinus pinus* Freeman) is a native, episodic insect pest that is distributed sympatrically with jack pine (Howse 1984). Outbreaks of this foliage-feeding insect occur regularly in the Lake States, about every six to ten years (Volney and McCullough 1994). During a jack pine budworm (JPBW) outbreak, severe defoliation can occur locally and over a widespread area. JPBW defoliation can result in reduced tree growth, mortality of the terminal leader of the tree (top-kill), and tree mortality (Graham 1935;

Kulman et al. 1963; Gross 1992; McCullough et al. 1996). Significant losses in merchantable volume of jack pine can result from a single JPBW outbreak (Gross and Meating 1994).

For economic and environmental considerations, forest managers in the Lake States do not currently use insecticides to combat JPBW infestations (Benzie 1977; Heym et al. 1993; McCullough et al. 1994). Instead, current management recommendations are based on the use of silvicultural guidelines, harvest scheduling, salvage, or cover-type conversion to minimize JPBW impact. Current management recommendations in the Lake States include eliminating overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area) to reduce competition, the number of suppressed trees in overstocked stands, and the number of wolf trees in understocked stands (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

Forest managers of public lands are under increasing pressure to maximize all benefits from forested land, including benefits from timber production, wildlife habitat protection, watershed protection, and recreational use. Faced with these often conflicting goals and the inevitable timber loss associated with insect pests such as the JPBW, forest managers need information to help them make efficient resource allocation decisions. Despite the importance of the JPBW as a pest and a number of studies quantifying the impact of individual outbreaks, reductions in timber yield resulting from JPBW outbreaks is not generally known (Hall et al. 1993).

The purpose of this chapter was to quantify stand-level financial loss associated with a single JPBW outbreak in one region of the Lake States and to examine patterns of financial loss in relation to stand characteristics and JPBW management recommendations. Specifically, the objectives of this chapter were to: (*i*) quantify the merchantable volume and financial losses that resulted from the 1991-1993 JPBW outbreak in the Raco Plains area in the Hiawatha National Forest in the Upper Peninsula of Michigan; (*ii*) examine the patterns of merchantable volume and financial loss in relation to stand characteristics of age, site index, basal area, suppressed tree proportion, and wolf tree proportion; and (*iii*) evaluate current JPBW management recommendations used in the Lake States. Specifically, I tested the following null hypotheses:

H_0: There is no difference in standing value loss between "young" stands (< 50 yrs) and "old" stands (≥ 50 yrs).

H_0: There is no difference in standing value loss between low site index stands (< 15.2 m) and high site index stands (≥ 15.2 m).

H_0: There is no difference in standing value loss among poorly stocked (< 1,300 TPH, < 16.1 m^2/ha), well stocked (1,300-1,734 TPH, 16.1-25.3 m^2/ha), or overstocked stands (> 1,734 TPH, > 25.3 m^2/ha).

H_0: There is no difference in standing value loss between stands with few suppressed trees (≤ 10%) and stands where suppressed trees were common (> 10%) (20-year-old or older stands, only).

H_0: There is no difference in standing value loss between stands with wolf trees and stands without wolf trees (20-years-old or older stands, only).

Methods

To quantify the merchantable volume and financial losses that resulted from the 1991-1993 JPBW outbreak, I determined the current composition of the jack pine stands in the Raco Plains area and estimated the impact attributable to the 1991-1993 JPBW outbreak. Impact estimates were used to reconstruct the composition of these stands in the absence of the 1991-1993 JPBW outbreak. I then compared volume and value of the timber in these stands with and without JPBW impact.

Study Site

The Raco Plains is a 18,200 ha (45,000 ac) area located in the Hiawatha National Forest in the Upper Peninsula of Michigan (Figure 3-1). This area is characterized by level to gently rolling terrain, sandy glacial outwash soils of the Rubicon, Croswell, and Kalkaska types, and large tracts of even-aged jack pine forest (Heym et al. 1993).

In 1991, a JPBW outbreak was first observed in the Raco Plains area, and aerial surveys indicated an estimated 6,560 ha (16,000 ac) were defoliated (Heym et al. 1993; McCullough et al. 1996). Defoliation increased the following year (1992), and an estimated 75% of the jack pine stands in this area suffered moderate to severe defoliation (McCullough et al. 1996). By 1993, the JPBW population was declining, although noticeable defoliation was still observed in the area (McCullough et al. 1996). No defoliation was observed in 1994 when the JPBW population returned to endemic levels.

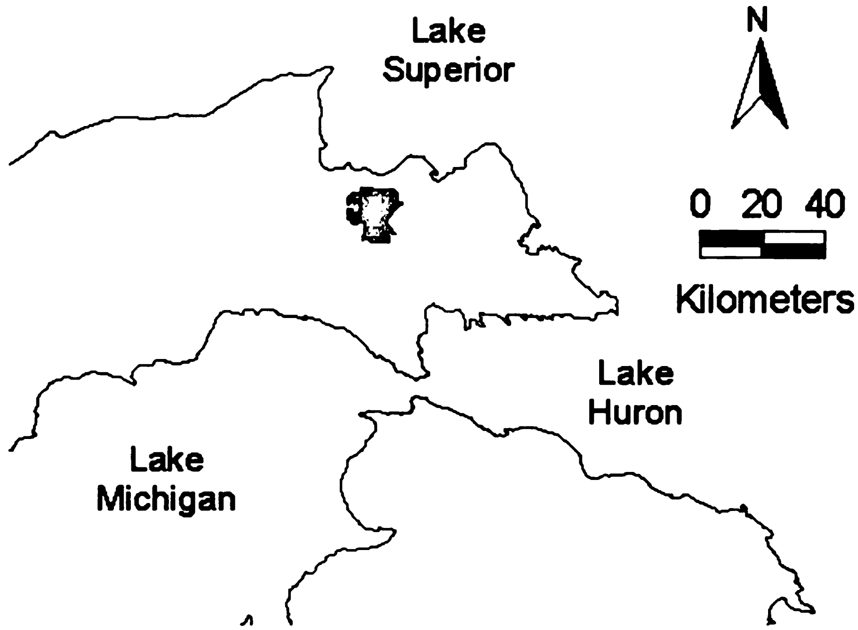

Figure 3-1 – The Raco Plains area of the Hiawatha National Forest located in the eastern Upper Peninsula of Michigan.

Sampling in the Raco Plains area has been performed annually since 1992 in four USDA Forest Service compartments (compartment numbers 49, 58, 78, and 79) (Figure 3-2). The four compartments average 730 ha (1,800 ac) in size and contain a total of 240 stands. All survey compartments were visited by USDA Forest Service personnel from 1991-1994, and inventory characteristics (e.g., forest type, stand age, site index, etc.) and stand boundaries were updated. All stands with at least 50% of the basal area in jack pine were surveyed in each compartment.

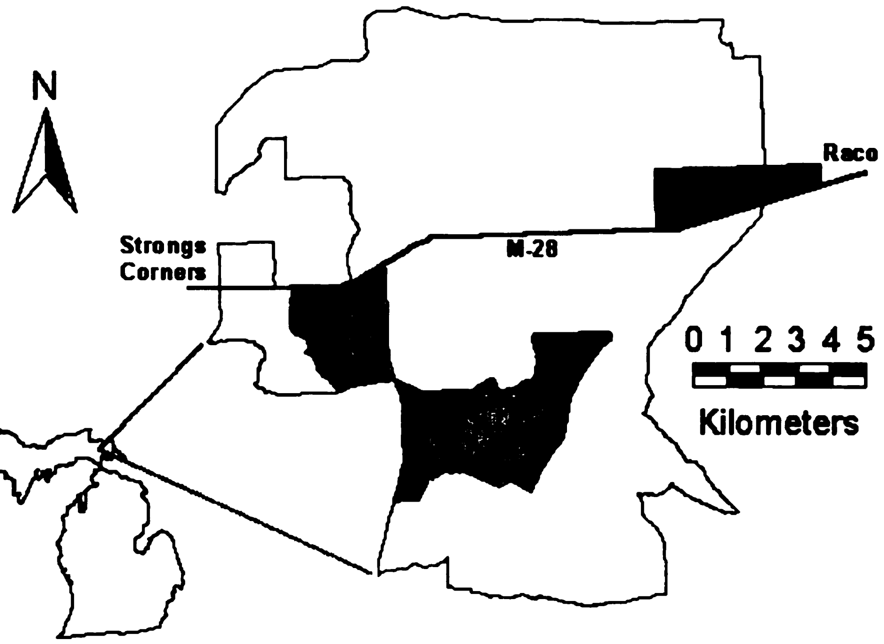

Figure 3-2 – USDA Forest Service management compartments in the Raco Plains area of the Hiawatha National Forest sampled from 1992 to 1996.

In 1996, a total of 99 stands, covering 1,480 ha (3,600 ac), were surveyed in the Raco Plains area (Figure 3-3). Summary statistics for area, age, site index, basal area, and trees per hectare of the 99 sample stands are given in Table 3-1. Age of the 99 sample stands was positively correlated with site index (r = 0.21; P = 0.041) and basal area (r = 0.75; P < 0.0001). Site index of the 99 sample stands was positively correlated with basal area (r = 0.35; P < 0.0001) and trees per hectare (r = 0.25; P = 0.013).

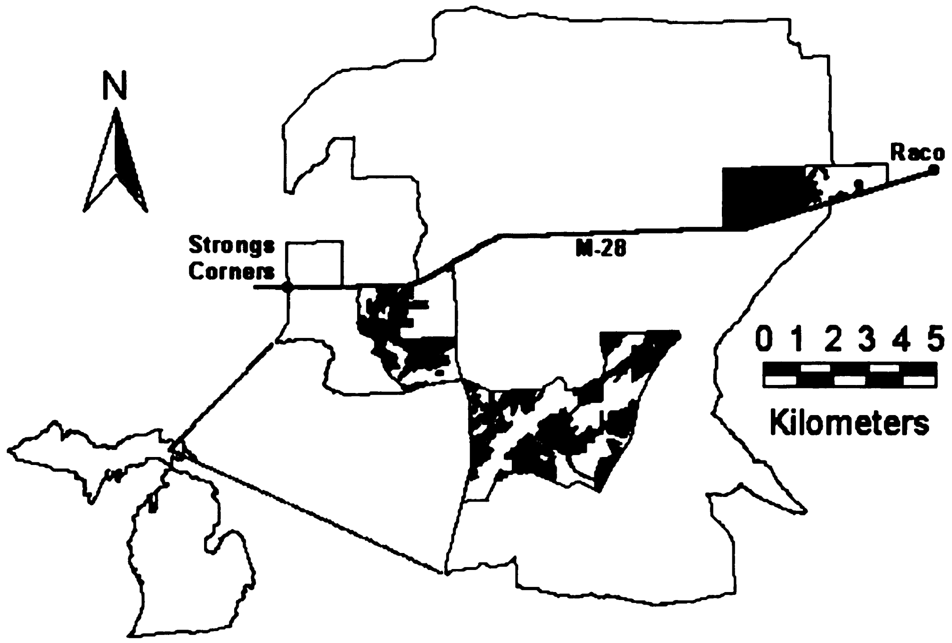

Figure 3-3 – Stands sampled in 1996 in the Raco Plains area of the Hiawatha National Forest.

Table 3-1 – Summary statistics for jack pine stands sampled in 1996 (*n* = 99).

