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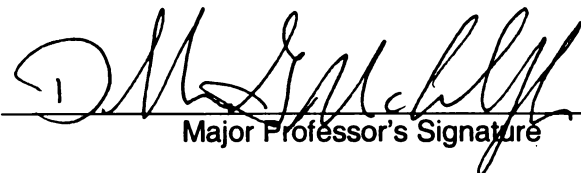
THE JACK PINE RESOURCE IN MICHIGAN: AN
ASSESSMENT OF VOLUME, GROWTH, MORTALITY, AND
COARSE WOODY DEBRIS

presented by

Andrew Thomas Klein

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THE JACK PINE RESOURCE IN MICHIGAN: AN ASSESSMENT OF VOLUME,
GROWTH, MORTALITY, AND COARSE WOODY DEBRIS

By

Andrew Thomas Klein

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Forestry

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ABSTRACT

THE JACK PINE RESOURCE IN MICHIGAN: AN ASSESSMENT OF VOLUME, GROWTH, MORTALITY, AND COARSE WOODY DEBRIS

By

Andrew Thomas Klein

Jack pine (*Pinus banksiana* Lambert.) is economically and ecologically important in the Lake States region and throughout much of Canada. The current state of the jack pine resource was assessed in six regions in Michigan and one region in Wisconsin by quantifying standing live and dead volume, mortality, top-kill, annual radial growth patterns, and coarse woody debris volume in one 0.01 ha circular plot per stand. Overall, live and dead volume was higher on state land in the western Upper Peninsula of Michigan than in the other six surveyed regions averaging 448.5 m³/ha live volume and 68.4 m³/ha dead volume. Accumulation of coarse woody debris volume was highest in the Ottawa National Forest (64.2 m³/ha) and the Huron-Manistee National Forest (60.1 m³/ha). Stand age had the most consistent relationship with all variables except radial growth rates across all regions. Stands 50+ yrs old generally had higher levels of standing volume, more mortality, and higher accumulation of coarse woody debris volume than younger stands. Under-stocked stands had less volume, mortality, and lower amounts of coarse woody debris volume than well-stocked or over-stocked stands. Patterns among standing volume, mortality, radial growth rates, and site index were unclear within regions. Among crown classes, mortality was generally higher in intermediate and suppressed trees than dominant trees. However, more dead volume was concentrated in dominant trees than in intermediate or suppressed trees.

To my Mom, Judy Kay Klein
(1954 – 1995)

ACKNOWLEDGEMENTS

I would like to thank Dr. Deborah G. McCullough and Dr. Larry A. Leefers for their patience, guidance, and friendship during the course of this study. I would also like to thank my graduate committee member, Dr. Donald I. Dickmann. Other thanks go towards Dr. Daniel Keathley, Chairperson of the Dept. of Forestry at Michigan State University, who provided appreciated advice and encouragement, and to other faculty members in the Dept. of Forestry who provided welcome encouragement, especially Dr. Michael Walters and Dr. Karen Potter-Witter. I am grateful to field cooperators who provided assistance with gathering compartment maps and stand inventory data used to locate research plots. Special thanks go to Bob Heyd, Les Homan and Roger Mech with the Michigan Department of Natural Resources, Doug Born, Larry Melstrom, Charlotte Bofinger, Quent McNichols, Steve Katovich, and Linda Haugen with the USDA Forest Service, and Tim Beyer with the Wisconsin Department of Natural Resources. I would also like to thank Dr. Raymond Miller, and everyone at the Upper Peninsula Tree Improvement Center for their assistance in measuring annual radial growth data. Finally, I need to thank my family, who have all been there when I needed them throughout this project. Special thanks go to my fiancée Elizabeth McDonald, my daughter Emma Klein, and my Dad, Bill Klein. They have given me tremendous support, encouragement, and love in the last three years, which has been greatly appreciated. Funding for this study was provided by the USDA Forest Service PTIPS program.

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INTRODUCTION

Thesis Objectives

Baseline data was collected from jack pine (*Pinus banksiana* Lambert.) stands to assess the current state of jack pine in northern Michigan and Wisconsin to establish a framework to monitor long-term impacts of jack pine budworm (*Choristoneura pinus pinus* Freeman) (JPBW), an important defoliator of jack pine. The long-term goal for collection and analysis of this data is to validate and modify an existing jack pine management model, the Lake States Jack Pine Budworm Decision Support System (Conway et al. 1998), which was developed from empirical data collected in the Raco Plains area of the Hiawatha National Forest in the eastern Upper Peninsula of Michigan (Conway et al. 1999a; Conway et al. 1999b; McCullough et al. 1996). This study is the first to quantify and compare stand-level impact data among several different regions in the Lake States area.

The overall objectives of this study were to:

1. Establish a network of permanent plots across seven regions in Michigan and Wisconsin to gather baseline data to assess the current state of jack pine and monitor long-term impacts of JPBW defoliation.
2. Quantify jack pine mortality, top-kill, standing volume, annual radial growth rates, and accumulation of coarse woody debris among surveyed regions of jack pine. These variables were of interest, because they could be affected by JPBW defoliation.

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3. Evaluate relationships between site and stand variables (tree age, stand age, site index, and basal area), and jack pine mortality, top-kill, standing volume, annual radial growth rates, and accumulation of coarse woody debris.

Specific hypotheses are as follows, and each is given as a research hypothesis:

H₁: Jack pine mortality, top-kill, standing volume, annual radial growth rates, and accumulation of coarse woody debris differ among the seven surveyed regions in Michigan and Wisconsin.

H₂: Jack pine mortality, standing volume, annual radial growth rates, and accumulation of coarse woody debris are related to tree, stand, and site variables within the seven surveyed regions in Michigan and Wisconsin.

H₃: Relationships between jack pine mortality, standing volume, annual radial growth rates, and accumulation of coarse woody debris and tree, stand, and site variables differ among the seven surveyed regions in Michigan and Wisconsin.

Thesis Organization

This thesis is divided into three chapters. Some repetition may occur in each chapter, particularly the introduction and methods sections. In the first chapter, standing live volume, mortality, top-kill, and standing dead volume are quantified and compared among regions. All impact variables, excluding top-kill, are examined in relation to tree and stand characteristics within regions, and relationships between live and dead volume and stand variables, land ownership, and regional location are assessed. The second chapter describes patterns of annual radial growth, and compares those patterns among regions. Annual radial growth data is then examined in relation to tree and stand characteristics within regions. In

the third chapter, accumulation, size, and decay level of coarse woody debris volume are quantified and compared among regions, and then examined in relation to stand age and basal area. The major results for this study and areas for future research of the impact and management of the JPBW in the Lake States are presented in a concluding chapter. Finally, Appendix A lists the geographical and plot center locations in all seven surveyed regions, while Appendix B lists measurement conversions related to this study.

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CHAPTER 1

AN ASSESSMENT OF MORTALITY, TOP-KILL, AND STANDING LIVE AND DEAD VOLUME IN MICHIGAN AND WISCONSIN JACK PINE STANDS

Introduction

Jack pine (*Pinus banksiana* Lambert) is an important resource in the Great Lakes region of the U.S. and throughout much of Canada. In Michigan and Wisconsin, jack pine forests occur on nearly 485,000 ha (1.2 million acres) (Piva 1997). Jack pine is a rapid colonizer in early forest succession, tolerates relatively poor, sandy soils, and has qualities desirable for the commercial pulpwood industry (Rudolph and Laidly 1990). Jack pine forests provide habitat for game and non-game species, including the endangered Kirtland's Warbler (*Dendroica kirtlandii*), and also provide recreational opportunities such as hunting, camping, and bird watching (Benzie 1977). More than 270,000 cords of jack pine are annually harvested for wood fiber, amounting to a stumpage value of nearly \$10.1 million (USDA-Forest Service 2002). Management intensity in jack pine forests has escalated because of the enhanced economic value of jack pine pulp, which sold at roughly \$4/cord in 1991 and \$35/cord in 2002 (McCullough and Leefers 2000; USDA-Forest Service 2002), leading to more emphasis on optimization of harvest rotations.

In northern Michigan and Wisconsin, jack pine forests experience multiple natural disturbances, such as wind, heavy snow, or fire, which can injure trees or cause tree death. At present, major fires occur at approximate 30 year intervals (Rouse 1986), while strong wind events can be localized or widespread (Zhang et al. 1999). Return intervals for catastrophic winds can be measured in centuries, but localized storms with winds

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sufficient to break or uproot trees in individual stands can occur every decade or less (Canham et al. 2001; Foster and Boose 1992).

Biotic disturbances, including insect outbreaks, can also affect tree mortality by killing trees or branches, or predisposing trees to attack by secondary pests (Conway 1998). Outbreaks of jack pine budworm (*Choristoneura pinus pinus* Free.) (JPBW), a prominent native defoliator, occur at six to ten year intervals, and typically persist two to four years (McCullough 2000). Heavy defoliation can result in death of the terminal leader (top-kill), tree mortality, and tree volume loss (Graham 1935; Gross 1992; Gross and Meating 1994; Kulman et al. 1963). Mortality typically accumulates for two to three years following the collapse of high density JPBW populations, and up to 16% of trees can die following an outbreak (Conway et al. 1999a; Gross 1992; Gross and Meating 1994; McCullough et al. 1996).

Silvicultural guidelines have been developed to reduce tree mortality and volume loss caused by JPBW defoliation. Current recommendations include prioritizing over-mature stands for harvest or salvage, maintaining shorter rotation ages on lower quality sites than on higher quality sites, and maintaining proper stocking levels (16.1 – 25.3 m²/ha basal area) (Benzie 1977). Other recommendations for managing the vulnerability of jack pine stands to JPBW impact include reducing the proportion of suppressed trees in a stand, maintaining within stand tree diversity, and decreasing the amount of stand edge (Kouki et al. 1997; McCullough et al. 1994).

Several previous studies have addressed impacts of JPBW, including jack pine mortality and standing volume loss. Kulman et al. (1963) and Gross (1992) reported jack pine mortality within crown classes in Minnesota and Ontario, respectively. Gross (1992)

noted factors other than JPBW that contributed to mortality of intermediate and suppressed trees in jack pine stands. A few studies have focused on the economic impacts that JPBW defoliation can have on jack pine stands (Conway et al. 1999a; Nyrop et al. 1983; Rose 1974). A few investigations have also looked at the growth and productivity of jack pine in relation to soil and site characteristics. Studies in Canada found that the growth of jack pine was more productive in soils with greater moisture-holding capacity and with a lower percentage of glacial sands (Beland and Bergeron 1996; Hamilton and Krause 1985). Pawluk and Arneman (1961) also found that jack pine stands growing in soils with higher moisture content, as well as higher cation exchange capacities in the Lake States region were more productive than stands growing in droughty soils with higher contents of coarse sand. No previous studies, however, have evaluated potential differences in jack pine mortality, top-kill, or standing live and dead volume among regions.

A study was initiated in 2001 to assess the current status of the jack pine resource and to collect baseline data to quantify long-term impacts of JPBW defoliation in six regions of northern Michigan and one region in Wisconsin. Within each region, I established a network of permanent plots to: (1) quantify jack pine mortality, top-kill, and standing live and dead volume; (2) compare these variables among surveyed regions; and (3) evaluate relationships between site and stand variables and jack pine mortality, standing live volume, and standing dead volume. I hypothesized that jack pine mortality, top-kill, and live and dead volume would differ among the seven regions because of variations in management guidelines among regions, site characteristics, climatic factors, and stand structure. Secondly, I hypothesized that mortality and live and dead volume

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would be positively related to stand age and stocking, because mortality and standing volume accumulates as trees increase in size and as stands increase in density, and site quality, because higher quality sites can support a higher volume of trees.

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Methods

Study sites

Permanent plots were established from May to August in 2001 – 2003 in six regions of northern Michigan and one region in Wisconsin to assess the current state of jack pine and to monitor long-term impacts of JPBW, including mortality, top-kill, and volume loss. I selected these seven regions based upon the relative abundance of jack pine in the area, and the historical importance of JPBW outbreaks. These regions included state land in the north-central Lower Peninsula of Michigan (NL-State), the Huron-Manistee National Forest in the northeastern Lower Peninsula (NL-HNF), the Raco Plains area of the Hiawatha National Forest in the eastern Upper Peninsula of Michigan (UP-Raco), two regions of state land in the Upper Peninsula (UP-East and UP-West), the Ottawa National Forest in the western Upper Peninsula (UP-ONF), and state land in west-central Wisconsin (WI-State) (Figure 1-1). Soils were generally moderately drained to droughty, except for two regions (UP-East and WI-State), which contained areas of poorly drained peat soils (Table 1-1). The terrain was generally level to gently sloping, with moderately steep areas in the UP-West and UP-ONF regions, while the WI-State region had scattered sandstone mounds (Table 1-1).

Stand selection and establishment of plots

A stratified random sampling approach was used to select jack pine stands in each of the seven regions for sampling. Stratification was based on stand age, site index, and basal area (Table 1-2), because of their documented relationship with tree mortality and jack pine volume (Conway et al. 1999a, 1999b; McCullough et al. 1996), and because

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these variables are routinely collected and used operationally by forest managers. These variables were acquired for all jack pine stands from each respective forest management agency's database. After stands were grouped by age, site index, and basal area, I randomly selected jack pine stands from each group, based on the percentage of the total number of stands that were assigned to each stand variable category. Number of stands used per region ranged from 35 stands in the NL-State region to 78 stands in the UP-Raco region. If stands had been recently harvested or were not accessible, a replacement stand was selected from the same group.

Permanent plots were established in a total of 356 jack pine stands encompassing 6,374 ha (15,750 acres) in northern Michigan and Wisconsin from 2001 to 2003 (Table 1-3). Stand age ranged from 10 yr in the UP-ONF region to 117 yr in the UP-Raco region. Site index (at 50 yrs) ranged from 9.2 m (30 ft) in the UP-East region to 22.3 m (73.2 ft) in the UP-ONF region and basal area ranged from 2.3 m²/ha (10 ft²/ac) in the NL-State, NL-HNF, UP-East, and WI-State regions to 50.6 m²/ha (220 ft²/ac) in the UP-Raco region (Table 1-3).

Stand composition, mortality, and top-kill

One circular, 0.01 ha (0.025 acre) fixed-radius plot was randomly located in each stand using compartment maps overlaid with a transparent grid. Grid cells were selected at random for plot center location, and a compass and pacing was used to establish the permanent plot center in the field. I established one survey plot per stand in all regions except NL-State. Multiple plots per stand were established in the NL-State region in 2001 to assess within-stand variability. Within each of the NL-State stands, I established at least two plots; three plots for stands larger than 8.5 ha (21 acres), four plots for stands

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larger than 20.7 ha (51 acres), and five plots for stands larger than 40.5 ha (100 acres). For analysis, I used mean values, based on the number of established plots per stand at the NL-State region. In all other regions, I chose to establish one plot per stand to ensure that a wide range of jack pine forest could be surveyed, and jack pine stands were generally fairly small (mean and median stand acres = 44 and 32, respectively), and tree age and stocking tends to be fairly homogenous within stands.

Within each plot, I measured the height, diameter at breast height (DBH; 1.37 m above ground), length of the dead terminal leader on top-killed trees, dominance class, and crown ratio of all jack pine trees. This study was limited to analysis of jack pine trees only, so other associated species in each plot were not measured. The percentage of jack pine trees that were dead or top-killed was calculated for each plot.

Live and dead volume

The volume of each jack pine tree (m³) per plot was calculated using the standard jack pine volume equation from the LS-TWIGS model:

$$V = 43 * SI^{0.249415} * (1 - EXP(-1.0 * 0.0633760 * D))^{3.3981}$$

where V = jack pine volume (m³), D = DBH (cm), and SI = site index (m). Live volume, including standing live and top-killed jack pine trees, and dead volume, representing standing dead jack pine trees, was determined. Volume of jack pine trees measured within each plot was summed, and then expanded to a per hectare value to estimate stand volume. In the NL-State region, where multiple plots per stand were established, jack pine live and dead volumes were summed for all plots then divided by the number of plots to generate a mean jack pine volume per stand.

Statistical analysis

Stand level estimates of mortality, top-kill, and live and dead volume were grouped for analysis based on categories or threshold values for age, site index, and basal area typically used for jack pine management in the Lake States (Table 1-2) (Benzie 1977), and previous studies that related these variables to JPBW impact (Conway et al. 1999a, 1999b; McCullough et al. 1996). Stands were divided into two categories based on age (< 50 yrs, 50+ yrs), and three categories based on basal area (< 16.1 m²/ha (< 70 ft²/ac), 16.1 – 25.3 m²/ha (70 – 110 ft²/ac), > 25.3 m²/ha (> 110 ft²/ac)) (Benzie 1977; Conway 1999a; McCullough et al. 1996). Comparisons of mortality and dead volume among basal area categories were made using data acquired from each forest manager's inventory database. I then calculated stand basal area values using jack pine data from live dominant trees, which were collected from my permanent plots and compared those values with the basal area data used for the mortality and dead volume comparisons to check for accuracy of the manager's inventory databases using a standard t-test ($p < 0.05$). Basal area values from inventory data were used in analyses.

Categories for site index were based on mean and median site index of jack pine stands per region. Mean and median site index values ranged from 14.7 m (48.2 ft) to 15.3 m (50.2 ft) for the NL-State, NL-HNF, UP-Raco and UP-East regions (Table 1-3), so I chose 14.9 m (49 ft) as the division between low and high quality site index for these regions. Mean and median values for the UP-ONF and WI-State regions ranged from 16.4 m (53.8 ft) to 17.2 m (56.3 ft), so I chose 16.8 m (55 ft) as the division between low and high quality site index for these regions. Mean and median values for the UP-West

region ranged from 18.0 m (59.1 ft) to 18.3 m (60 ft), so I chose 18.3 m (60 ft) as the division between low and high quality site index (Table 1-3).

A test of normality for mortality data was significant in the NL-State and WI-State regions using the Shapiro-Wilk procedure (Kuehl 2000). For these regions, I analyzed associations between mortality data and stand age and site index categories using a t-test, and basal area categories using one-way analysis of variance (ANOVA) procedures. If the ANOVA test was significant, treatment means were separated using the Fisher's least square difference procedure (Kuehl 2000) at the 0.05 level of confidence. Log transformation normalized live volume data in all regions except the UP-Raco and UP-ONF regions, and dead volume data in the NL-State region. Within these regions, associations between live volume, dead volume, and stand age, site index, and basal area categories were analyzed using either a t-test or ANOVA.

Log transformations of overall mortality, top-kill, and volume data ($n = 356$) did not normalize data, so I used a one-way non-parametric ranked F test for regional comparisons ($p < 0.05$) (Neter et al. 1996). Analysis of within-region comparisons of mortality, and live and dead volume data which were not normalized by log transformations, were analyzed using a one-way non-parametric ranked F test ($p < 0.05$) (Neter et al. 1996). If the F-test was significant, treatment means were separated using a non-parametric multiple comparison procedure ($p < 0.05$) (Zar 1984). All non-parametric pairwise comparisons were analyzed by first ranking the data, then using a t-test. Interactions among non-normal jack pine mortality and live and dead volume data, and stand age, site index, and basal area categories for all regions combined ($n = 356$) were analyzed using a two-way ranked F test (Neter et al. 1996).

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Linear associations between jack pine live volume (m^3/ha of standing live trees), dead volume (m^3/ha of standing dead trees), and stand inventory variables were evaluated among all regions combined, and within each region, using Spearman's nonparametric correlation coefficient (r_s). Standing live and dead volume were used as response variables, and stand age, site index, and basal area were used as predictor variables. Backward stepping linear regression was used to assess relationships between log transformed live and dead volume data and stand inventory variables. Backward stepping procedures were used in order to adjust models for the effect of potential collinearity among predictor variables, and to most efficiently find the most powerful predictors of live and dead volume.

Within each region, I used stand age, site index, and basal area as predictor variables of live and dead volume data. With all regions combined, I used the same stand inventory variables as linear predictors of live and dead volume data, and tested for significance of land ownership (USDA Forest Service owned vs. MI Department of Natural Resources owned), and physio-region (northern lower Michigan regions (NLMI) vs. eastern Upper Peninsula regions (EUP) vs. western Upper Peninsula regions (WUP)) using dummy variables. Data were analyzed using SAS statistical software (SAS Institute, Inc. 2000) at the $p < 0.05$ level of significance.

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Results

Jack pine volume, mortality and top-kill

Overall, volume of live jack pine averaged $220.8 \pm 10.64 \text{ m}^3/\text{ha}$. On average, $20.4 \pm 0.96\%$ of the jack pine trees in our plots were dead, and $5.1 \pm 0.51\%$ of the jack pine had dead tops. Volume of dead jack pine averaged $35.0 \pm 3.51 \text{ m}^3/\text{ha}$.