	Mean[a]	Median	Minimum	Maximum
Area (ha)	14.9 (1.68)	10.9	0.8	101.7
Stand Age (years)	44 (2.1)	51	10	71
Site Index (m)	15.0 (0.15)	15.2	11.3	18.0
Basal Area (m^2/ha)	15.2 (0.87)	16.0	0.4	34.5
Number of Trees (per ha)	1353 (67.8)	1288	347	4293

[a] Standard error of the mean in parentheses

Stand Composition, Top-kill, and Tree Mortality

To quantify top-kill and tree mortality resulting from the 1991-1993 JPBW outbreak, at least two fixed-radius, 0.01 ha (1/40 ac) circular plots were located in each of the 99 stands. Plots were randomly located each year. For the 1996 sampling, stands 8-19 ha (20-49 ac) in size were sampled with three plots. Those 20-39 ha (50-99 ac) in size received four sample plots. Stands 40-79 ha (100-199 ac) in size had five plots. Two stands had areas greater than 80 ha (200 ac), and they received six plots each. This number of plots per stand represented a practical compromise between sampling effort and accuracy. A total of 277 plots were sampled.

In all sample years, the total number of jack pine trees in each plot was tallied and the status of each tree (i.e., surviving, top-killed, or dead) was recorded. Each top-killed and dead jack pine tree was visually examined to determine if damage had occurred recently (i.e., as a result of the 1991-1993 JPBW outbreak) or before the 1991-1993 JPBW outbreak. This determination was based on the overall form of the tree, the presence of fine twigs, bark tightness, and other indicators of decay (McCullough et al. 1996).

In 1996, I measured diameter at breast height (1.37 m) and visually estimated crown ratio of all jack pine trees in each plot. Crown ratio is the percentage of live crown of each tree or the ratio of the length of living crown to the total tree height (Wenger 1984). In addition, I ranked all jack pine trees as dominant/ codominant, intermediate, suppressed, or wolf as defined by Smith (1986). Information on 2,899 trees was collected.

In 1996, total height and length of dead tops of all top-killed jack pine trees were measures using a clinometer. I also measured the height of at least one randomly selected live tree from the dominant/codominant crown class in each plot.

Tree Growth

In 1996, seven trees from each of the 12 strata, a total sample of 84 trees, were selected from the sample stands in the Raco Plains area. Chapter 2 contains a detailed description of the stratification and sample tree selection process. To ensure that growth of top-killed and dead trees was measured, two of the seven sample trees in each stratum were recently top-killed and two were trees that recently died.

Each sample tree was felled, and two- to four-centimeter (1-2 in.) thick discs were taken at several locations along the bole of each tree. Discs were cut at stump height (0.30 m), breast height (1.37 m), and every 2 meters above breast height, without corresponding to branch nodes. A minimum of three discs were taken from each tree.

To measure annual ring width, I kiln-dried, sanded one face, and located two average radii on each disc. I measured and cross-dated annual ring widths along these radii to the nearest 0.01 mm using an optical digitizing scanner and WinDENDRO image analysis software (Regent Instruments, Inc., Quebec, Quebec) (Guay et al. 1992).

Growth Loss Estimation

I used non-outbreak growth before the 1991-1993 JPBW as the reference to measure growth loss. Similar studies of jack pine growth in Saskatchewan and Ontario, Canada following JPBW defoliation (Cerezke 1986; Gross 1992) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth in British Columbia, Canada following western spruce budworm (*Choristoneura occidentalis*

Freeman) defoliation (Alfaro et al. 1982; Thomson and Van Sickle 1980) also used this approach.

To estimate growth loss by extrapolating non-outbreak growth, Thomson and Van Sickle (1980) suggested two methods. The first method involved fitting a least-squares regression line to the mean radial increment of each disc excluding outbreak and recovery years. The least-squares line equation was then used to estimate growth during outbreak and recovery years. In the second method, the authors used 5-year-mean increments of growth before the outbreak and after recovery to determine two points. These two points were connected with a line segment which represented growth during outbreak and recovery years.

Although the first method may estimate actual volume more accurately, the second method more accurately reflects short-term growth patterns and gives a better estimate of growth in outbreak and recovery years. Due to variability in long-term growth between outbreaks and sharply decreasing long-term growth trends in many older trees, I used the second method.

I used the breast height disc from surviving and top-killed trees (n = 60) to estimate radial growth loss. Annual radial increment was plotted against year to examine the patterns of growth loss and recovery from past JPBW outbreaks. Periodic reductions in growth were observed in many sample trees. To determine if these reductions in growth were the result of JPBW defoliation or other stress events such as drought stress, I studied Annual Forest Pest Reports published by Michigan Department of Natural Resources from 1950-1994. These Annual Forest Pest Reports provided a historic record of JPBW activity in the eastern Hiawatha National Forest from which I was able to determine past patterns of growth loss and recovery from JPBW outbreaks.

I calculated the mean radial increment for each sample tree for the five non-outbreak years (1982, 1987-1990) before the 1991-1993 JPBW outbreak. The years 1983 to 1986 were not included because a JPBW outbreak and recovery occurred in the study area at that time (Heym et al. 1993). This five-year mean radial increment and the 1995 radial increment, after recovery from the 1991-1993 outbreak, were used as end points (set at 1990 and 1995, respectively) that determined a line segment. The equation of this line segment was used to calculate growth loss for 1991-1993 (outbreak) and 1994 (recovery) for each sample tree by subtracting predicted growth from observed growth. If observed growth was greater than predicted growth, I assumed that growth loss was zero.

Growth and Yield Model

To determine the merchantable volume yield of the jack pine stands in the Raco Plains area, I used the information collected in our field survey described above, along with a USDA Forest Service growth and yield model, the Lake States TWIGS variant of the Forest Vegetation Simulator (LS-TWIGS) (Bush and Brand 1995; Miner et al. 1988). LS-TWIGS is a distance-independent, individual-tree growth and yield model. Data collected during the 1996 field season were used to generate tree lists for each stand. A tree list is a list of characteristics of individual sample trees in a stand that is used to represent the stand in LS-TWIGS. Tree lists contained information on individual tree species, status (alive or dead), diameter at breast height (DBH), crown ratio, and height.

General stand and sampling information such as site index, plot size, number of plots, and stand area were also included (Teck 1995). LS-TWIGS does not recognize trees as being top-killed. In addition, the loss in merchantable volume to dead wood in top-killed portion of the stem was negligible (see Research Note in Appendix A). For these reasons top-kill was not included as a factor in determining merchantable volume loss.

Tree List Adjustments

LS-TWIGS was used to estimate merchantable volume yield of each sample stand in the Raco Plains area twice – once in its current state in 1996 (with JPBW impact) and once in an adjusted state (without JPBW impact resulting from the 1991-1993 outbreak). Tree list adjustments were made by changing the status of trees that had died and by adding diameter growth that was lost as a result of the 1991-1993 JPBW outbreak.

To adjust tree mortality rate, I first determined an endemic rate of tree mortality. From the 1992 survey data, I observed a 1% average tree mortality rate. I believe this rate was approximately equal to endemic jack pine mortality rates (Buchman et al. 1983), and in lieu of other data, these data were used to adjust the tree mortality rate in each tree list. Due to salvage operations and updated stand inventory data, some stands sampled in 1996 had not been sampled in 1992. To determine an endemic tree mortality rate for all sample stands, I calculated the mean and standard deviation of the endemic tree mortality rate for each stratum defined in the stratification scheme (see Chapter 2, Table 2-2). These statistics were used to create normal probability distributions for endemic tree mortality for each stratum. An endemic tree mortality rate was randomly selected from the probability distribution of the stratum for each sample stand. The mortality rate of each stand was adjusted to the endemic rate by changing the status of randomly selected dead trees in the tree list.

Similarly, not all stands were sampled for radial growth loss. Diameter growth adjustments were made by determining the mean and standard deviation of total growth loss (i.e., the sum of the growth loss in years 1991-1994) for each stratum. These statistics were used to create normal probability distributions for the growth loss for each stratum. For each tree in the tree list, an amount of growth was randomly selected from these probability distributions and added to the DBH of each tree.

Merchantable Volume Loss Estimation

I computed the merchantable volume loss for the stands in the Raco Plains area in two ways – standing volume loss and projected volume loss. LS-TWIGS was used in both computations.

Standing Volume Loss

The current and adjusted tree lists for all stands (*n* = 99) were entered into LS-TWIGS to calculate current and adjusted merchantable volume yield in 1996 for each stand. Yield for both pulpwood and sawtimber was summed in each stand to produce total volume yield. The difference between current and adjusted yield was the loss in merchantable volume in each stand attributable to the 1991-1993 JPBW outbreak.

Projected Volume Loss

Some of the sample stands in the Raco Plains area had no merchantable volume in 1996. While some volume may have been lost in these stands due to impact from the 1991-1993 JPBW outbreak, this volume reduction will not be realized as a merchantable loss until these stands are harvested. To examine the eventual reduction in merchantable volume in these stands, I projected all stands younger than 50 years old (in 1996) to age 50 (n = 49). The projection age of 50 years was chosen based on recommended rotation ages for the management areas surveyed in this study and on current JPBW management recommendations used in the Lake States (Benzie 1977; McCullough et al. 1994; USDA Forest Service 1986).

To determine merchantable volume yield, current and adjusted tree lists for these stands were projected to age 50 with LS-TWIGS. Yield for both pulpwood and sawtimber was summed in each stand to produce a total projected volume yield. The difference between current and adjusted yield after projection was the projected merchantable volume loss for each stand attributable to the 1991-1993 JPBW outbreak. Stands over 50 years old or older were not projected and were not included in the projected volume loss calculation.

Financial Loss Estimation

As with merchantable volume loss estimation, I calculated financial loss of jack pine timber in the Raco Plains area in two ways – standing value loss and projected value loss.

Standing Value Loss

To determine the standing value loss, I used the standing volume loss estimates described above. Price data were collected from USDA Forest Service jack pine timber sales in the Raco Plains area in 1996. Pulpwood and sawtimber price per unit for these five sales were approximately equal (i.e., there was no premium for jack pine sawtimber). Because no differentiation in price was made between pulpwood and sawtimber, I used average 1996 pulpwood and sawtimber price ($14.58/m^3). The standing value loss that resulted from the 1991-1993 JPBW outbreak was calculated by multiplying standing volume loss for each stand by the mean 1996 timber price. Costs were not included in our estimates of standing value loss.

Projected Value Loss

Projected value loss was calculated for each stand younger than 50 years old (in 1996) using the following equation:

$$\textit{Projected Value Loss} = \frac{Q\,P\,(1+b)^{t}}{(1+r)^{t}} \qquad [1]$$

Where:

Q = projected merchantable volume loss (m^3/ha)
P = jack pine timber price ($/m^3)
b = annual real rate of increase of jack pine timber price (%)
r = discount rate (%)
t = time period (years)

The parameter Q was the projected volume loss described above. Jack pine timber price (P) was set at the mean 1996 timber price in the Raco Plains area ($14.58/m^3), as described above. Data from annual USDA Forest Service "Cut and Sold" reports (Timber Cut and Sold on National Forests Under Sales and Land Exchanges) from 1977-1996 were used to determine annual real rate of change of jack pine timber price (*b*). Nominal price per cubic meter for jack pine pulpwood from five National Forests in Wisconsin (Chequamegon and Nicolet) and Michigan (Hiawatha, Huron-Manistee, and Ottawa) were converted to constant 1996 dollars (real prices) using the annual Producer Price Index for all commodities (U.S. Department of Labor, Bureau of Labor Statistics). Implicit in our use of data from five regional National Forests was the assumption that the market for jack pine timber is regional and that timber sales in the Raco Plains area may be purchased by harvesters likely to bid on timber sales in any of these five National Forests. To determine the real rate of price increase, I took the natural log of real price and ran a linear ordinary least-squares regression against year using the following equation:

$$ln(P) = a + b\,(year) \qquad [2]$$

Where:

P = real jack pine timber price ($\$/m^3$)
a = constant
b = annual real rate of increase of jack pine timber price (%)

The regression analysis indicated a significant model (F = 5.43; P = 0.022; df = 1) with annual real rate of increase of jack pine timber price (b) equal to 2.67% ($S.E.$ = 1.15). Discount rate (r) was set at 4%, the standard discount rate used by the USDA Forest Service for evaluating long-term investments in resource management (Row et al. 1981). The discounting time period (t) was the length of time in years of the LS-TWIGS projection for each stand (1-40 years). Again, costs were not included in our estimates of projected value loss.

Analysis of Merchantable Volume and Financial Loss

Descriptive statistics for standing merchantable volume and value loss were calculated. To examine the distribution of standing value loss, I plotted standing value loss per hectare for each stand, and I ranked total standing value loss from smallest to largest and plotted these values against total area. Absolute loss (loss/ha), as opposed to proportional loss (%), was presented because I felt absolute loss may be more relevant to the forest manager. For example, a stand that losses only 10% of its volume but produces 120 m^3/ha (absolute loss of 12 m^3/ha) may be of greater concern to the forest manager than a stand that losses 30% of its volume but can produce only 30 m^3/ha (absolute loss of 9 m^3/ha).

To compare standing and projected loss for stands younger than 50 years old (in 1996), I calculated descriptive statistics for volume and value losses for these stands. To further evaluate the differences between standing and projected value loss for these stands, I plotted standing and projected value loss per hectare. Finally, total standing and projected value loss were ranked from smallest to largest and plotted against total area.

Analysis of Stand Characteristics

Standing value loss was examined in relation to stand characteristics of age, site index, basal area, suppressed tree proportion, and wolf tree proportion. Total standing value loss was sorted and plotted against each stand characteristic so that I could evaluate the distribution of value losses among stands with different characteristics. Kendall's nonparametric coefficient of rank correlation (τ) was computed to evaluate associations between standing value loss per hectare and each stand characteristic because standing value loss per hectare did not conform to the assumptions of normality (Sokal and Rohlf 1995).

Analysis of Management Recommendations

To evaluate current JPBW management recommendations used in the Lake States, statistical tests of the null hypotheses stated in the objectives were performed. Standing value loss data did not conform to the assumptions of normality, and the Kruskal-Wallis test, a nonparametric test analogous to a parametric one-way analysis of variance, was used to evaluate effects of treatments on the response level (Lehmann 1975; Sokal and Rohlf 1995). Significance of the Kruskal-Wallis test statistic (H) was assessed by the univariate χ^2. The Kruskal-Wallis test was performed to test for significant differences in standing value loss between poorly stocked, well stocked, and overstocked stands; stands with few versus abundant suppressed trees; and stands with no verus some wolf trees. If interactions were significant, the Scheire-Ray-Hare extension of the Kruskal-Wallis test was used. This test is a nonparametric test analogous to a two-way analysis of variance (Sokal and Rohlf 1995). Again, significance of the Scheire-Ray-Hare extension of the Kruskal-Wallis test statistic (H) was assessed by the univariate χ^2.

Only stands 20 years old or older were used to test for significant differences in suppressed tree class and wolf tree class. This minimum age was chosen because younger stands were not likely to have reached canopy closure or to have developed stratified canopies.

Results

Annual growth of a single surviving jack pine tree is presented in Figure 3-4. Examination of the Michigan DNR Forest Pest Reports indicated that five JPBW outbreaks have occurred in the Raco Plains area since 1950. In the sample tree presented in Figure 3-4 and in most other surviving and top-killed sample trees, JPBW defoliation affected radial growth for an average of two years during the outbreak and one year (recovery) following outbreak collapse.

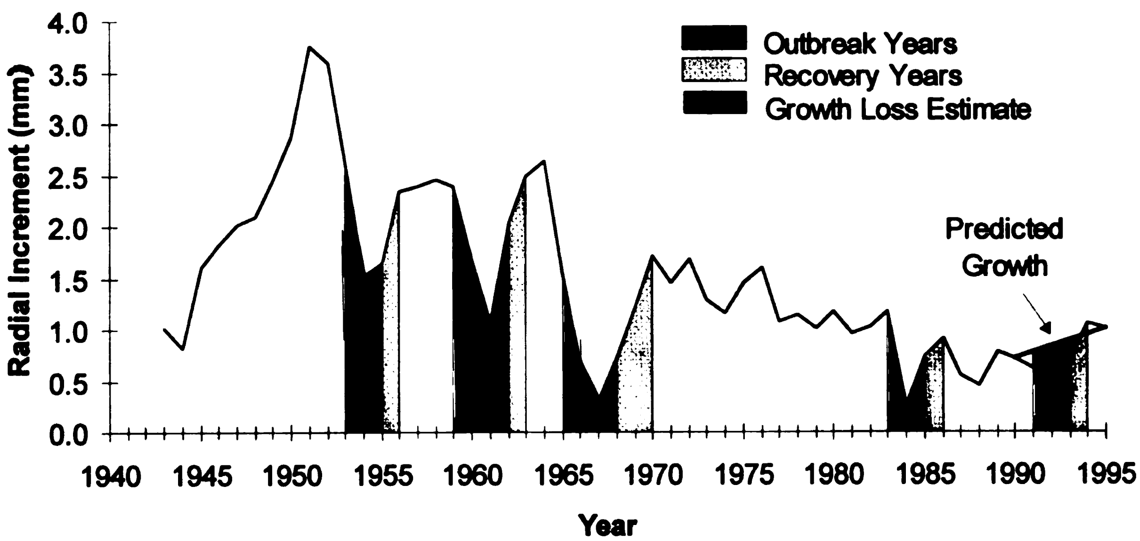

Figure 3-4 – Annual radial increment at breast height for a single surviving sample tree with historic JPBW outbreaks and growth loss estimation highlighted.

Analysis of Merchantable Volume and Financial Loss

Descriptive statistics of standing merchantable volume and value loss are presented in Table 3-2. Standing volume and value loss averaged 13.3 m^3/ha (2.3 cds/ac) and \$194/ha (\$78/ac), respectively. Standing volume loss totaled

19,500 m^3 (8,200 cds) for the entire 1,480 ha (3,600 ac) sample area. Total standing value loss was $289,800.

Table 3-2 – Descriptive statistics for standing merchantable volume and value loss.

	N[a]	Mean[b]	Median	Minimum	Maximum
Standing					
Volume Loss (m^3/ha)	99	13.3 (2.03)	5.6	0	109.5
Volume Loss (%)	82[c]	14.1 (1.23)	12.3	0	43.8
Value Loss ($/ha)	99	$194 (29.6)	$82	$0	$1,597

[a] Number of stands
[b] Standard error of mean in parentheses
[c] 17 stands had no standing merchantable volume and were not included in volume loss (%) statistics

Seventeen stands had no standing merchantable volume in 1996 and therefore, sustained no standing merchantable volume loss. These stands were not included in the proportional volume loss (%) statistics. Two of the remaining 82 stands had no standing volume loss.

A single stand (7% of the area) suffered 17% of the total standing value loss, the largest single-stand loss. This was the largest stand in the sample (102 ha). It was a well stocked (25.3 m^2/ha), 56-year-old stand on a high site index site (16.8 m) that experienced a high mortality rate (44%) and a heavy reduction in basal area (28%) as a result of the 1991-1993 JPBW outbreak.

The heaviest losses per hectare were concentrated in only a few stands (Figures 3-5 and 3-6). Seventy-four stands (75% of the sample) experienced less than $200/ha standing value loss (Figure 3-5). Only eight stands (23% of the area) accounted for over half the total standing value loss ($145,400) (Figure 3-6). These eight stands averaged 40 m^3/ha (6.8 cds/ac) standing volume loss (25% reduction in standing volume) and $587/ha ($237/ac) standing value loss.

Descriptive statistics for the stand characteristics of these eight stands is given in Table 3-3.

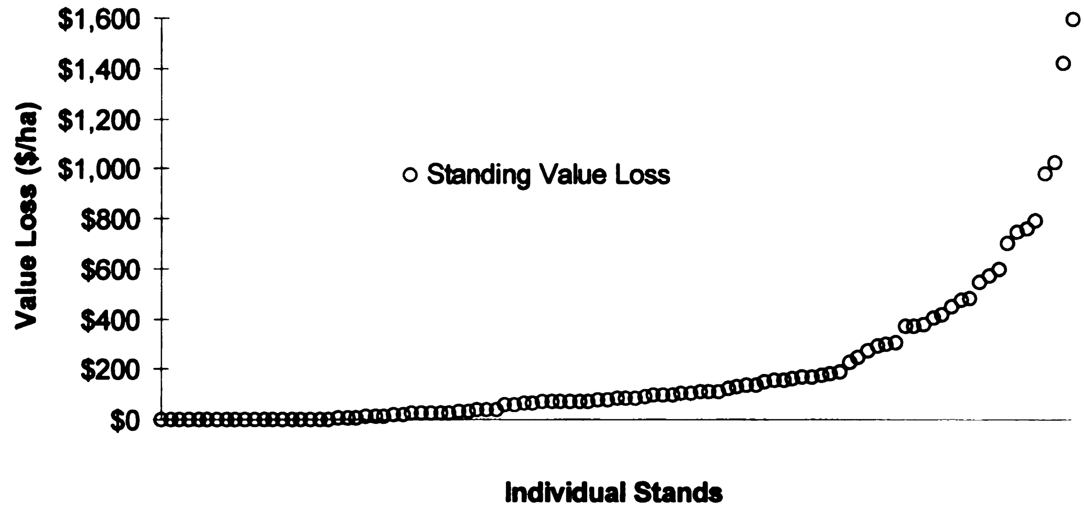

Figure 3-5 – Standing value loss per hectare for all sample stands (n = 99).

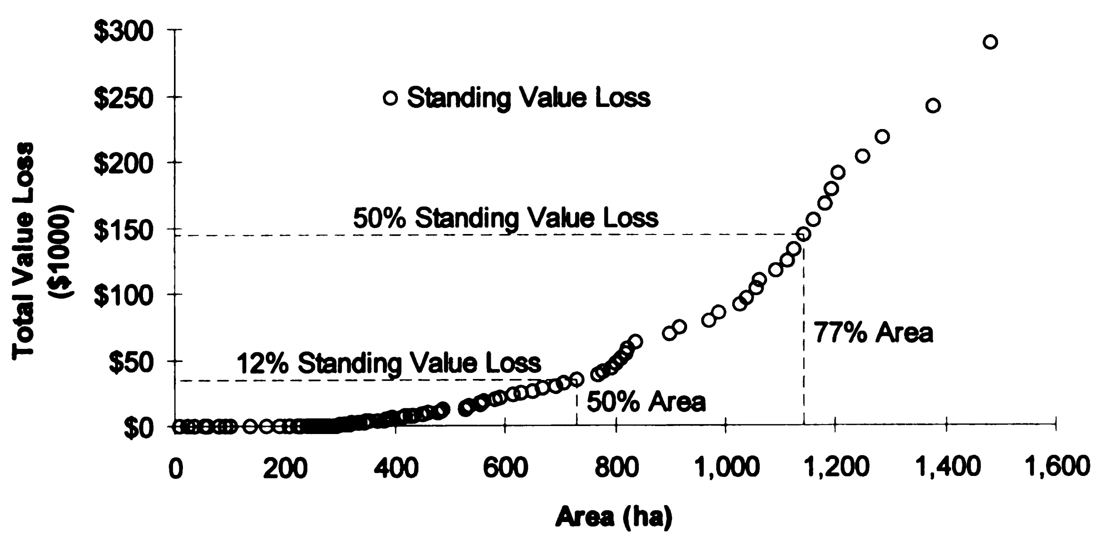

Figure 3-6 – Total standing value loss for the entire sample area (n = 99).

Table 3-3 – Descriptive statistic for the stand characteristics of eight[a] stands sustaining the greatest standing value losses.