Overall, live volume was generally similar among regions, however the UP-West region had a significantly higher average live volume per hectare than the UP-ONF, UP-East, NL-HNF, WI-State, UP-Raco, and NL-State regions. Live jack pine volume was also significantly higher in the UP-ONF region than in the WI-State, UP-Raco, and NL-State regions ($F = 17.04$, $P < 0.0001$, d.f. = 6, 349) (Table 1-4). In the UP-West stands, live jack pine volume averaged $448.5 \pm 44.83 \text{ m}^3/\text{ha}$, approximately one and a half to three times higher than the other six regions (Table 1-4). Live jack pine volume averaged $245.6 \pm 22.73 \text{ m}^3/\text{ha}$ in the UP-ONF stands, approximately 33% to 65% higher than the WI-State, UP-Raco, and NL-State regions (Table 1-4).

Percentage mortality was generally variable among regions, and stand variability was also high within regions. The UP-ONF and WI-State regions had significantly more dead jack pine trees per stand than the UP-Raco and NL-State regions ($F = 4.74$, $P = 0.0001$, d.f. = 6, 349) (Table 1-4), but other differences among regions were not significant. On average, the UP-ONF and WI-State stands had $28.0 \pm 2.95\%$ and $27.3 \pm 2.67\%$ mortality, respectively, while only $13.2 \pm 1.46\%$ and $15.0 \pm 1.96\%$ of the jack pine trees in plots were dead in the UP-Raco and NL-State regions.

Percentage top-kill was generally similar among all regions, except for the UP-Raco region, which had a significantly higher percentage of jack pine trees with dead

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tops than the UP-West, NL-HNF, WI-State, and UP-ONF regions ($F = 4.84$, $P < 0.0001$, d.f. = 6, 349) (Table 1-4). On average, $9.9 \pm 1.58\%$ of jack pine were top-killed in UP-Raco stands, approximately two and a half to four times higher than stands in the UP-West, NL-HNF, WI-State, and UP-ONF regions.

Trends in the amount of dead volume were similar to those of standing live volume among regions. Volume of dead jack pine trees was significantly higher in the UP-West region than in the UP-East, NL-HNF, UP-Raco, and NL-State regions ($F = 4.79$, $P = 0.0001$, d.f. = 6, 349) (Table 1-4). There was an average of $68.4 \pm 17.85 \text{ m}^3/\text{ha}$ of dead jack pine volume in the UP-West region, nearly two to four and a half times more than stands in the UP-East, NL-HNF, UP-Raco, and NL-State regions (Table 1-4).

Mortality, dead volume, and tree characteristics

The majority of dead jack pine trees were in the intermediate or suppressed crown classes, while most of the dead volume was in the dominant and co-dominant crown class. Suppressed trees accounted for only 11.2% of the dead jack pine volume, while intermediate trees represented 37.3% of dead volume (Table 1-5). The NL-State, UP-ONF, and UP-Raco regions were the only areas where a higher percentage of dead volume occurred in the intermediate and suppressed crown classes than in the dominant crown class (Table 1-5). Dead volume in the intermediate and suppressed crown classes in these regions accounted for 64.7%, 65.1%, and 67.3% of the total dead volume, compared with the other regions, which had only 30% to 40.5% of the total dead volume in the intermediate and suppressed crown classes (Table 1-5).

Overall, 17.6% of the dead trees and 51.5% of the dead volume were in the dominant or co-dominant crown class in the seven regions (Table 1-5). The NL-HNF

region had the highest percentage of dead jack pine trees in the dominant crown class at 24.2%, while the WI-State region had the highest percentage of dead volume in the dominant crown class at 69.5% (Table 1-5). The NL-State region had the lowest number of dead dominants at 6.3%, while the UP-Raco region had the least percentage of dead volume in the dominant class at 32.7% (Table 1-5). Most of the dead jack pine were classed as suppressed or intermediate trees. Mortality of suppressed and intermediate trees ranged from 16.0% in the WI-State region to 62.5% at the same region.

Stand inventory variables

Mortality of jack pine trees and the ratio of dead to live volume of jack pine seemed to be highest in stands that were 50+ yrs old among all regions. I calculated a ratio of dead to live volume for within region comparisons because I felt that this would standardize the proportion of dead volume relative to the proportion of live volume in each stand. Overall, significantly more mortality occurred in stands that were 50+ yrs old than in stands younger than 50 yrs ($t = 6.81$, $P < .0001$, $d.f. = 1, 311$). However, a significant interaction occurred between stand age and site index ($F = 5.05$, $P < .0001$, $d.f. = 5, 350$). Stands that were 50+ yrs old growing on higher quality sites across all regions had higher levels of mortality than younger stands growing on higher quality sites. Stands 50 yrs old or older averaged $25.2 \pm 1.26\%$ mortality, while younger stands averaged $13.0 \pm 1.25\%$ mortality. Significantly more mortality occurred in stands that were 50+ yrs old than in younger stands in the NL-HNF ($t = 3.13$, $P = 0.0033$, $d.f. = 1, 40$), UP-Raco ($t = 3.92$, $P = 0.0002$, $d.f. = 1, 75$), UP-East ($t = 4.03$, $P = 0.0002$, $d.f. = 1, 41$), and UP-ONF ($t = 3.22$, $P < 0.0001$, $d.f. = 1, 48$) regions (Figure 1-2A). Trends were similar in the other three regions, but not significant. Mortality in stands that were 50+ yrs old ranged from

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20.8 ± 2.68% in the UP-Raco region to 32.4 ± 3.38% in the UP-ONF region, while mortality of stands less than 50 yrs old ranged from 7.1 ± 2.25% in the UP-Raco region to 12.3 ± 2.77% in the UP-ONF region (Figure 1-2A).

Overall, the ratio of dead to live volume was significantly higher in stands that were 50+ yrs old than in younger stands ($t = 6.77$, $P < .0001$, d.f. = 1, 310). Stands younger than 50 yrs old averaged a ratio of $8.5 \pm 1.90 \text{ m}^3/\text{ha}$ dead to live volume, while stands that were 50+ yrs old averaged a ratio of $22.9 \pm 2.46 \text{ m}^3/\text{ha}$ dead to live volume.

Among all regions, stand age was consistently the most powerful predictor of live and dead volume. Both live volume ($r_s = 0.51$, $P < .001$) and dead volume ($r_s = 0.43$, $P < .001$) were significantly correlated with stand age (Table 1-6). Results from the linear regression model indicated that stand age was a significant predictor of live volume ($r^2 = 0.45$, $P < .0001$) and dead volume ($r^2 = 0.26$, $P < .0001$) among all regions ($n = 356$) (Table 1-7). The effect of land ownership was also significant in predicting live volume ($r^2 = 0.46$, $P < .0001$), and the effect of physio-region was significant in predicting dead volume ($r^2 = 0.28$, $P < .0001$) (Table 1-7).

Within regions, stand age was also consistently the most important factor in predicting live and dead volume. Stands that were 50+ yrs old had a higher ratio of dead to live volume (Table 1-8), ranging from an average ratio of $9.4 \pm 3.74 \text{ m}^3/\text{ha}$ dead to live volume in the NL-State region to $36.5 \pm 6.90 \text{ m}^3/\text{ha}$ dead to live volume in the UP-ONF region. Comparisons between the ratio of dead to live volume and stand age were significant in the NL-HNF ($t = 2.39$, $P = 0.0213$, d.f. = 1, 42), UP-Raco ($t = 3.23$, $P = 0.0019$, d.f. = 1, 72), UP-East ($t = 6.07$, $P < .0001$ d.f. = 1, 46), and UP-West ($t = 2.50$, $P = 0.0183$, d.f. = 1, 30) regions (Table 1-8).

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All regions except the NL-State region had significant correlations between live and dead volume, and stand age (Table 1-6). In the linear regression models, stand age was a significant predictor of live volume in all regions except the UP-West region, where there was no linear model. Stand age was also a significant predictor of dead volume in all regions except the NL-State and UP-West regions, where there were no significant linear models (Table 1-7). However, stand age was significantly correlated with site index in the UP-ONF region ($r_s = 0.41$, $P = 0.003$), indicating that older stands were growing on higher quality sites in this region.

Within regions, site index appeared to be an inconsistent factor for comparisons of jack pine mortality and the ratio of dead to live volume. However, when all stands were combined, mortality in stands on higher quality sites ($23.0 \pm 1.44\%$) was significantly higher than in stands on lower quality sites ($18.1 \pm 1.27\%$) ($t = 2.44$, $P = 0.0151$, d.f. = 1, 351). A marginal interaction occurred between site index and basal area ($F = 3.82$, $P = 0.0515$, d.f. = 5, 350), indicating that more mortality potentially accumulates in over-stocked, higher quality stands when all regions were combined. Mortality was significantly greater in higher quality stands than in lower quality stands only in the UP-Raco region ($t = 2.10$, $P = 0.0386$, d.f. = 1, 76) (Figure 1-2B). This trend was the same for all other regions except for the UP-West region, where there was virtually no difference (Figure 1-2B).

Comparisons between the ratio of dead to live volume and site index categories were consistently insignificant within regions (Table 1-8). Only the NL-HNF ($r_s = 0.34$, $P = 0.017$), UP-Raco ($r_s = 0.30$, $P = 0.007$), and UP-ONF ($r_s = 0.43$, $P = 0.002$) regions had significant correlations between live volume and site index, and the low r_s values suggest

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high variability among stands within the regions. No significant relationships occurred between dead volume and site index within regions (Table 1-6), and linear regression models within regions also indicated that site index was a significant predictor of live volume only in the NL-HNF region ($r^2 = 0.35$, $P = 0.0001$), and was not a significant predictor of dead volume within any regions (Table 1-7). However, results of Spearman's correlation analysis indicated that both live volume ($r_s = 0.42$, $P < .001$) and dead volume ($r_s = 0.25$, $P < .001$) were significantly correlated with site index when all regions were combined (Table 1-6). Linear regression models using all regions combined also indicated that site index was consistently a significant predictor of both live and dead volume (Table 1-7).

Differences between basal area data calculated from permanent plots for live dominant jack pine trees and inventory database basal area data provided by cooperating agencies were significant only in the NL-HNF ($t = 2.24$, $P = 0.0275$, d.f. = 1, 98) and UP-West ($t = 4.43$, $P < .0001$, d.f. = 1, 96) regions. Within regions, permanent plot basal area data averaged 0.3 m²/ha, 0.5 m²/ha, and 2.2 m²/ha lower than inventory database basal area data in the UP-ONF, UP-Raco, and NL-State regions, while permanent plot basal area data averaged 0.4 m²/ha, 2.6 m²/ha, 4.2 m²/ha, and 8.3 m²/ha higher than inventory database basal area data in the WI-State, UP-East, NL-HNF, and UP-West regions. However, when all regions were combined, a Pearson's test of linear correlation resulted in a low r-value ($r = 0.35$), suggesting high variability and a lack of a linear relationship between permanent plot basal area data and inventory database basal area data used for stand category analysis.

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Generally, jack pine stands that were well-stocked (basal area of 16.1 – 25.3 m²/ha) or over-stocked (basal area > 25.3 m²/ha) had more mortality and a higher ratio of dead to live volume than stands that were under-stocked (basal area < 16.1 m²/ha), however, some variability among regions occurred. Overall, mortality was significantly higher in well to over-stocked stands than in under-stocked stands ($F = 25.47$, $P < .0001$, d.f. = 2, 353). Stands that were well-stocked or over-stocked averaged $25.6 \pm 1.44\%$ and $28.3 \pm 2.97\%$ mortality, respectively, while under-stocked stands averaged $13.4 \pm 1.22\%$ mortality. Mortality of jack pine was significantly higher in stands that were well-stocked or over-stocked than in stands that were under-stocked in the NL-HNF ($F = 5.09$, $P = 0.0100$, d.f. = 2, 47), UP-Raco ($F = 10.85$, $P < 0.0001$, d.f. = 2, 75), UP-ONF ($F = 4.43$, $P = 0.0173$, d.f. = 2, 47), and WI-State ($F = 6.22$, $P = 0.0044$, d.f. = 2, 41) regions (Figure 1-2C).

Overall, the ratio of dead to live volume was significantly higher in well to over-stocked stands than in under-stocked stands ($F = 19.83$, $P < .0001$, d.f. = 2, 353). Stands that were well-stocked or over-stocked averaged a ratio of 21.0 ± 2.71 m³/ha and 22.1 ± 5.14 m³/ha dead to live volume, respectively, while under-stocked stands averaged a ratio of 12.4 ± 2.36 m³/ha dead to live volume. When all regions were combined, both live volume ($r_s = 0.47$, $P < .001$) and dead volume ($r_s = 0.43$, $P < .001$) were significantly correlated with basal area (Table 1-6), probably because of the significant relationship between basal area and stand age ($r_s = 0.49$, $P < .001$) and site index ($r_s = 0.35$, $P < .001$). Significantly higher ratios of dead to live volume occurred in well-stocked stands than in under-stocked stands in the NL-State ($F = 4.75$, $P = 0.0156$, d.f. = 2, 32), NL-HNF ($F = 5.65$, $P = 0.0063$, d.f. = 2, 47), and UP-Raco ($F = 5.91$, $P = 0.0042$, d.f. = 2, 75) regions

(Table 1-8). This trend was the same for all other regions except the UP-East region, which averaged an approximate ratio of 10 m³/ha of dead to live volume for under, well, and over-stocked stands. The UP-ONF region had a significantly lower ratio of dead to live volume in over-stocked stands than in well-stocked stands ($F = 3.80$, $P = 0.0295$, d.f. = 2, 47) (Table 1-8). All regions except the NL-HNF and UP-West regions had significant correlations between live volume and basal area, and all regions except the UP-ONF region had significant correlations between dead volume and basal area (Table 1-6), probably a result of the significant correlations between basal area and stand age and site index.

Discussion

Overall, live volume of jack pine seemed to be higher than previous Lake States studies have found (Rudolph and Laidly 1990), but relatively similar to studies in Canada (Gross 1992). Mortality and top-kill of jack pine in Michigan and Wisconsin more closely resemble what other Lake States studies have reported (Conway et al. 1999a; McCullough et al. 1996). Rudolph and Laidly (1990) reported that un-managed stands of jack pine in all age classes in the Lake States region averaged approximately 136.5 m³/ha live volume. Estimates of live volume from this study were probably higher because the highly productive jack pine regions in the western Upper Peninsula of Michigan were included in the analysis. Gross (1992) found that jack pine stands in Ontario averaged approximately 202.3 m³/ha standing volume. However, one of the four stands had a relatively high percentage (71%) of associated species, while this study accounted for jack pine volume only.

In the 30,000 ha Raco Plains area of the Hiawatha National Forest in Michigan, McCullough et al. (1996) and Conway et al. (1999a) found that one to two years following defoliation by JPBW, mortality of jack pine averaged 8% and 16%, respectively, while Kulman et al. (1963) reported roughly 30% mortality of jack pine in Minnesota. Mortality results from this study were similar to these previous studies, indicating that mortality of jack pine varies within and among stands, depending upon stand age, and whether or not a severe disturbance, such as defoliation by JPBW, has recently occurred. Results from studies of top-kill in Saskatchewan (Hall et al. 1998), and in the Raco Plains area of the Hiawatha National Forest (McCullough et al. 1996)

indicated relatively higher levels of top-kill than what our study suggests, probably because of the amount of dead jack pine trees that were likely top-killed.

Jack pine volume, mortality, and top-kill

In most regions, jack pine was relatively similar, however, some variability did occur among regions. Possible reasons for overall similarities among some regions could be because of the general homogeneity of age and density among jack pines stands, or because of relatively similar site conditions (Table 1-1). Because jack pine is a prolific pioneer species, regeneration of stands is generally even-aged, and because jack pine can grow on very droughty sites where other, more competitive species may have more difficulty establishing, so stands can be relatively low in species diversity (Rudolf 1958). Jack pine stands in regions that were most similar in terms of live volume, dead volume, and mortality generally grew in similar site conditions; droughty to moderately drained sands with very little moisture holding capacity that are of lower site quality than the other regions (Johnson 1990; Werlein 1998; Whitney 1992). Standing live volume of jack pine was especially high in the UP-West region. In this region, jack pine typically grows on much higher quality sites than in most other regions, except the UP-ONF region, which has generally similar growing conditions (Schwenner 1991). It has been well documented that jack pine can grow faster and to larger sizes on better quality sites than on lower quality sites (Rudolf 1958; Rudolph and Laidly 1990). Mean and median site index values for jack pine in the UP-West region were generally 1.0 to 3.5 m higher than all other regions, where average live volume estimates were significantly less.

The high percentage of dead trees in the UP-ONF and WI-State regions could be related to several factors, including stand age and basal area, the frequency and severity

of JPBW outbreaks within each region, the frequency of other disturbances, or differing management guidelines. Stands in the UP-ONF region were generally old and fairly well to over-stocked, while stands in the WI-State region were generally young and under-stocked. So, the question arises as to why these two seemingly different regions have such high, equal amounts of mortality. Several of the old stands in the UP-ONF region were located in designated 'buffer' riparian areas, where harvesting was not allowed (Larry Melstrom, personal communication). Jack pine, being a short-lived species, can quickly accumulate mortality beyond ages 50 to 60 yrs, depending upon site conditions (Benzie 1977). The high levels of mortality in relatively young stands in the WI-State region were probably a result of natural thinning processes occurring from ages 35 yrs to 45 yrs. The relatively higher percentage of top-kill in the UP-East, NL-State, and UP-Raco regions is likely related to the frequency and severity of JPBW outbreaks that have occurred (Heym et al. 1993; MI Dept. of Natural Resources 1980 – 1994). High levels of dead standing jack pine volume in the UP-West and UP-ONF are likely related to generally higher levels of live volume and mortality in the regions, as well as generally higher frequencies of older aged, heavier stocked stands.

Genetic variation between populations of jack pine across geographical regions has been well documented (Hyun 1976; Gauthier et al. 1992). Variation in the genetics of different populations can affect the susceptibility of individuals to mortality caused by biotic and abiotic stresses which occur across the landscape. Genetic variation can potentially affect stand volume growth, as well as variations in the production of serotinous and non-serotinous cones. Jack pine stands where non-serotinous cones are produced more frequently may have higher percentages of intermediate or suppressed

trees, which can succumb to mortality from insect defoliation or other natural thinning processes (Kenkel et al. 1989).

Differences in management guidelines among regions can also affect the amount of live and dead volume, and the percentage of dead trees which occur in a stand. Results indicated that older aged, heavier stocked stands seem to be most vulnerable to individual tree mortality, suggesting that rotation ages and compliance with stocking guidelines should be among the most important management rules to follow to maintain the highest levels of economic viability for jack pine. Results from the linear regression analysis further indicate that land ownership, i.e. different management, may affect the structure of jack pine stands among regions. Rotation ages may be different, based upon market values of jack pine in different areas. Jack pine stands used for pulp vs. stands used for dimension lumber vs. stands that are whole-tree harvested could be managed with different intermediate or late stand treatment methods, thus reflecting the potential variation among regions and ownerships. This suggests that human-caused disturbance, i.e. harvesting for wood products, could be just as an important factor as naturally-caused disturbances, such as JPBW outbreaks, in explaining the current jack pine status in Michigan. Linear regression analysis also indicated that a regional effect may exist in explaining the amount of dead volume in jack pine stands. This could be explained by many of the factors I just suggested which affect the structure of jack pine stands; frequency of JPBW outbreaks, severity of randomly occurring abiotic disturbance (weather events, etc.), or genetic variation.

Mortality, dead volume, and tree characteristics

The occurrence of jack pine mortality in different crown levels can be important because the majority of economic impacts occur when dominant, merchantable trees die. The largest percentage of trees that died in all regions were either in the suppressed or intermediate crown levels of the stand. Yet, the greatest percentage of standing volume that was dead occurred in the dominant class. Kulman et al. (1963) found that mortality of intermediate and suppressed trees following successive years of JPBW defoliation in Minnesota ranged from 25% to 70%, while mortality of dominant and co-dominant trees ranged from an average of 12% to 17%. Gross (1992) found that dominant and co-dominant jack pine trees averaged less than 1% mortality after a JPBW outbreak in Ontario, while intermediate and suppressed trees ranged from an average of 9% to 60% mortality. My results were generally similar with these studies, except the percentage of mortality in the dominant and co-dominant crown classes were higher than the results reported by Gross (1992). This implies that impacts from within stand competition or natural disturbances such as defoliation by JPBW, can act as natural thinning agents in over-stocked stands by freeing up resources to surviving individuals by disposing of less vigorous suppressed trees. In regions where the dominant class is more heavily affected by tree mortality and volume loss, emphasis should be placed on salvage or pre-salvage operations so that the economic value of vulnerable trees can be saved (Conway 1999a).

Mortality, live and dead volume, and stand inventory variables

There are a few reasons why there were such confounding differences between basal area data that I calculated from live dominant jack pine trees from permanent plots and basal area data received from cooperating forest manager's databases. The

differences were likely due to the fact that my plot-level data was taken from jack pine trees only, while most stands were not complete monocultures of jack pine, e.g. plantations, and forest manager's likely include data on other companion species in stands while updating their stand inventory databases. On average, basal area data calculated from my plots were generally higher in four of the seven regions. These results could reflect the potential that the stand inventory data I received from managers may not have reflected the density of the stand during while I was collecting data.