	Mean[b]	Median	Minimum	Maximum
Area (ha)	42.0 (12.8)	28	12	102
Stand Age (years)	58.1 (2.62)	59	48	69
Site Index (m)	16.4 (0.16)	16.5	15.5	16.8
Basal Area (m^2/ha)	23.6 (1.88)	25.2	15.3	31.6

[a] Stand numbers: 58008, 58011, 58018, 58053, 58063, 78004, 78052, 78069
[b] Standard error of the mean in parentheses

Comparison of standing volume and value loss and projected volume and value loss descriptive statistics for all projected stands (n = 49) is given in Table 3-4. Total standing volume loss for the 49 stands (4,700 m^3) was less than total projected volume loss for the 49 stands (5,900 m^3). While mean and median absolute standing volume losses (m^3/ha) were less than projected volume losses, proportional standing volume loss (%) was greater than projected volume losses. Total standing value loss for the 49 stands ($68,300) was also less than total projected value loss for the 49 stands ($74,400).

Table 3-4 – Comparison of standing and projected merchantable volume and value loss.

	N[a]	Mean[b]	Median	Minimum	Maximum
Standing					
Volume Loss (m^3/ha)	49	6.0 (1.79)	1.3	0.0	52.4
Volume Loss (%)	32[c]	12.8 (1.80)	11.2	0.0	40.5
Value Loss ($/ha)	49	$87 (26.1)	$19	$0	$764
Projected					
Volume Loss (m^3/ha)	49	6.4 (1.23)	3.2	-1.8	40.5
Volume Loss (%)	49	4.8 (0.80)	2.6	-1.0	24.8
Value Loss ($/ha)	49	$77 (16.2)	$33	-$17	$575

[a] Number of stands
[b] Standard error of mean in parentheses
[c] 17 stands had no standing merchantable volume and were not included in volume loss (%) statistics

Minimum projected volume and value losses were negative (i.e., volume gains) in five sample stands. All five stands experienced very small volume gains (> 2 m^3/ha), and all were 15 years old or younger when the outbreak began in 1991. There is no clear explanation as to why tree list adjustment (i.e., resurrection of trees that had died and the addition of lost diameter growth) resulted in a lower final volume. I speculate that in these young stands the JPBW outbreak acted as a type of precommercial thinning that allowed the residual trees to increase in volume more than they might otherwise have.

Figure 3-7 illustrates the differences in the standing and projected value loss estimates for each of the projected stands. Standing value loss estimates were less than projected value loss estimates in 34 stands (68%). Standing value loss estimates were greater than projected value loss estimates in 12 stands (24%). Three stands had equal projected and standing value loss estimates. Each of these three stands had zero standing and projected value loss estimates. The most extreme discrepancy between projected and standing value losses was seen in a 20-year-old stand that lost \$764/ha in standing value but gained (negative loss) \$17/ha in projected value (i.e., projection resulted in greater value with JPBW impact than without JPBW impact).

Analysis of Stand Characteristics

The pattern of increasing slope with increasing stand age in Figure 3-8 indicates that total standing value loss was concentrated in older stands. Stands over 50 years old (54% of the area) accounted for 76% of the total standing value loss. A similar pattern was seen with site index. Total standing value loss

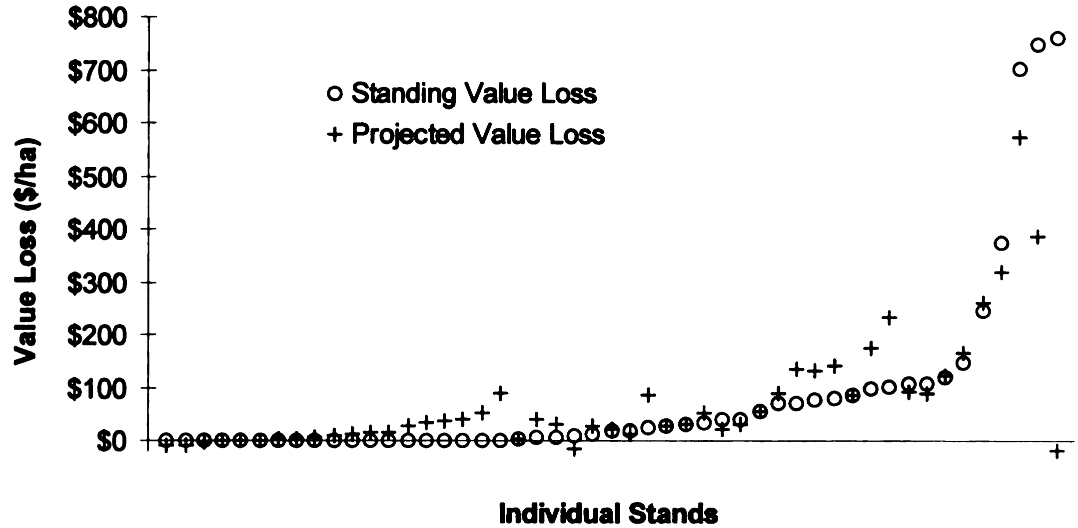

Figure 3-7 – Standing and projected value loss per hectare for each projected stand (n = 49).

was concentrated in higher site index stands (Figure 3-9). Stands with site index 15.2 m (50 ft) or higher (61% of the area) accounted for 82% of the total standing value loss. Figure 3-10 indicates that standing loss was concentrated in stands with moderate basal area. Poorly stocked stands with less than 16.1 m^2/ha (70 ft^2/ac) (44% of the area) accounted for only 21% of the total standing value loss. Overstocked stands with more than 25.3 m^2/ha (110 ft^2/ac) (22% of the area) accounted for 23% of the total standing value loss. The remaining 56% of the total standing value loss occurred in well stocked stands with basal area between 16.1-25.3 m^2/ha (70-110 ft^2/ac) (34% of the area). Total standing value loss was concentrated in stands with a low proportion of either suppressed trees (< 15%) or wolf trees (<10%) (Figures 3-11 and 3-12).

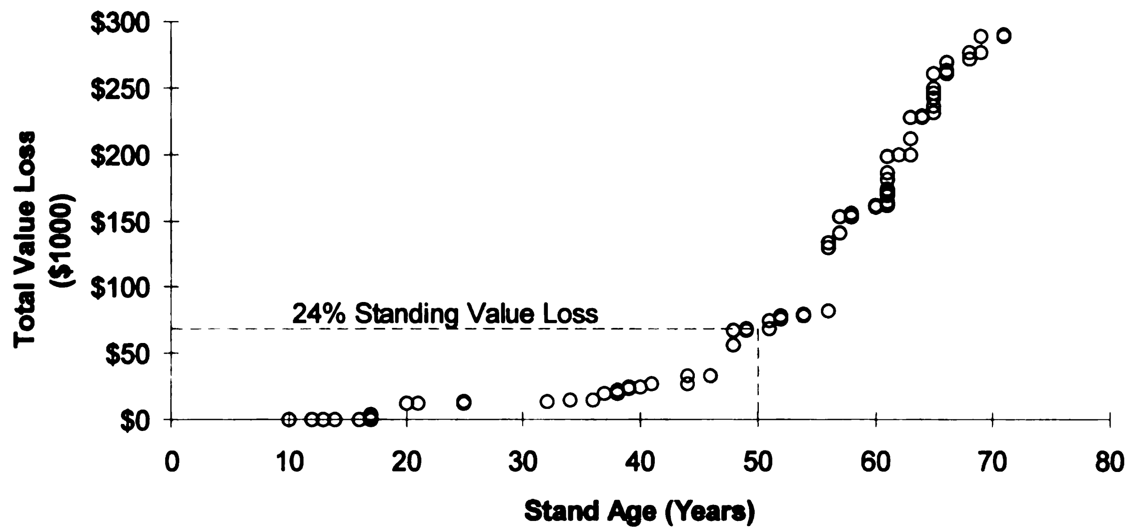

Figure 3-8 – Total standing value loss ordered by stand age.
Note: points may overlap.

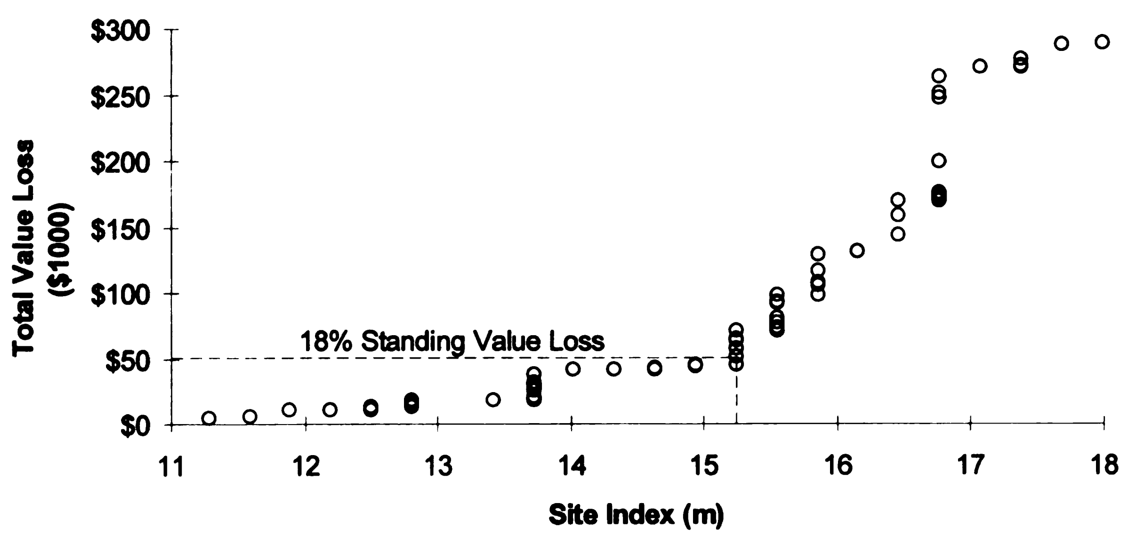

Figure 3-9 – Total standing value loss ordered by site index.
Note: points may overlap.

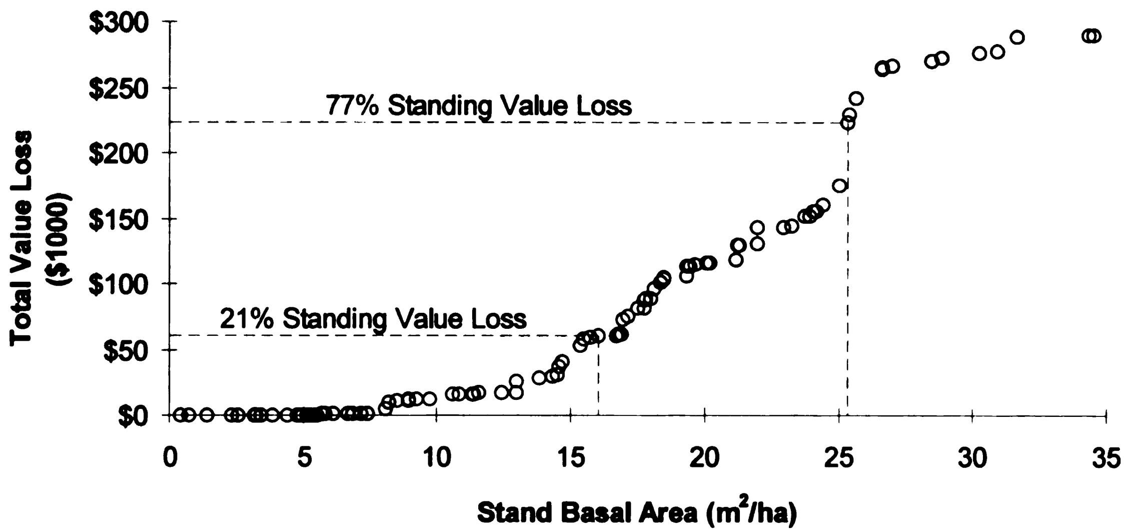

Figure 3-10 – Total standing value loss ordered by stand basal area.
Note: points may overlap.

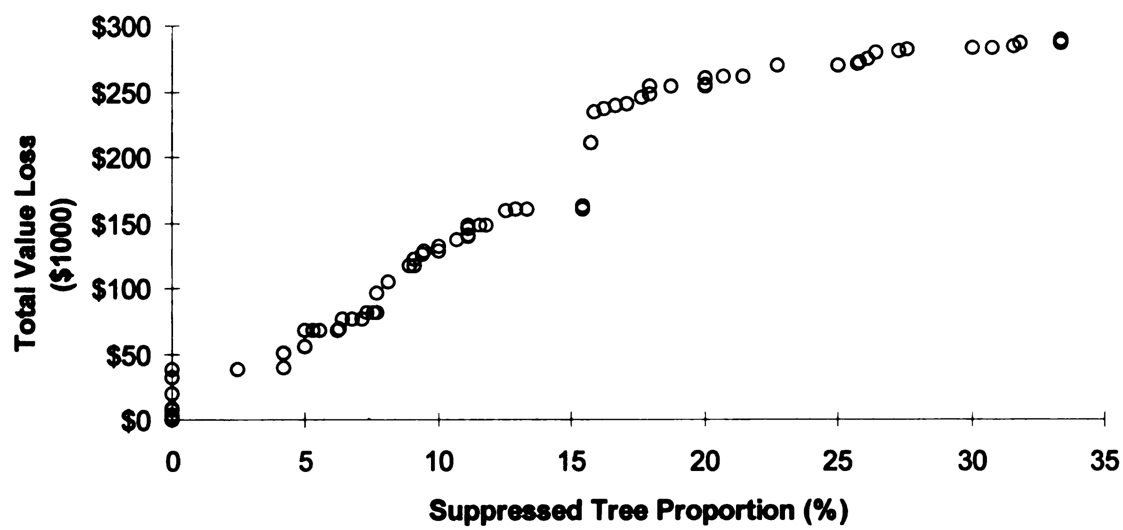

Figure 3-11 – Total standing value loss ordered by suppressed tree proportion.
Note: points may overlap.

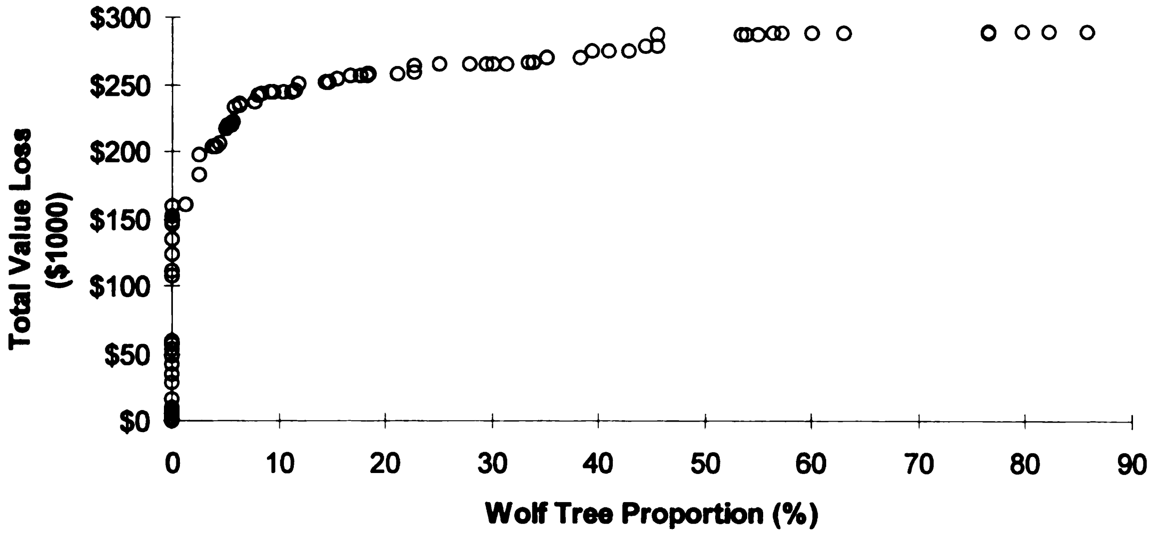

Figure 3-12 – Total standing value loss ordered by wolf tree proportion.
Note: points may overlap.

Standing value loss was positively correlated with stand age, site index, stand basal area, and suppressed tree proportion (Table 3-5). Standing value loss was negatively correlated with wolf tree proportion (Table 3-5).

Table 3-5 – Kendall's coefficient of rank correlation (τ) for standing value loss ($/ha) and stand characteristics.

	Standing Value Loss
Stand Age	0.52 **
Site Index	0.18 *
Stand Basal Area	0.55 **
Suppressed Tree Proportion	0.18 *
Wolf Tree Proportion	-0.40 **

** Significant at the 0.01 level (2-tailed)
* Significant at the 0.05 level (2-tailed)

Analysis of Management Recommendations

Current management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area).

Mean, median, and mean rank standing value loss per hectare for five management classes are presented in Table 3-7. A significant interaction between stand age and site index was present in the standing value loss per hectare data ($H = 4.33$; $P = 0.037$; $df = 1$). This interaction was somewhat difficult to interpret. Examining mean values suggested that it was a multiplicative interaction (i.e., interaction that affects magnitude of the differences but not direction) (Table 3-6). Median values suggested a qualitative interaction (i.e., interaction that affects direction of the differences) (Table 3-6). The Schiere-Ray-Hare extension of the Kruskal-Wallis test evaluated interaction of the mean ranks, and results agian suggested a qualitative interaction (Table 3-6).

Table 3-6 – Mean, median, and mean rank of standing value loss ($/ha) for age-site index interaction.

	N[a]	Mean[b]	Median	Mean Rank
Young (< 50 years)				
Low Site Index (< 15.2 m)	24	$46 (9.3)	$31	34.4
High Site Index (≥15.2 m)	25	$126 (49.5)	$0	32.3
Old (≥ 50 years)				
Low Site Index (<15.2 m)	17	$105 (17.0)	$91	52.2
High Site Index (≥15.2 m)	33	$399 (67.0)	$300	73.7

[a] Number of sample stands
[b] Standard error of the mean in parentheses

Table 3-7 – Mean, median, and mean rank standing value loss ($/ha) by management class.

	N[a]	Mean[b]	Median	Mean Rank[c]
Age Class (years)				
Young (< 50)	49	$87 (26.1)	$19	33.3*a*
Old (≥ 50)	50	$299 (48.6)	$166	66.4*b*
Site Index Class (m)				
Low (< 15.2)	41	$70 (9.9)	$67	41.7*a*
High (≥ 15.2)	58	$281 (46.9)	$139	55.9*b*
Stocking Class[d] (TPH, m^2/ha)				
Poor (< 1,300, < 16.1)	34	$174 (55.9)	$40	44.4*a*
Well (1,300-1,734, 16.1-25.3)	41	$214 (48.2)	$98	53.1*a*
Over (> 1,734, > 25.3)	24	$189 (45.7)	$97	52.8*a*
Suppressed Tree Class[e] (%)				
Few (≤ 10)	33	$308 (62.3)	$166	41.2*a*
Abundant (> 10)	42	$209 (42.7)	$106	35.5*a*
Wolf Tree Class[e] (%)				
Absent (0)	30	$380 (70.0)	$285	47.7*a*
Present (> 0)	45	$168 (34.4)	$91	31.5*b*
Total	99	$194 (29.6)	$82	50.0

[a] Number of sample stands
[b] Standard error of the mean in parentheses
[c] Mean ranks within a management class followed by the same letter were not significantly different ($\alpha = 0.05$)
[d] TPH - "young" stands, m^2/ha - "old" stands
[e] 20-year-old or older stands, only

There were no significant differences in standing value loss per hectare among stocking classes ($H = 2.02$; $P = 0.365$; $df = 2$) or between suppressed tree classes ($H = 1.27$; $P = 0.2.60$; $df = 1$). Standing value loss was significantly greater in stands without wolf trees than in stands with wolf trees ($H = 9.97$; $P = 0.002$; $df = 1$).

Discussion

My results focused principally on analysis of the standing value loss, but it is important to note that all results and interpretation can be extended to standing volume loss. Standing volume and value loss differ only in magnitude because standing value loss equals standing volume loss multiplied by a constant (price).

Costs were not included in our estimates of financial loss. Therefore, I cannot interpret my financial loss results as representing the net loss; rather they are gross loss estimates. I have not included costs in our estimates for several reasons. First, very little stand-level cost data is available from the USDA Forest Service in general and the Hiawatha National Forest in particular (D. Heym, Hiawatha National Forest, pers. comm.). Second, I am not assuming that these stands will harvested. Costs are not likely to be incurred by the USDA Forest Service until the sale of these stands is administered. However, ignoring costs probably has little effect on our loss estimates. Costs of administering a timber sale can be considered independent of JPBW outbreaks assuming the timing of the sale is independent of JPBW outbreaks and thus, are the same with or without the impact from the 1991-1993 outbreak. Because I am concerned with the difference in value with and without the outbreak, costs have no effect on the magnitude of the value loss.

Merchantable Volume and Financial Loss

In hindsight, it is clear that the USDA Forest Service could have dramatically reduced the timber losses by harvesting or salvage cutting only a few additional stands. By harvesting the eight stands with the heaviest losses (336 ha) in 1991 or 1992, the Forest Service could have potentially reduced their losses by one-half. Certainly, 336 ha is a considerable area to cut in a short period of time, and this amount of timber on the market over a short period of time may have resulted in lower sale prices. However, this action may have been justifiable considering the magnitude of eventual losses.

In fairness to the USDA Forest Service, pre-salvage or salvage cuts for jack pine were performed in 15 stands, 332 ha (823 ac), in the four management compartments from 1992-1996 (Heym et al. 1993). Given the disproportionate financial impact I observed in eight of the remaining stands, it is easy to image a much greater total standing value loss estimate had the loss in these 15 stands been measured.

The fact that the eight stands with the largest total standing volume loss estimates were all well to overstocked, old stands on high quality sites (Table 3-3) suggests that these types of stands should receive priority for management activities such as salvage or pre-salvage harvest operations. Jack pine stands with these characteristics sustained high levels of tree mortality (Chapter 1) and growth loss (Chapter 2), and they typically carry larger merchantable volumes than stands with other characteristics.

Although differences between standing and projected value loss estimates were observed, the magnitude of these differences was not great for two reasons. First, stands that currently do not have any merchantable volume (i.e., young stands) suffered low levels of tree mortality (Chapter 1) and limited reduction in growth (Chapter 2). Second, because these stands were projected into the future, the present value of the loss in these stands was reduced due to the discounting preformed. Also, it is important to remember that I am concerned only with the 1991-1993 JPBW outbreak. Because of the periodicity of JPBW outbreaks, many stands are likely to experience one or more JPBW outbreaks during the time they were projected. Including the impact of future outbreaks would undoubtedly increase projected value loss estimates.

In most projected stands, projected value loss estimates were greater than standing value loss estimates. In these stands some volume may have been lost due to impact from the 1991-1993 JPBW outbreak, but this volume reduction was not realized as a merchantable loss until these stands were projected. In a few projected stands, standing value loss estimates were greater than projected value loss estimates. The most likely explanation for this observation was that residual tree growth during the projection period partially offset the reduction in volume caused by the 1991-1993 JPBW outbreak.