Jack pine mortality and average dead to live volume ratio seemed to be closely related to stand age and basal area among all regions. However, because basal area was closely associated with stand age, it should be interpreted as a less important indicator of mortality and dead volume. The generally strong correlation between basal area and stand age suggested that well-stocked to over-stocked stands were over-aged. From earlier discussion, more mortality and dead volume should occur in older stands. Linear regression results within regions further describe the importance of stand age on volume loss resulting from tree death, suggesting that jack pine stands should be harvested at optimum rotation periods to lessen economic losses by damaging disturbances, such as defoliation by JPBW. Many studies have noted higher levels of jack pine mortality and dead volume in older stands (Conway et al. 1999a; McCullough et al. 1996; Volney 1998). Most of the regions surveyed had extensively higher amounts of mortality in older stands, except the NL-State and WI-State regions, which had relatively high percentages of dead jack pine in younger stands. As an explanation, higher levels of mortality within these regions occurred in the intermediate and suppressed crown classes in well or over-stocked stands. Mortality in younger stands could have been a result of natural thinning,

thus allowing a subsequent rapid increase in the growth and productivity potential of dominant, vigorous trees.

McCullough et al. (1996) and Conway et al. (1999a) found that mortality and volume loss was higher in higher quality stands in the Raco Plains area of the Hiawatha National Forest in Michigan. They suggested that trees growing on higher quality sites may have lower root-to-shoot ratios and would potentially be less tolerant of defoliation by JPBW than trees growing on lower quality sites. Even though the results showed that mortality was generally higher on higher quality sites among all regions, that comparison was significant only in the UP-Raco region. Four regions (NL-State, UP-East, UP-West, WI-State) had proportionally more dead volume on higher quality sites, while the other three regions (NL-HNF, UP-Raco, UP-ONF) had a higher proportion of dead volume on lower quality sites.

The variation in impact on different sites could be attributed to moisture or nutrient holding capacities of the soils in different regions, or to the percentage of dead dominant or suppressed trees in older or relatively higher quality stands. The variability of the amount of dead trees and proportion of dead volume among regions could also be related to the occurrence of salvage or pre-salvage operations, which remove recently killed, merchantable trees. My results indicated an inconsistent pattern of loss of dominant trees in higher quality stands, which suggests that further research should be done specifically looking at mortality in relation to site characteristics in different areas.

Summary and conclusions

This study is the first to collect baseline data to describe the current status of the jack pine resource in Michigan and Wisconsin for monitoring long-term impacts of

JPBW. Within stands, age seems to be the most important factor to predict mortality of jack pine, yet tree death occurs most frequently among the suppressed and intermediate crown classes. Stands experiencing high mortality in the dominant crown class should be prioritized for harvest. Interestingly, only a few regions varied significantly from the rest, with respect to live and dead volume, and mortality and top-kill. These results will be used to modify a current decision support model (Conway et al. 1998), so that it can be applicable to forest managers across the surveyed regions.

Table 1-1. Description of terrain, soils, and location of regions surveyed including state land in the northern Lower Peninsula (N. C. 1970)

Table 1-1. Description of terrain, soils, and location of regions surveyed including state land in the northern Lower Peninsula (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State).

Region	Terrain	Soil Description	Latitude	Longitude
Lower Michigan				
NL-State	Level to gently sloping	Droughty to moderately drained Grayling-Graycalm-Croswell series	84° 12' - 85° 15' W	44° 16' - 44° 48' N
NL-HNF	Level to gently sloping	Droughty to moderately drained Grayling-Graycalm-Croswell series	83° 21' - 84° 36' W	44° 09' - 44° 25' N
Upper Michigan				
UP-Raco	Level to gently sloping	Droughty to moderately drained Grayling-Graycalm-Croswell series and Rubicon-Kalkaska sands	84° 44' - 84° 55' W	46° 18' - 46° 24' N
UP-East	Level to gently sloping	Droughty sands to very poorly drained peat muck of Deer Park-Dawson-Au Gres series	84° 58' - 85° 53' W	46° 25' - 46° 46' N

Table 1-1 (cont.)

Region	Terrain	Soil Description		Latitude	Longitude
UP-West	Level to moderately steep	Moderately to excessively drained, with moraine mixtures of Graying-Rubicon, Keweenaw-Trimountain, Kalkaska-Waiska series	Berndt 1988; Schwenner 1991	87° 16' - 87° 53' W	46° 15' - 46° 46' N
UP-ONF	Level to moderately steep	Moderately to excessively drained, with moraine mixtures of Graying-Rubicon, Keweenaw-Trimountain, Kalkaska-Waiska series	Berndt 1988; Schwenner 1991	89° 37' - 89° 58' W	46° 32' - 46° 40' N
Central Wisconsin					
WI-State	Level with scattered sandstone mounds	Moderately to excessively drained sand/sandstone of Tarr-Boone-Rockdam series and poorly to very poorly drained sand, gravel, and peat of Ironrun-Ponycreek-Dawsil series	Langton and Simonson 2001	90° 33' - 90° 50' W	44° 11' - 44° 25' N

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Table 1-2. Characteristics used to stratify jack pine stands for evaluation of jack pine live and dead volume (m^3/ha), mortality and top-kill, and total and average annual radial growth rates from 1991 - 2000 in six regions of Michigan and one region of Wisconsin.

Age (years)	Site Index (m) ¹	Basal Area Class (m ² /ha) ²	Number of Stands
Young (< 50)	Low	Under	69
		Well	16
		Over	0
	High	Under	25
		Well	24
		Over	5
Old (50+)	Low	Under	39
		Well	50
		Over	12
	High	Under	28
		Well	56
		Over	32
TOTAL			356

¹Site index was stratified differently among regions: the Ottawa National Forest in the west Upper Peninsula and state land in west-central Wisconsin (low SI ≤ 16.8 m < high SI), state land in the west-central Upper Peninsula (low SI ≤ 18.3 m < high SI), other four regions (low SI ≤ 14.9 m < high SI).

²Basal area categories represent stands considered to be: Under-stocked = (< 16.1 m^2/ha); Well-stocked = (16.1 - 25.3 m^2/ha); Over-stocked = (> 25.3 m^2/ha).

Table 1-3. Number of jack pine stands and trees and characteristics of stands surveyed in seven regions of Michigan and Wisconsin to assess standing live and dead volume (m^3/ha), mortality and top-kill, total and average annual radial growth rates of jack pine trees, and coarse woody debris volume (m^3/ha).

Regions surveyed included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in Wisconsin (WI-State) (SEM = standard error of the mean).

Region	NL-State	NL-HNF	UP-Raco	UP-East	UP-West	UP-ONF	WI-State
No. stands	35	50	78	50	49	50	44
No. trees	1020	499	826	561	559	488	518
Age (years)							
Mean	54.7	55.7	48.5	53.9	58.0	57.1	43.1
SEM	2.58	2.33	2.43	2.84	1.93	2.26	2.26
Median	54	57	57	60	60	64	38
Min	23	16	13	20	32	10	20
Max	79	87	117	101	86	96	71
Site Index (m)							
Mean	14.7	15.0	14.9	14.8	18.2	17.2	16.4
SEM	0.32	0.25	0.14	0.26	0.28	0.26	0.24
Median	15.0	15.3	15.3	15.3	18.3	16.8	16.8
Min	10.7	10.7	12.5	9.2	12.2	14.6	12.2
Max	18.3	19.5	18.0	18.6	21.4	22.3	19.8
Basal Area (m^2/ha)							
Mean	15.3	14.7	18.2	17.0	18.6	19.6	14.5
SEM	1.49	1.05	1.13	1.12	0.79	1.20	1.36
Median	16.1	13.8	16.9	16.1	18	18.4	15.5
Min	2.3	2.3	19.0	2.3	9.2	3.5	2.3
Max	39.1	34.5	50.6	32.2	29.9	34.5	34.5

Table 1-4. Comparison of mean ($\pm$ SE) volume (m^3/ha) of live and dead jack pine trees per stand, mean ($\pm$ SE) percentage of dead jack pine trees, and mean ($\pm$ SE) percentage of jack pine trees with dead tops in the seven surveyed regions. Regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Letters indicate significant differences among regions ($p < 0.05$).

Region	Live Volume (m^3/ha)	Mortality (%)	Top-Kill (%)	Dead Volume (m^3/ha)
NL-State	144.8 $\pm$ 12.95 c	13.2 $\pm$ 1.46 b	5.2 $\pm$ 1.24 ab	15.0 $\pm$ 6.00 bc
NL-HNF	201.6 $\pm$ 22.16 bc	18.1 $\pm$ 2.31 ab	3.5 $\pm$ 1.09 b	20.1 $\pm$ 5.04 bc
UP-Raco	150.6 $\pm$ 17.08 c	15.0 $\pm$ 1.96 b	9.9 $\pm$ 1.58 a	20.0 $\pm$ 3.69 c
UP-East	209.5 $\pm$ 22.02 bc	20.8 $\pm$ 2.75 ab	5.2 $\pm$ 1.03 ab	29.3 $\pm$ 6.27 bc
UP-West	448.5 $\pm$ 44.83 a	22.1 $\pm$ 2.59 ab	3.8 $\pm$ 1.32 b	68.4 $\pm$ 17.85 a
UP-ONF	245.6 $\pm$ 22.73 b	28.0 $\pm$ 2.95 a	2.3 $\pm$ 0.98 b	62.6 $\pm$ 9.48 ab
WI-State	191.3 $\pm$ 23.46 c	27.3 $\pm$ 2.67 a	3.0 $\pm$ 0.79 b	32.5 $\pm$ 9.31 abc

Table 1-5. Comparison of the percentage of dead volume (m³/ha) and percentage of jack pine trees that were dead in dominant, intermediate, and suppressed crown classes in the seven surveyed regions. Surveyed regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State).

Region	Dominant		Intermediate		Suppressed	
	Dead Volume	Mortality	Dead Volume	Mortality	Dead Volume	Mortality
NL-State	35.3	6.3	48.2	41.5	16.5	52.1
NL-HNF	59.5	24.2	36.9	52.6	3.6	23.2
UP-Raco	32.7	17.7	41.2	38.5	26.1	43.1
UP-East	70.1	20.7	28.2	52.3	1.7	27.0
UP-West	59.5	20.0	38.0	35.7	2.5	44.3
UP-ONF	34.9	15.6	40.5	43.0	24.6	41.4
WI-State	69.5	21.5	30.2	62.5	0.3	16.0
ALL	51.5	17.6	37.3	46.3	11.2	36.0

Table 1-6. Number of stands sampled and Spearman's non-parametric correlations (r_s) between live volume (m^3/ha), dead volume (m^3/ha), and stand characteristics in each region. Regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Significant correlations are in bold and p values are in parentheses. ($p < 0.05$).