Stand Characteristics

I observed strong positive associations between standing value loss, age, and basal area (Table 3-5). I would expect age and basal area to have similar associations with standing value loss because these two stand characteristics were highly correlated.

Younger age and lower basal area may affect standing value loss in two ways. First, younger stands and lower basal area stands were probably carrying less volume and value when the outbreak occurred. Therefore, I would expect greater absolute losses in older stands and in stands with higher basal area. Second, younger stands and lower basal area stands tended to suffer lower proportional tree mortality and growth loss than did older or higher basal area stands (Chapters 1 and 2).

While the trend was not as clear as that of age or basal area, standing value loss was positively associated with site index. Again, this could be due to more volume and value on higher quality sites leading to greater absolute loss. A more likely explanation relates to the hypothesis that higher tree mortality occurred in high site index stands, suggested in Chapter 1. That is, when stress occurs, physiological changes occur in the tree in an attempt to minimize the strain of that stress. These physiological changes can be both immediate, such as stomatal closure with the onset of drought stress, and long-lasting, such as changes in carbon allocation (i.e., root-to-shoot ratios) or increases in root membrane permeability (Ibrahim et al. 1997; Johnson 1987; Laurence et al. 1994). In addition, these physiological changes can be cross-adaptive. For example, physiological changes brought about by one stress, such as nutrient deficiency, may enhance the tree's ability to minimize the strain of other types of stress, such as drought stress (Johnson 1987). Jack pine growing on lower quality sites may experience higher frequency of water or nutrient stress and thus, may be better able to cope with defoliation stress. These trees may be less vulnerable to JPBW impact, which translated into lower volume and value losses.

There was a slight, but significant, positive association between standing value loss and the proportion of suppressed trees in the stand. This study and others have found disproportionately heavy impact to suppressed trees (Batzer and Jennings 1980; Graham 1935; Hodson and Zehngraff 1946; Kulman et al. 1963). However, I would expect suppressed trees to have little merchantable volume or value, and thus, volume and value losses from suppressed tree mortality would have little effect on total losses sustained by the stand. Although many suppressed trees died, their proportion in the stand does not appear to greatly affect the value loss sustained by the stand as a whole.

Finally, I observed a clear negative association between standing value loss and the proportion of wolf trees in the stand. This association may arise from the negative association between wolf tree proportion and stand density. Low density stands are likely to have high proportions of wolf trees and less volume and value to lose as a result of JPBW defoliation. The pattern observed in this case may reflect the effect of stand density on standing value loss, rather than lower JPBW impact in wolf trees.

Management Recommendations

I observed a significant interaction between age class and site index class. Interpreting this interaction as qualitative (i.e., interaction that affects direction of differences), I observed that "young", low site index stands experienced greater standing value loss than "young", high site index stands, while the opposite was true for "old" stands. This effect could be explained by our hypothesis related to jack pine physiological response to stress described above. That is, "young", low site index stands have probably not experienced stress events needed to elicit long-term physiological changes. Without this cross-adaptation, these stands may be more vulnerable to JPBW impact than "young", high site index stands because they may be growing less vigorously. Older, low site index stands are more likely to have experienced cross-adaptive stress events, and therefore, have lower vulnerability to JPBW impact than older, high site index stands.

Another possible explanation is that the most vulnerable trees in older, low site index stands have succumbed to previous stress or defoliation during previous JPBW outbreaks and died before the 1991-1993 JPBW outbreak. This would result in lower vulnerability to JPBW impact in the stand as a whole.

Based on the positive association between standing value loss and age, and the greater mean, median, and mean rank of standing value loss in "old" stands (Table 3-5), I can conclude that management recommendations to eliminate overmature stands through harvesting and shorter rotations are appropriate from a financial perspective. A number of other workers have come to similar conclusions (Albers et al. 1995; Jones and Campbell 1986; McCullough et al.

1994; Nyrop et al. 1983; Rose 1973; Rose 1974; Weber 1986; Weber 1995; Williams and Nautiyal 1992). My results indicate that stands over 50 years old accounted for over 75% of the reduction in total standing value due to the 1991-1993 JPBW outbreak. Obviously, had these stands been on shorter rotations, I would most likely have observed notably lower value losses. I believe that stand age is the most important factor to be considered in the management of JPBW impact because operationally, forest managers have more control over rotation lengths than over site quality or stand density.

The management recommendation to select higher quality sites for jack pine stands may need to be reconsidered. Standing value loss was positively associated with site index, and stands with site index over 15.2 m (50 ft) accounted for over 80% of the total standing value loss. In addition, older stands experienced greater standing value loss on high site index sites than on low site index stands.

Other studies have found that impact from forest insect pests may be site dependent. For example, tree mortality of oak species (*Quercus* spp.) defoliated by a native looper complex in the central and southern Appalachians (Crow and Hicks 1990) and defoliated by gypsy moth (*Lymantria dispar* L.) in Pennsylvania (Quimby 1987) was higher on better quality sites than on poorer quality sites. Another study to predict susceptibility to gypsy moth defoliation found that while stands on dry ridges and sands sustained more frequent defoliation events (i.e., higher susceptibility), these stands were less likely to sustain high mortality than stands on mesic slopes and bottom sites (i.e., lower vulnerability) (Houston and Valentine 1977).

Trees on higher quality sites may have higher foliar nitrogen levels, which are positively associated with JPBW larval survival on young jack pine (McCullough and Kulman 1991a; McCullough and Kulman 1991b). Also, higher soil nitrogen levels have been shown to stimulate pollen cone production (McCullough and Kulman 1991b), which in turn may increase JPBW survival (Nealis and Loomic 1994).

I observed no significant differences in standing value loss among poor, well, and overstocked stands. However, I did observe a positive association between standing value loss and basal area. While it is difficult to comment on the appropriateness of the 16.1-25.3 m^2/ha (70-110 ft^2/ac) basal area recommendation or on the efficacy of silvicultural management of stand density (i.e., thinnings, optimal planting densities, etc.), I can conclude that higher density stands are likely to be carrying more timber volume and value than low density stands. Therefore, the highest density stands are likely to suffer the greatest absolute loss following a JPBW outbreak. For the forest manager concerned with minimizing timber loss, this means that the highest density stands should be given management priority for harvest scheduling, salvage, or cover-type conversion.

Related to stand density is the issue of the presence or abundance of suppressed trees and wolf trees in the stand, and effects of these trees on the merchantable volume and value loss in the stand. I found no significant differences in standing value loss among stands with few and abundant suppressed trees and only a slight positive association between standing value loss and the proportion of suppressed trees in the stand. These results suggest that suppressed trees have relatively little importance from a management perspective. While suppressed trees may suffer disproportionate impact or act as refugia for JPBW (Batzer and Jennings 1980; Kulman et al. 1963), their presence in the stand does not appear to adversely affect the volume or value loss in the stand. Managers should probably give a low priority to management operations designed to eliminate or reduce suppressed trees such as non-commercial thinnings from below or planting or seeding activities that ensure even spacing. The presence of wolf trees in the stand was negatively associated with standing value loss, and significantly more standing value was lost in stands with no wolf trees. This reinforces our previous conclusion that low density stands (i.e., stands likely to contain wolf trees) should be given the lowest management priority for harvest scheduling, salvage, or cover type conversion.

Conclusions

The 1991-1993 JPBW outbreak eliminated an average of 14% (13.3 m^3/ha) of the standing merchantable volume, valued at $289,000, from the jack pine stands in four management compartments in the Raco Plains area. The average standing value loss for these stands was $194/ha.

Standing value loss was observed to be positively associated with age, basal area, and to a lesser extent, site index and the proportion of suppressed trees in the stand. These associations were probably the result of higher absolute volume and value and higher tree mortality and growth loss in these stands. Standing value loss was negatively associated with wolf tree proportion, but this pattern may be more a reflection of stocking than of lower impact to wolf trees.

With regard to management recommendations, I can conclude that standing value loss can be reduced by harvesting overmature stands and shortening rotation ages to less than 50 years. Low quality sites, once intuitively considered inappropriate for jack pine stands, may actually produce stands that are less vulnerable to JPBW impact. The observed interaction between age and site index lends support to our theory about the increased stress tolerance of trees growing on low quality sites. Management priority should be given to the highest density stands and attempts should be made to reduce the occurrence of overstocked stands. Finally, the abundance of suppressed trees in the stand did not seem to adversely affect standing value loss. Reduction or elimination of these trees should probably be given low priority.

CHAPTER 4

CONCLUSIONS, LIMITATIONS, AND FUTURE RESEARCH

Conclusions

From 1991-1993, a jack pine budworm (*Choristoneura pinus pinus* Freeman) outbreak occurred in the Raco Plains area of the Hiawatha National Forest in the Upper Peninsula of Michigan. Moderate to severe defoliation occurred during this outbreak in most jack pine (*Pinus banksiana* Lamb.) stands in the Raco Plains area. This research project was performed to evaluate and quantify the impact in the form of top-kill, tree mortality, growth loss, merchantable volume loss, and financial value loss that resulted from the 1991-1993 jack pine budworm (JPBW) outbreak in the Raco Plains area.

Top-kill and Tree Mortality

Top-kill accumulated rapidly following the onset of defoliation, increasing from a stand-level mean of 5% in 1992 to 19% in 1993. Top-kill appeared to have leveled off with a mean of 18% in 1996. Tree mortality that resulted from the 1991-1993 outbreak accumulated more slowly than top-kill, averaging only 1% in 1992 and increasing to a stand-level average of 16% in 1995.

In 1996, 70% of all top-killed trees in these stands were dominant/ codominant crown class trees. Proportionally fewer top-killed trees were intermediate (16%) or suppressed (14%). One-third of the intermediate trees in the sample stands and one-half of the suppressed trees in the sample stands had died presumably as a result of the 1991-1993 JPBW outbreak. Mortality in the sample stands was approximately equally distributed among suppressed, intermediate, and dominant/codominant crown classes.

Top-kill was greater in "old" stands (≥ 50 years old) than in "young" stands (< 50 years old). Tree mortality was greater in "old" stands (≥ 50 years old) than in "young" stands (< 50 years old), in high site index stands (≥ 15.2 m) than in low site index stands (< 15.2 m), and in well stocked (1,300-1,734 TPH, 16.1-25.3 m^2/ha) or overstocked stands (> 1,734 TPH, > 25.3 m^2/ha) than in poorly stocked stands (< 1,300 TPH, < 16.1 m^2/ha). Mortality was also greater in stands where wolf trees were absent than in stands where wolf trees were present.

Growth Loss

The pattern of growth of the jack pine trees in the Raco Plains area shows distinct, periodic reductions in growth attributable to defoliation during JPBW outbreaks. Tree growth patterns and Annual Forest Pest Reports published by the Michigan Department of Natural Resources indicate that five JPBW outbreaks have occurred in this area since 1953. Trees that survived the 1991-1993 outbreak showed significantly reduced growth in 1992 and 1993 compared to pre-outbreak growth levels but recovered to pre-outbreak growth levels in 1994. Average growth of top-killed trees was similar to average growth of surviving trees until 1993. From 1993 through 1995, however, average growth of top-killed trees was significantly less than average growth of surviving trees.

Top-killed trees had not recovered to pre-outbreak growth levels by 1995. Average growth of trees that died as a result of the 1991-1993 JPBW outbreak was significantly less than average growth of either surviving or top-killed trees in all years after 1989.

Growth of surviving and top-killed trees during the 1991-1993 outbreak was significantly greater in trees from "young" stands (< 50 years old) than in trees from "old" stands (≥ 50 years old). Tree growth was not significantly affected by site index or stand basal area.

Merchantable Volume and Financial Value Loss

Total standing merchantable volume loss resulting from the 1991-1993 JPBW outbreak in the 1,480 ha (3,600 ac) sample area was estimated to be 19,500 m^3 (8,200 cds). On average, standing merchantable volume loss for the 99 sample stands was 13.3 m^3/ha (2.3 cds/ac) or 14% of standing volume. Total standing value loss was estimated to be $289,800. Average standing value loss for the 99 sample stands was $194/ha ($78/ac).

Standing value losses that resulted from the 1991-1993 JPBW outbreak were concentrated in only a few stands. Only eight stands (23% of the area) accounted for over half the total standing value loss ($145,400).

Standing value loss was greater in "old" stands (≥ 50 years old) than in "young" stands (< 50 years old) and in high site index stands (≥ 15.2 m) than in low site index stands (< 15.2 m). Stands where wolf trees were absent sustained lower standing value loss than stands where wolf trees were present.

Management Recommendations

Current JPBW management recommendations in the Lake States include shortening rotation lengths and harvesting overmature stands (older than 50-55 years), favoring high quality sites (site index over 15.2 m), and maintaining proper stocking (16.1-25.3 m^2/ha basal area) (Albers et al. 1995; Jones and Campbell 1986; McCullough et al. 1994; Weber 1986; Weber 1995).

Stand age was clearly an important factor affecting JPBW impact. Reducing rotation length and harvesting overmature jack pine is, perhaps, the single most important objective for forest managers. The oldest stands should be given the highest priority for management such as harvest or salvage.

Both tree mortality and standing value loss were greater on higher quality sites, an unexpected result given long-held assumptions that trees on low quality sites should be more vulnerable to JPBW impact. There are some compelling physiological reasons that favor revising the management recommendation to favor high quality sites for jack pine. However, the consistency of this relationship must be validated with data from other areas.

Poorly stocked stands sustained lower tree mortality than did well or overstocked stands. The management recommendation to eliminate overstocked stands seems valid, and the highest density stands should be prioritized for management.

Although suppressed trees suffered disproportionately high rates of mortality, there was no clear association between the relative abundance of suppressed trees and overall impact in the stand. Practices designed to reduce the abundance of suppressed trees will probably have little effect on reducing the volume and value loss of stands sustaining severe defoliation.

Tree mortality and standing value loss were negatively associated with the abundance of wolf trees, and poorly stocked stands sustained relatively low tree mortality. Due to the low volume and low JPBW impact, I suggest that poorly stocked stands be given low priority for salvage, harvest, or related silvicultural activity.

Limitations

One of the most important limitations of this research project was that the primary focus was on impact to timber in the Raco Plains area. No attempt was made to address the ecological consequences of the 1991-1993 JPBW outbreak. Ecological effects of a JPBW outbreak go far beyond reduction to jack pine timber volume observed in this study. JPBW is a native insect that co-evolved with its host, and as such, it may regulate, or even increase, forest productivity over time. JPBW feeding activity plays an important role in nutrient cycling in jack pine forests. JPBW defoliation often creates wildlife habitat trees, and JPBW larvae may also provide an important food source to wildlife species.

Another limitation of this study is that our estimates of impact following the 1991-1993 JPBW outbreak are probably conservative. From 1992-1996, the USDA Forest Service harvested jack pine from 15 stands in the study management compartments (Heym et al. 1993). These stands were cut to limit timber losses associated with the outbreak, and the stands selected for harvest were those the Forest Service believed to be the most vulnerable to impact

(Heym et al. 1993). If these stands suffered heavy impact, then the 1996 data likely underestimated the true volume and financial losses attributable to the 1991-1993 JPBW outbreak.

Other limitations of this study relate to the methods I used to quantify the financial impact of the 1991-1993 JPBW outbreak. In the estimation of projected value losses, I considered only a single JPBW outbreak. Projected value loss estimates would have been considerable different had I more realistically considered multiple JPBW outbreaks likely to occur over the course of a rotation. Costs were not include in the financial value estimation due to difficulty I encountered trying to quantify costs at the stand-level.

Future Research

The patterns of impact that are presented in this thesis are the result of a single JPBW outbreak in one 1,480 ha area. Extension of the results and recommendations from this study to other areas should be made cautiously. Patterns identified in this study should be validated for other JPBW outbreaks and in other jack pine forests, to evaluate the consistency and applicability of the conclusions and recommendations presented here.

Although validation and perhaps, modification of the patterns and recommendations is in order, the information presented in this study can be used to develop tools that will aid forest managers in the decision-making process. Decision support systems can be very useful in forest planning, timber supply projection, and management resource allocation.

There are still a number of areas related to the biology of the JPBW that are poorly understood and should be addressed in future research. The release phase of the JPBW population cycle is not well understood. For example, it is apparent that abundant jack pine pollen cones are associated with JPBW outbreaks, but we still do not understand factors the regulate pollen cone production or why pollen cones tend to be more abundant in some years and on some trees.

It was assumed throughout this study was that the dramatic increase in tree mortality I recorded was the direct result of defoliation during the 1991-1993 JPBW outbreak. While certainly defoliation was a factor in high mortality rate observed in the Raco Plains area, it was presumably not the only factor involved. Relationships between JPBW defoliation and susceptibility and vulnerability to pathogens, such as *Armillaria* root rot (*Armillaria* spp.) or pine gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka (=*Peridermium harknessii* J.P. Moore)), and secondary insect pests, such as pine engraver beetle (*Ips pini* Say).

APPENDICES

APPENDIX A

APPENDIX A

Research Note

While growth loss and tree mortality are obviously important components of timber volume loss, some debate exists over the importance of top-kill (Kulman et al. 1963; Hall et al. 1993; Gross and Meating 1994). It was apparent from our data that rarely does the dead wood in the top-killed portion of the stem reduce the amount of merchantable volume in the tree. Less than 1% of the 395 top-killed trees sampled in 1996 had a top-kill margin below the 10 cm (4 in) diameter merchantable limit. Nonetheless, there is some evidence suggesting that top-kill may be an important contributing factor in subsequent tree mortality (Kulman et al. 1963; Gross and Meating 1994; Mallett and Volney 1990). Also, top-kill may increase susceptibility of the tree to other damaging insects or pathogens by providing an infection court. Top-kill may cause young trees to develop poor crown form with crooked or multiple leaders, and loss of apical dominance may severely impact the future growth of the tree. However, other workers who assessed reductions in merchantable volume due to the JPBW concluded that the reduction in merchantable volume due to top-kill was negligible (Gross and Meating 1992). More research is needed to determine how top-kill affects tree growth, survival, susceptibility to secondary pathogens, and vulnerability to JPBW.

APPENDIX B

APPENDIX B

Measurement Conversions

Table B-1 – Metric - English conversion table.

Metric	English
Length	
1 m	3.281 ft
Area	
1 m^2	10.76 ft^2
1 ha	2.477 ac
1 m^2/ha	4.346 ft^2/ac
Volume	
1 m^3	35.32 ft^3
1 m^3	0.4205 cds
1 m^3/ha	14.26 ft^3/ac
1 m^3/ha	0.1698 cds/ac
Site Index	
15.2 m	50 ft
Basal Area	
16.1 m^2/ha	70 ft^2/ac
25.3 m^2/ha	110 ft^2/ac
Trees per Unit Area	
1300 TPH[a]	525 TPA[b]
1734 TPH	700 TPA

[a] Trees per hectare
[b] Trees per acre

LIST OF REFERENCES

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Albers, J., Carroll, M., and Jones, A. 1995. Jack pine budworm in Minnesota: past trends and changing perspectives. *In* Jack Pine Budworm Biology and Management: Proc. of the Jack Pine Budworm Symp., Jan. 1995, Winnipeg, Man. *Edited by* W.J.A. Volney, V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley. Can. For. Serv. Inf. Rep. NOR-X-342. pp. 11-18.

Alfaro, R.I., Van Sickle, G.A., Thomson, A.J., and Wegwitz, E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12: 780-787.

Batzer, H.O., and Jennings, D.T. 1980. Numerical analysis of a jack pine budworm outbreak in various densities of jack pine. Environ. Entomol. 9: 514-534.

Benzie, J.W. 1977. Manager's handbook for jack pine in the North Central states. USDA For. Serv. Gen. Tech. Rep. NC-32. 18 p.

Buchman, R.G., Pederson, S.P., and Walters, N.R. 1983. A tree survival model with application to species of the Great Lakes region. Can. J. For. Res. 13: 601-608.

Bush, R.R., and Brand, G. 1995. The Lake States TWIGS Variant of the Forest Vegetation Simulator. USDA For. Serv. Fort Collins, CO. 29 p.

Carmean, W.H. 1975. Forest site quality evaluation in the United States. Adv. Agron. 27: 209-269.

Carmean, W.H., and Lenthall, D.J. 1989. Height-growth and site-index curves for jack pine in north central Ontario. Can. J. For. Res. 19: 215-224.

Cayford, J.H. 1970. The role of fire in the ecology and silviculture of jack pine. Proc. 10th Ann. Tall Timbers Fire Ecol. Conf., Oct. 1970, Tall Timbers Research Station, Tallahassee, FL. pp. 221-224.

Cerezke, J.H. 1986. Impact studies of the jack pine budworm, *Choristoneura pinus pinus*, in Nisbet Provincial Forest, Saskatchewan. *In* Jack Pine Budworm Information Exchange, Jan. 1986, Winnipeg, Man. Manitoba Natural Resources, Forest Protection Branch, Winnipeg, Man. pp. 25-38.

Clancy, K.M., Giese, R.L., and Benjamin, D.M. 1980. Predicting jack-pine budworm infestations in northwestern Wisconsin. Environ. Entomol. 9: 743-751.

Clancy, K.M., Wagner, M.R., and Reich, P.B. 1995. Ecophysiology and insect herbivory. *In* Ecophysiology of Coniferous Forests. Academic Press, San Diego, CA. pp. 125-180.

Crow, G.R., and Hicks, R.R. 1990. Predicting mortality in mixed oak stands following spring insect defoliation. For. Sci. 36: 831-841.

Duff, G.H., and Nolan, N.J. 1957. Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in *Pinus resinosa* Ait. Can. J. Bot. 35: 527-572.

Foltz, J.L., Knight, F.B., and Allen, D.C. 1972. Numerical analysis of population fluctuations of the jack pine budworm. Ann. Entomol. Soc. Am. 65: 82-89.

Graham, S.A. 1935. The spruce budworm on Michigan pine. University of Michigan, School of Forestry and Conservation, Ann Arbor, MI. Bull. No. 6, 56 p.

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. Can. J. For. Res. 22: 818-831.

Gross, H.L., and Meating, J.H. 1994. Impact of the 1982-1986 jack pine budworm infestation on jack pine in northeastern Ontario. Can. For. Serv., Ont. Reg., Great Lakes For. Cent. Inf. Rep. O-X-431. 19 p.

Guay, R., Gagnon, R., and Morin, H. 1992. A new automatic and interactive tree ring measurement system based on a line scan camera. For. Chron. 68: 138-141.

Haack, R.A. 1993. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae): biology, management considerations, and data gaps. *In* Proceedings of the 9th Central Hardwoods Forest Conference, Mar. 1993, West Lafayette, IN. *Edited by* A.R. Gillespie, G.R. Parker, P.E. Pope, and G. Rink. USDA For. Serv. Gen. Tech. Rep. NC-161. pp. 83-100.

Hackett, R.L., and Piva, R.J. 1994. Pulpwood production in the North-Central region, 1992. USDA For. Serv. Res. Bull. NC-159. 41 p.

Hall, R.J., Titus, S.J., and Volney, W.A.J. 1993. Estimating top-kill volumes with large-scale photos on trees defoliated by the jack pine budworm. Can. J. For. Res. 23: 1337-1346.

Hodson, A.C., and Zehngraff, P.J. 1946. Budworm control by forest management. J. For. 44: 198-200.