Region	N	Live Volume (m^3/ha)			Dead Volume (m^3/ha)		
		Age	Site Index	Basal Area	Age	Site Index	Basal Area
NL-State	35	0.29 (0.092)	0.29 (0.092)	0.48 (0.004)	0.17 (0.323)	0.27 (0.113)	0.45 (0.007)
NL-HNF	50	0.44 (0.001)	0.34 (0.017)	0.12 (0.399)	0.42 (0.002)	0.12 (0.391)	0.50 (0.002)
UP-Raco	78	0.60 (<0.001)	0.30 (0.007)	0.55 (<0.001)	0.41 (0.002)	0.18 (0.109)	0.47 (<0.001)
UP-East	50	0.57 (<0.001)	0.20 (0.169)	0.57 (<0.001)	0.62 (<0.001)	0.01 (0.954)	0.43 (0.002)
UP-West	49	0.29 (0.044)	0.19 (0.201)	0.16 (0.272)	0.39 (0.006)	0.23 (0.107)	0.39 (0.006)
UP-ONF	50	0.44 (0.001)	0.43 (0.002)	0.45 (0.001)	0.32 (0.025)	0.18 (0.207)	0.21 (0.142)
WI-State	44	0.64 (<0.001)	0.27 (0.075)	0.52 (0.003)	0.54 (0.002)	0.27 (0.079)	0.37 (0.013)
ALL	356	0.51 (<0.001)	0.42 (<0.001)	0.47 (<0.001)	0.43 (<0.001)	0.25 (<0.001)	0.43 (<0.001)

Table 1-7. Results of linear regression analysis for jack pine live volume (m³/ha) and dead volume (m³/ha) predicted by stand age (yrs), site index (SI) (m), and basal area (BA) (m²/ha) within each region, and by stand age (yrs), site index (SI) (m), basal area (BA) m²/ha), land ownership (USDA - Forest Service or MI Dept. of Natural Resources), and physio-region (northern lower Michigan (NLM), eastern Upper Peninsula (EUP), western Upper Peninsula (WUP)) among all regions. Rows with no values indicate a non-significant predicting model (p < 0.05).

Region	Response	Predictors	Coefficient(s) ± SE	F-value	P-value	r ²
NL-State	Live Volume (m ³ /ha)	Intercept	5.267 ± 0.903			
		Age	0.014 ± 0.007			
		BA	0.005 ± 0.003	4.15	0.0139	0.24
	Dead Volume (m ³ /ha)	--	--	--	--	--
NL-HNF	Live Volume (m ³ /ha)	Intercept	4.640 ± 0.704			
		Age	0.018 ± 0.005			
		SI	0.045 ± 0.013	8.40	0.0001	0.35
	Dead Volume (m ³ /ha)	Intercept	-1.002 ± 3.106			
		Age	0.042 ± 0.021			
		BA	0.032 ± 0.011	6.49	0.0009	0.30
UP-Raco	Live Volume (m ³ /ha)	Intercept	4.108 ± 1.309			
		Age	0.031 ± 0.006	20.51	<.0001	0.43
	Dead Volume (m ³ /ha)	Intercept	-2.062 ± 3.754			
		Age	0.042 ± 0.018			
		BA	0.017 ± 0.009	9.56	<.0001	0.28

Table 1-7 (cont.)

Region	Response	Predictors	Coefficient(s) $\pm$ SE	F-value	P-value	r^2
UP-East	Live Volume (m ³ /ha)	Intercept	4.771 $\pm$ 1.345			
		Age	0.028 $\pm$ 0.009			
		BA	0.010 $\pm$ 0.005	14.70	<.0001	0.48
	Dead Volume (m ³ /ha)	Intercept	-1.199 $\pm$ 3.388			
UP-West	Live Volume (m ³ /ha)	Age	0.088 $\pm$ 0.013	13.32	<.0001	0.45
		--	--	--	--	--
	Dead Volume (m ³ /ha)	--	--	--	--	--
UP-ONF	Live Volume (m ³ /ha)	Intercept	5.784 $\pm$ 1.006			
		Age	0.028 $\pm$ 0.008			
		BA	0.006 $\pm$ 0.004	10.77	<.0001	0.41
	Dead Volume (m ³ /ha)	Intercept	1.373 $\pm$ 3.692			
		Age	0.080 $\pm$ 0.029	3.15	0.0338	0.16
WI-State	Live Volume (m ³ /ha)	Intercept	4.112 $\pm$ 1.194			
		Age	0.024 $\pm$ 0.009			
		BA	0.007 $\pm$ 0.003	9.54	<.0001	0.39
	Dead Volume (m ³ /ha)	Intercept	-0.227 $\pm$ 3.515			
		Age	0.057 $\pm$ 0.028	3.91	0.0153	0.21
All Regions	Live Volume (m ³ /ha)	Intercept	3.807 $\pm$ 0.336			
		Age	0.027 $\pm$ 0.003			
		SI	0.040 $\pm$ 0.006			

Table 1-7 (cont.)

Region	Response	Predictors	Coefficient(s) $\pm$ SE	F-value	P-value	r^2
All Regions	Live Volume (m ³ /ha)	BA	0.004 $\pm$ 0.001	96.37	<.0001	0.45
	Dead Volume (m ³ /ha)	Intercept	-2.566 $\pm$ 1.072			
		Age	0.050 $\pm$ 0.009			
		SI	0.052 $\pm$ 0.020			
<i>With Land Ownership</i>	Live Volume (m ³ /ha)	BA	0.016 $\pm$ 0.004	41.12	<.0001	0.26
		Intercept	3.807 $\pm$ 0.333			
		Age	0.027 $\pm$ 0.003			
		SI	0.039 $\pm$ 0.006			
		BA	0.004 $\pm$ 0.001			
		Land Ownership	0.234 $\pm$ 0.086	75.45	<.0001	0.46
<i>With Physio-region</i>	Dead Volume (m ³ /ha)	Intercept	-2.567 $\pm$ 1.072			
		Age	0.051 $\pm$ 0.009			
		SI	0.053 $\pm$ 0.020			
		BA	0.016 $\pm$ 0.004	31.26	<.0001	0.26
	Live Volume (m ³ /ha)	Intercept	4.535 $\pm$ 0.423			
		Age	0.026 $\pm$ 0.003			
		SI	0.027 $\pm$ 0.008			
		BA	0.005 $\pm$ 0.001			
		Land Ownership	0.233 $\pm$ 0.088	45.93	<.0001	0.46

Table 1-7 (cont.)

Region	Response	Predictors	Coefficient(s) $\pm$ SE	F-value	P-value	r ²
All Regions	Dead Volume (m ³ /ha)	Intercept	0.144 $\pm$ 1.359			
		Age	0.054 $\pm$ 0.009			
		BA	0.016 $\pm$ 0.004			
		NLMI	-1.485 $\pm$ 0.498			
		EUP	-1.413 $\pm$ 0.467	20.02	<.0001	0.28

Table 1-8. Comparison of the mean ($\pm$ SE) ratio of dead volume to live volume (m^3/ha) per stand grouped by stand age (yrs), site index (m), and basal area (m^2/ha) in the seven regions. Surveyed regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), two areas of state land in the Upper Peninsula of Michigan (UP-East & UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Different letters indicate significant differences among stand categories within regions ($p < 0.05$).

Region	NL-State	NL-HNF	UP-Raco	UP-East	UP-West	UP-ONF	WI-State
Age (yrs)							
< 50	4.8 $\pm$ 2.52 a	3.2 $\pm$ 1.23 b	7.0 $\pm$ 2.87 b	1.8 $\pm$ 1.39 b	4.0 $\pm$ 2.09 b	16.3 $\pm$ 9.07 a	18.9 $\pm$ 7.08 a
50+	9.4 $\pm$ 3.74 a	19.8 $\pm$ 6.36 a	21.2 $\pm$ 6.14 a	16.2 $\pm$ 3.47 a	26.3 $\pm$ 6.68 a	36.5 $\pm$ 6.90 a	22.7 $\pm$ 7.88 a
Site Index ¹							
Low	4.8 $\pm$ 2.00 a	18.5 $\pm$ 9.06 a	17.1 $\pm$ 7.38 a	7.7 $\pm$ 2.63 a	11.9 $\pm$ 3.37 a	34.4 $\pm$ 7.82 a	17.2 $\pm$ 7.04 a
High	10.9 $\pm$ 4.87 a	10.7 $\pm$ 3.69 a	13.5 $\pm$ 2.97 a	12.2 $\pm$ 3.53 a	33.8 $\pm$ 11.63 a	28.6 $\pm$ 8.80 a	26.4 $\pm$ 7.81 a
Basal Area (m^2/ha)							
< 70	3.0 $\pm$ 2.03 b	5.7 $\pm$ 2.27 b	11.4 $\pm$ 4.90 b	11.4 $\pm$ 4.68 a	11.8 $\pm$ 6.89 a	27.5 $\pm$ 10.71 ab	19.5 $\pm$ 9.13 a
70 - 110	10.1 $\pm$ 2.97 a	26.4 $\pm$ 10.16 a	19.1 $\pm$ 7.55 a	9.1 $\pm$ 2.39 a	17.6 $\pm$ 6.23 a	43.3 $\pm$ 8.88 a	18.4 $\pm$ 4.37 a
111+	15.5 $\pm$ 13.37 ab	8.7 $\pm$ 1.03 ab	21.1 $\pm$ 9.17 ab	10.7 $\pm$ 3.37 a	52.7 $\pm$ 27.69 a	20.6 $\pm$ 10.51 b	30.8 $\pm$ 24.45 a
TOTAL²	7.4 $\pm$ 2.40 d	13.8 $\pm$ 4.23 bcd	15.2 $\pm$ 3.81 bc	10.4 $\pm$ 2.36 cd	20.4 $\pm$ 5.12 ab	32.0 $\pm$ 5.82 a	9.2 $\pm$ 1.51 cd

¹Site index was stratified differently among regions: the Ottawa National Forest in the west Upper Peninsula and state land in west-

central Wisconsin (low SI $\leq$ 16.8 m < high SI), state land in the west-central Upper Peninsula (low SI $\leq$ 18.3 m < high SI), other four regions (low SI $\leq$ 14.9 m < high SI).

²Different letters indicate significant differences among regions.

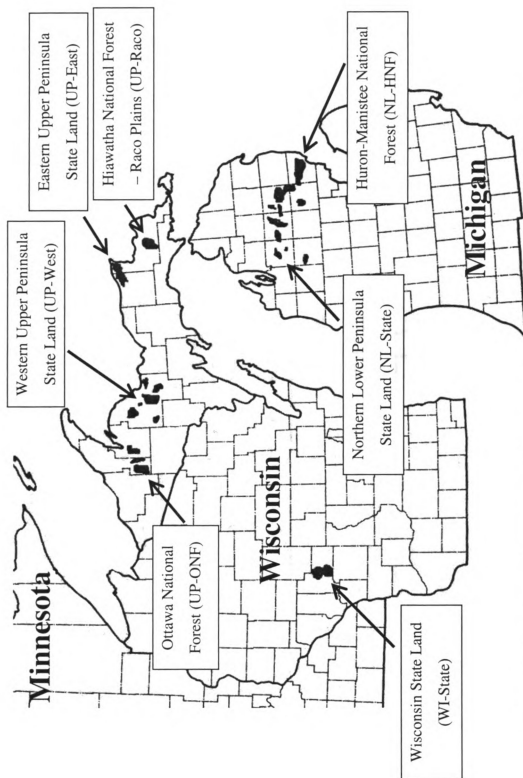
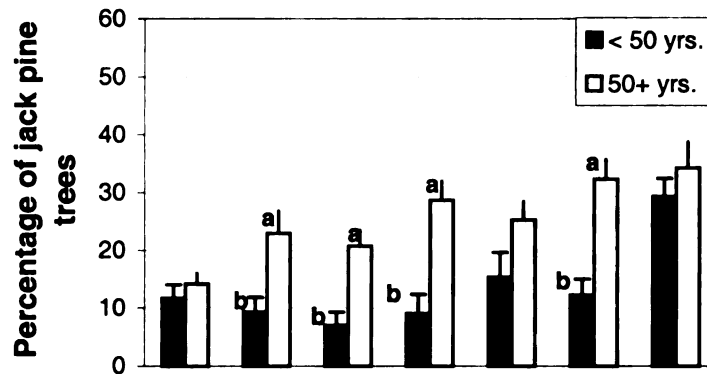
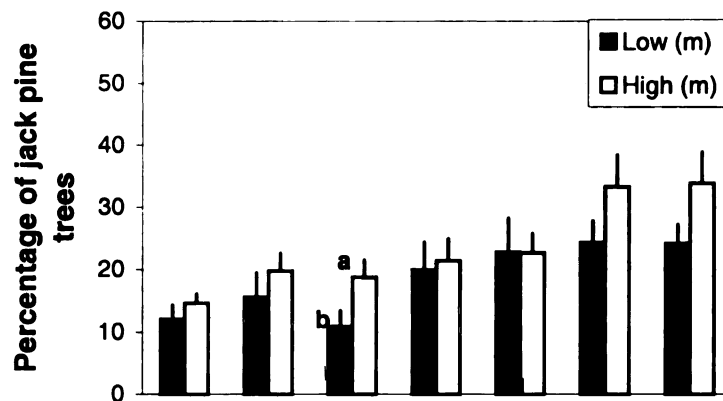


Figure 1-1. Locations of permanent plots surveyed in six regions of Michigan and one region in Wisconsin from 2001 to 2003.

(A) Stand Age (yrs.)



(B) Site Index (m)



(C) Basal Area (m²/ha)

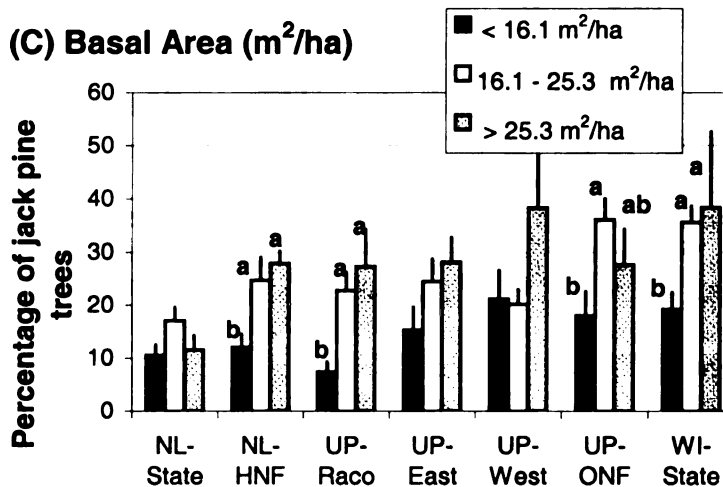


Figure 1-2. Mean ($\pm$ SE) percentage of dead jack pine trees in seven regions in Michigan and Wisconsin grouped by (A) stand age, (B) site index (m), and (C) basal area (m²/ha). Different letters indicate significant differences among groups within regions ($p < 0.05$).

CHAPTER 2

ANALYSIS OF ANNUAL RADIAL GROWTH RATES OF JACK PINE ACROSS NORTHERN MICHIGAN AND WISCONSIN

Introduction

Annual radial growth rings have long been used to evaluate effects of environmental and climatic factors on tree growth (Hainze and Benjamin 1984; Jeong and Rao 1996; Larsen and MacDonald 1995; Watson and Luckman 2002), and to predict growth and yield of economically important species (Boyer 1987; Johnson et al. 1981). Tree ring analysis has been used to evaluate effects of defoliating insects on radial growth, such as western spruce budworm (*Choristoneura occidentalis* Freeman) (Weber and Schweingruber 1995), spruce budworm (*Choristoneura fumiferana* Clements) (Piene 1989; Shore and Alfaro 1986), and Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) (Brubaker 1978). Outbreak years can generally be identified by a pronounced decrease in radial growth due to heavy defoliation.

Jack pine (*Pinus banksiana* Lambert) is an important species in the Lake States region of the U.S. and throughout much of Canada. It is a fast growing, shade intolerant species which can grow on relatively poor soils, and is important for the commercial pulpwood industry (Rudolph and Laidly 1990). In Michigan and Wisconsin, jack pine forests occur on nearly 485,000 ha (1.2 million acres) (Piva 1997). More than 270,000 cords of jack pine are annually harvested for wood fiber, amounting to a stumpage value of nearly \$10.1 million (USDA-FS timber price list 2002). Management intensity in jack pine forests has escalated because of the enhanced value of jack pine pulp (from \$4/cord in 1991 to \$35/cord in 2002) (McCullough and Leefers 2000; USDA-FS timber price list 2002), leading to emphasis on optimization of harvest rotations.

Every year, jack pine forests in the Lake States region experience multiple natural disturbances, which can affect patterns of annual radial growth in jack pine, including drought stress and other weather events. Jack pine budworm (JPBW) is among the most important biotic disturbances in jack pine ecosystems. Outbreaks occur every 6 - 10 years, typically lasting two to four years (McCullough 2000). During a JPBW outbreak, heavy defoliation can result in radial growth reduction, death of the terminal leader (top-kill), and tree mortality (Gross 1992; Kulman et al. 1963).

Because of the economic importance and demand for jack pine in Michigan and Wisconsin (Piva 1997), it is important to quantify annual growth patterns in jack pine. Advances in annual radial growth research can aid forest managers in decision making processes, so that proper stand attributes, including stand density and age, can be identified for the most efficient growth of economically viable trees. Important stand-level disturbances that greatly affect annual growth patterns can also be recognized and stands can then be managed properly to lessen annual growth losses.

A large-scale project was initiated in 2001 to assess the current status of the jack pine resource and to quantify long-term impacts of JPBW defoliation in six regions of Michigan and one region of Wisconsin. Objectives of this study were to (1) quantify annual radial growth of jack pine in a network of recently established permanent plots, (2) assess relationships between radial growth and crown class and stand variables, and (3) evaluate radial growth patterns in jack pine among regions related to tree and stand level disturbance. I hypothesized that patterns of annual radial growth for jack pine would differ among the seven regions, because of variation in JPBW outbreaks, and climatic patterns. Within a given region, I hypothesized that radial growth patterns would be

negatively related to tree age and stocking level, and positively related to site quality and dominance class.

Methods

Study sites

Permanent plots were established from May to August in 2001 – 2003 in six regions of northern Michigan and one region in Wisconsin to assess the current state of jack pine and to monitor long-term impacts of JPBW and annual radial growth rates of jack pine. These seven regions were selected based upon the relative abundance of jack pine in the area, and the frequency of JPBW outbreaks. These regions included state land in the north-central Lower Peninsula of Michigan (NL-State), the Huron-Manistee National Forest in the northeastern Lower Peninsula (NL-HNF), the Raco Plains area of the Hiawatha National Forest in the eastern Upper Peninsula of Michigan (UP-Raco), two regions of state land in the Upper Peninsula (UP-East and UP-West), the Ottawa National Forest in the western Upper Peninsula (UP-ONF), and state land in west-central Wisconsin (WI-State) (Figure 1-1). Soils were generally moderately drained to droughty, except for two regions (UP-East and WI-State), which contained areas of poorly drained peat soils (Table 1-1). The terrain was generally level to gently sloping, with moderately steep areas in the UP-West and UP-ONF regions. The WI-State region had scattered sandstone mounds (Table 1-1).

Stand selection

A stratified random sampling approach was used to select jack pine stands in each of the seven regions for sampling. Stratification was based on stand age, site index, and basal area (Table 1-2), because of their documented relationship with tree mortality, jack pine volume, and annual radial growth (Conway et al. 1999a, 1999b; McCullough et al.

1996), and because these variables are routinely collected and used operationally by forest managers. These variables were acquired from each respective forest management agency's database. After stands were grouped by age, site index, and basal area, we randomly selected jack pine stands from each group, based on the percentage of the total number of stands that were assigned to each stand variable category. Number of stands used per region ranged from 35 stands in the NL-State region 78 stands in the UP-Raco region. If stands had been recently harvested or were not accessible, a replacement stand was selected from the same group.

Permanent plots were established in a total of 356 jack pine stands encompassing 6,374 ha (15,750 acres) in northern Michigan and Wisconsin from 2001 to 2003 (Table 1-3). Stand age ranged from 10 yr in the UP-ONF region to 117 yr in the UP-Raco region. Site index ranged from 9.2 m (30 ft) in the UP-East region to 22.3 m (73.2 ft) in the UP-ONF region and basal area ranged from 2.3 m²/ha (10 ft²/ac) in the NL-State, NL-HNF, UP-East, and WI-State regions to 50.6 m²/ha (220 ft²/ac) in the UP-Raco region (Table 1-3).