Hopkin, A.A., and Howse, G.M. 1995. Impact of the jack pine budworm in Ontario: a review. *In* Jack Pine Budworm Biology and Management: Proc. of the Jack Pine Budworm Symp., Jan. 1995, Winnipeg, Man. *Edited by* W.J.A. Volney, V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley. Can. For. Serv. Inf. Rep. NOR-X-342. pp. 111-120.

Houston, D.R., and Valentine, H.T. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. Can. J. For. Res. 7: 447-461.

Howse, G.M. 1984. Insect pests of jack pine: biology, damage and control. *In* Jack Pine Symposium, Oct. 1983, Timmins, Ont. *Edited by* C.R. Smith and G. Brown. Can. For. Serv. Great Lakes For. Res. Cent. COJFRC Symp. Proc. O-P-12. pp. 131-138.

Howse, G.M. 1986. Jack pine budworm in Ontario. *In* Jack Pine Budworm Information Exchange, Jan. 1986, Winnipeg, Man. Manitoba Natural Resources, Forest Protection Branch, Winnipeg, Man. pp. 47-50.

Heym, D., Evans, D.J., Katovich, S., Keach, K., Kurz, T., Lanasa, M., Miller, M., and Whitcomb, L. 1993. Raco Plains jack pine ecosystem project. USDA For. Serv., Sault Ste. Marie Ranger District, Hiawatha National Forest. Sault Ste. Marie, MI. Project Report. 231 p.

Ibrahim, L., Proe, M.F., and Cameron, A.D. 1997. Main effects of nitrogen supply and drought stress upon whole-plant carbon allocation in poplar. Can. J. For. Res. 27: 1413-1419.

Johnson, J.D. 1987. Stress physiology of forest trees: the role of plant growth regulators. Plant Growth Regulation 6: 193-215.

Jones, A.C., and Campbell, J. 1986. Jack pine budworm: the Minnesota situation. *In* Jack Pine Budworm Information Exchange, Jan. 1986, Winnipeg, Man. Manitoba Natural Resources, Forest Protection Branch, Winnipeg, Man. pp. 7-9.

Kouki, J., McCullough, D.G., and Marshall, L.D. 1997. Effects of forest stand and edge characteristics on the vulnerability of jack pine stands to jack pine budworm (*Choristoneura pinus pinus*) damage. Can. J. For. Res. 27: 1765-1772.

Kulman, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16: 289-325.

Kulman, H.M., Hodson, A.C., and Duncan, D.P. 1963. Distribution and effects of jack pine budworm defoliation. For. Sci. 9: 146-157.

Laurence J.A., Amundson, R.G., Friend, A.L., Pell, E.J., and Temple, P.J. 1994. Allocation of carbon in plants under stress: an analysis of the ROPIS experiments. J. Environ. Qual. 23: 412-417.

Lehmann, E.L. 1975. Nonparametrics: Statistical Methods Based on Ranks. Holden-Day, San Francisco, CA. 457 p.

LeJeune, R.R. 1950. Effect of jack-pine staminate flowers on the size of larvae of the jack-pine budworm *Choristoneura* sp. Can. Entomol. 82: 34-43.

LeJeune, R.R., and Black, W.F. 1950. Populations of larvae of the jack pine budworm. For. Chron. 26: 1-5.

Levene, H. 1960. Robust tests for equality of variance. *In* Contributions to Probability and Statistics. Stanford University Press, Palo Alto, CA. pp. 278-292.

Little, C.H.A., and Savidge, R.A. 1987. The role of plant growth regulators in forest tree cambial growth. Plant Growth Regulation 6: 137-169.

Lysyk, T.J., and Nealis, V.G. 1988. Temperature requirements for development of the jack pine budworm (Lepidoptera: Tortricidae) and two of its parasitoids (Hymenoptera). J. Econ. Entomol. 81: 1045-1051.

MacAloney, H.J. 1944. Relation of root condition, weather, and insects to the management of jack pine. J. For. 42: 124-129.

MacLean, D.A. 1990. Impact of forest pests and fire on stand growth and timber yield: implications for forest management planning. Can. J. For. Res. 20: 391-404.

MacLean, D.A., and Porter, K.B. 1996. Role of forest inventory projection in the spruce budworm decision support system. *In* Decision Support Systems for Forest Pest Management: Proceedings of a Workshop at the Joint Meeting of the Entomological Societies of Canada and British Columbia, Oct. 1995, Victoria, BC. Can. *Edited by* T.L. Shore and D.A. MacLean. For. Serv. FRDA Rep. No. 260. pp. 15-24.

Mallett, K.I. 1995. Relationships among *Armillaria* root disease, jack pine budworm, and jack pine forest ecosystems. *In* Jack Pine Budworm Biology and Management: Proc. of the Jack Pine Budworm Symp., Jan. 1995, Winnipeg, Man. *Edited by* W.J.A. Volney, V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley. Can. For. Serv. Inf. Rep. NOR-X-342. pp. 107-110.

Mallett, K.I., and Volney, W.J.A. 1990. Relationships among jack pine budworm damage, selected tree characteristics, and *Armillaria* root rot in jack pine. Can. J. For. Res. 20: 1791-1795.

Mattson, W.J., Jr., and Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. Science (Washington, D.C.), 190: 515-522.

McCullough, D.G., and Kulman, H.M. 1991a. Differences in foliage quality of young jack pine (*Pinus banksiana* Lamb.) on burned and clearcut sites: effects on jack pine budworm (*Choristoneura pinus pinus* Freeman). Oecologia. 87: 135-145.

McCullough, D.G., and Kulman, H.M. 1991b. Effects of nitrogen fertilization on young jack pine (*Pinus banksiana* Lamb.) and on its suitability as a host for the jack pine budworm (*Choristoneura pinus pinus* Freeman). Can. J. For. Res. 21: 1447-1458.

McCullough, D.G., Katovich, S., Heyd, R.L., and Weber, S. 1994. How to manage jack pine to reduce damage from jack pine budworm. USDA For. Serv. NA-FR-01-94. 10 p.

McCullough, D.G., Marshall, L.D., and Buss, L. 1995. Effects of stand age and site index on jack pine budworm damage in the Raco Plains area of Michigan. *In* Jack Pine Budworm Biology and Management: Proc. of the Jack Pine Budworm Symp., Jan. 1995, Winnipeg, Man. *Edited by* W.J.A. Volney, V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley. Can. For. Serv. Inf. Rep. NOR-X-342. pp. 97-105.

McCullough, D.G., Marshall, L.D., Buss, L.J., and Kouki, J. 1996. Relating jack pine budworm damage to stand inventory variables in northern Michigan. Can. J. For. Res. 26: 2180-2190.

Miner, C.L., Walters, N.R., and Belli, M.L. 1988. A guide to the TWIGS program for the North Central United States. USDA For. Serv. Gen. Tech. Rep. NC-125. 105 p.

Nealis, V.G. 1990. Jack pine budworm populations and staminate flowers. Can. J. For. Res. 20: 1253-1255.

Nealis, V.G., and Lomic, P.V. 1994. Host-plant influence on the population ecology of the jack pine budworm, *Choristoneura pinus* (Lepidoptera: Tortricidae). Ecol. Entomol. 19: 367-373.

Nyrop, J.P., Olson, J.T., Mosher, D.G., and Simmons, G.A. 1983. Simulation of how jack pine budworm (Lepidoptera: Tortricidae) affects economic returns from jack pine timber production in Michigan. Great Lakes Entomol. 16: 157-165.

O'Neil, L.C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamb.). Can. J. Bot. 40: 273-280.

O'Neil, L.C. 1963. The suppression of growth rings in jack pine in relation to defoliation by the swaine jack-pine sawfly. Can. J. Bot. 41: 227-235.

Premo, D.B., Rogers, E.I., Apfelbaum, S.I., and Premo, K.F. 1994. A review of information on the federally endangered Karner blue butterfly *Lycaeides melissa samuelis* Nabokov (Lepidoptera: Lycaenidae). White Water Associates, Inc. Amasa, MI. Project Report. 80 p.

Quimby, J.W. 1987. Impact of gypsy moth defoliation on forest stands. *In* Coping With the Gypsy Moth, Symposium Proceedings of a Workshop for Forest Managers, Aug. 1987, Morgantown, WV. pp. 21-29.

Rauf, A., Benjamin, D.M., and Cecich, R.A. 1985. Insects affecting seed production of jack pine, and life tables of conelet and cone mortality in Wisconsin. For. Sci. 31: 271-281.

Rawat, J.K., Belli, K.L., Smith, S.M., and Nautiyal, J.C. 1987. A pest and timber management model: jack pine budworm and jack pine. Can. J. Agric. Econ. 35: 441-461.

Rose, D.W. 1973. Simulation of jack pine budworm attacks. J. Environ. Mgmt. 1: 259-276.

Rose, D.W. 1974. Economic implications of stocking and budworm attacks for jack pine management. Can. J. For. Res. 4: 349-360.

Row, C., Kaiser, H.F., and Sessions, J. 1981. Discount rate for long-term forest service investments. J. For. 79: 367-369.

Rudolph, T.D., and Laidly, P.R. 1990. *Pinus banksiana*, Lamb. - jack pine *In* Silvics of North America. Vol. 1. Conifers. R.M. Burns and B.H Honkala eds. Agric. Handbook 654. USDA For. Serv. Washington, D.C. 280-293.

Savidge, R.A. 1988. Auxin and ethylene regulation of diameter growth in trees. Tree Physiol. 4: 401-414.

Shea, S.R., and Armson, K.A. 1972. Stem analysis of jack pine (*Pinus banksiana* Lamb.): techniques and concepts. Can. J. For. Res. 2: 392-406.

Smith, D.M. 1986. The Practice of Silviculture. 7th ed. John Wiley & Sons, New York, NY. 527 p.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. 3rd ed. W.H. Freeman and Company, New York, NY. 887 p.

Teck, R. 1995. Forest Vegetation Simulator Submittal System Users Guide. USDA For. Serv. WO Timber Management Unit. Fort Collins, CO. 122 p.

Thomson, A.J., and Van Sickle, G.A. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10: 176-182.

USDA Forest Service. 1986. Final Environmental Impact Statement. Land and Resource Management Plan. Hiawatha National Forest. 189 p.

Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res. 8: 220-227.

Volney, W.J.A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. Can. J. For. Res. 18: 1152-1158.

Volney, W.J.A., and Mallett, K.I. 1992. Light rings and the age of jack pine trees. Can. J. For. Res. 22: 2011-2013.

Volney, W.J.A., and McCullough, D.G. 1994. Jack pine budworm population behaviour in northwestern Wisconsin. Can. J. For. Res. 24: 502-510.

Weber, S.D. 1986. Jack pine management. *In* Jack Pine Budworm Information Exchange, Jan. 1986, Winnipeg, Man. Manitoba Natural Resources, Forest Protection Branch, Winnipeg, Man. pp. 12-14.

Weber, S.D. 1995. Integrating budworm into jack pine silviculture in Northwest Wisconsin. *In* Jack Pine Budworm Biology and Management: Proc. of the Jack Pine Budworm Symp., Jan. 1995, Winnipeg, Man. *Edited by* W.J.A. Volney, V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley. Can. For. Serv. Inf. Rep. NOR-X-342. pp. 19-24.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press, Cambridge, United Kingdom. 346 p.

Williams, J.S., and Nautiyal, J.C. 1992. Integrating budworm and timber management: comparing preventative versus remedial strategies. Nat. Res. Model. 6: 409-433.

Wenger, K.L. 1984. Forestry Handbook. 2nd ed. John Wiley & Sons, New York, NY. 1335 p.

Wright, H.A., and Bailey, A.W. 1982. Fire Ecology, United States and Southern Canada. John Wiley & Sons, New York, NY. 501 p.