Tree core extraction

One circular, 0.01 ha (0.025 acre) fixed-radius survey plot was randomly located in each stand using compartment maps overlaid with a transparent grid. Grid cells were selected at random for plot center location, and a compass and pacing was used to locate the permanent plot center in the field. I established one survey plot per stand in all regions except NL-State. Multiple plots per stand were established in the NL-State region in 2001 to assess within-stand variability. Within each of the NL-State region stands, I established at least two plots; three plots for stands larger than 8.5 ha (21 acres), four

plots for stands larger than 20.7 ha (51 acres), and five plots for stands larger than 40.5 ha (100 acres). For analysis, I used mean values, based on the number of established plots per stand at the NL-State region. In all other regions, I chose to establish one plot per stand to ensure that a wide range of jack pine forest could be surveyed, and jack pine stands were generally fairly small (mean and median stand acres = 44 and 32, respectively). The age of jack pine trees and stocking also tends to be fairly homogenous within stands.

Each standing jack pine tree within each plot was identified as live, dead, or top-killed. Tree height, diameter at breast height (DBH; 1.37 m above ground), dominance class, and crown ratio were recorded on all jack pine trees in each plot. This study was limited to analysis of jack pine trees only, so other associated species in each plot were not measured. From two to six jack pine trees were randomly selected in each plot from a stratified combination of live, dead, or top-killed trees within jack pine crown classes (dominant/co-dominant, intermediate, or suppressed). The extraction of cores from a combination of trees depended upon whether or not those trees were present in the plot, and what condition the trees were in when cores were being extracted. For example, to extract a core from dominant live, dead, and top-killed trees, one of each of those trees would need to be present in a survey plot at the same time. Plus, if the tree was dead, its condition would have to be such that an adequate core could be extracted to achieve an accurate measurement of annual ring width.

One increment core from each tree was extracted at diameter at breast height using an increment borer. Following extraction, cores were placed in a straw, and labeled with the compartment, stand, and tree numbers from which they were extracted. In the

laboratory, cores were mounted and sanded. Annual ring width (to nearest 0.01 mm) was measured with an optical digitizing scanner and WINDENDRO image analysis software (Regent Instruments, Inc., Quebec, Que.). Because light or missing rings can occur in jack pine that have been affected by JPBW defoliation or other natural stresses (Kulman et al. 1963; O' Neil 1963), caution and precision was used when identifying annual ring sequences of jack pine cores after digitally scanning them into WINDENDRO.

I collected a total of 1,147 cores from live trees (836 cores), dead trees (168 cores), and top-killed trees (143 cores) that were either in the dominant/codominant, intermediate, or suppressed crown classes. Because the sample size was so un-balanced, I chose to statistically compare only the live trees among all regions. Sample sizes were also comparatively small for live intermediate (156 cores) and suppressed trees (21 cores), so data from those two crown classes were combined for statistical analysis.

Previous jack pine studies have used stem analysis to examine growth patterns and volume losses resulting from JPBW defoliation (Conway et al. 1999b; Kulman et al. 1963; Gross 1992). Increment cores were chosen because this study spanned a large geographical area, and non-destructive methods were chosen for tree core data collection. By using non-destructive increment cores, previously sampled trees can be re-visited, and future radial growth patterns can be compared with these results.

Annual radial growth and jack pine budworm defoliation

I plotted annual radial growth rates from 1991 – 2000 from a subset of tree cores which were collected from 55+ year old live dominant trees. From 1991 – 1994, widespread defoliation from JPBW occurred in all seven surveyed regions (Heym et al. 1993; MI Dept. of Natural Resources 1991 – 1994; WI Dept. of Natural Resources 1992

– 1994). The period 1991 – 2000 was chosen because the most recent regional outbreak of JPBW occurred during this time period.

Statistical analysis

Mean values of average and total annual radial growth rates from the years 1991 – 2000 were grouped for analysis based on categories or threshold values for age, site index, and basal area typically used for jack pine management in the Lake States (Table 1-2) (Benzie 1977), and previous studies that related these variables to JPBW impact (Conway et al. 1999b; McCullough et al. 1996). For analysis, trees were divided into three categories based on tree age (20 - 39 yrs, 40 - 59 yrs, 60+ yrs), and three categories based on stand basal area ($< 16.1 \text{ m}^2/\text{ha}$ ($< 70 \text{ ft}^2/\text{ac}$), $16.1 - 25.3 \text{ m}^2/\text{ha}$ ($70 - 110 \text{ ft}^2/\text{ac}$), $> 25.3 \text{ m}^2/\text{ha}$ ($> 110 \text{ ft}^2/\text{ac}$)) (Benzie 1977; McCullough et al. 1996). Comparisons of mean average annual radial growth rates from 1991 – 2000 among basal area categories were made using data acquired from each forest manager's inventory database. I then calculated stand basal area values using jack pine data from live dominant trees, which were collected from my permanent plots and compared those values with the basal area data used for annual radial growth rate comparisons to check for accuracy of the manager's inventory databases using a standard t-test ($p < 0.05$). Basal area values from inventory data were used for analyses.

Two categories for site index were chosen, based on mean and median site index of jack pine stands in each region. Mean and median site index values ranged from 14.7 m (48.2 ft) to 15.3 m (50.2 ft) for the NL-State, NL-HNF, UP-Raco and UP-East regions (Table 1-3). I chose 14.9 m (49 ft) as the division between low and high quality site index for these regions. Mean and median values for the UP-ONF and WI-State regions ranged

from 16.4 m (53.8 ft) to 17.2 m (56.3 ft), so I chose 16.8 m (55 ft) as the division between low and high quality site index for these regions. Mean and median values for the UP-West region ranged from 18.0 m (59.1 ft) to 18.3 m (60 ft), so I chose 18.3 m (60 ft) as the division between low and high quality site index (Table 1-3).

Results of the Shapiro-Wilk procedure (Kuehl 2000) indicated that all sets of data were normal. I used one-way analysis of variance (ANOVA) to assess differences in total annual radial growth of live dominant trees and live intermediate + suppressed trees among regions, and between the live dominant and live intermediate + suppressed crown classes among all regions combined. Average annual radial growth for live dominant jack pine trees among categories of tree age, site index, and stand basal area were also analyzed using one-way ANOVA. When the ANOVA results were significant, treatment means were separated using the Fisher's least square difference procedure ($p < 0.05$) (Kuehl 2000). Interactions between average annual radial growth and tree age, site index, and basal area categories among all regions ($n = 356$) were tested using a two-way ANOVA. Pairwise comparisons between average annual radial growth of live dominant jack pine trees and site index categories were analyzed using a t-test.

For analysis of annual radial growth rates and JPBW defoliation, I compared average radial growth rates of live dominant jack pine trees during outbreak years for each region (NL-State, NL-HNF, UP-Raco, UP-East, and UP-ONF = 1991 – 1993; UP-West = 1991 – 1994; WI-State = 1992 – 1994), including three years following the final year of outbreak against the remainder of years until the year 2000 (recovery years). A t-test was used to analyze statistical significance between average growth rates of outbreak and growth loss years and growth recovery years.

Linear associations between average annual radial growth of live dominant jack pine trees and stand inventory variables were evaluated using Pearson's correlation coefficient. Backward stepping multiple regression was used to assess relationships between average annual radial growth of live dominant trees and tree age, site index, and stand basal area for all regions combined ($n = 659$), and within regions (NL-State; $n = 118$, NL-HNF; $n = 76$, UP-Raco; $n = 100$, UP-East; $n = 105$, UP-West; $n = 79$, UP-ONF; $n = 90$, WI-State; $n = 91$). Backward stepping procedures were used in order to adjust models for the effect of potential collinearity among predictor variables, and to most efficiently find the most powerful predictors of average annual radial growth. Data were analyzed using SAS statistical software (SAS Institute, Inc. 2000) at the $p < 0.05$ level of significance.

Results

Overall growth of live jack pine

Overall, live jack pine trees in the dominant class, and growing in well-stocked and over-stocked stands, added significantly higher amounts of radial growth than trees that were growing in the suppressed crown class in under-stocked stands. However, results did show trends, though insignificant, in decreased annual radial growth as tree age increased. Among all regions, live dominant jack pine trees grew significantly more from 1991 – 2000 than live trees in the intermediate and suppressed crown classes ($t = 7.96$, $P < .0001$, d.f. = 1, 796) (Table 2-1). Live dominant trees averaged 27.4 ± 0.42 mm of total growth from 1991 – 2000, while live trees in the intermediate and suppressed classes averaged 20.2 ± 0.63 mm of growth during the same 10-yr period.

Regional differences

Live dominant jack pine trees grew significantly more from 1991 – 2000 in the UP-West region than the other six regions ($F = 16.45$, $P < .0001$, d.f. = 6, 652). Live dominant trees in the NL-State region grew the least, averaging only 22.0 ± 0.90 mm of growth per tree in the 10-yr period (Table 2-1). Total radial growth averaged between 25.8 mm and 31.8 mm per tree in the other five surveyed regions. Live trees in the intermediate and suppressed crown classes also grew significantly more in the UP-ONF and UP-West regions than in the UP-Raco and NL-State regions ($F = 4.00$, $P = 0.0009$, d.f. = 6, 170) (Table 2-1). Intermediate and suppressed trees in the UP-ONF and UP-West regions averaged 26.4 ± 2.54 mm and 26.3 ± 2.76 mm, respectively, of growth from 1991 – 2000, while growth of live trees in the intermediate and suppressed crown class

averaged from 17.8 ± 0.90 mm in the NL-State region to 22.8 ± 2.22 mm in the WI-State region during the 10-year period (Table 2-1).

Stand inventory variables

Among all regions, annual average radial growth rates of live dominant jack pine trees seemed to be marginally related to tree age and site index. Generally, variability of growth rates seemed to be high within and among stands. Among all regions combined, no significant differences occurred among average annual growth rates of live dominant trees from 1991 – 2000 among age classes ($F = 1.45$, $P = 0.2354$, d.f. = 2, 618) or between site index classes ($t = 1.84$, $P = 0.0662$, d.f. = 1, 638) (Table 2-2). Average annual growth rates of dominant trees among all regions were significantly correlated with tree age ($r = -0.08$, $P = .0490$) and site index ($r = 0.31$, $P < .0001$). However, the low r -values suggested high variability and a lack of a significant linear relationship. When all regions were combined, the linear regression model indicated that tree age and site index were significant predictors of average annual growth of live dominant jack pine during the 10-yr period ($F = 29.36$, $P < .0001$, $r^2 = 0.13$), but the low r^2 value again suggests high variability and a lack of a strong linear model.

Generally, average radial growth rates among age classes within regions were quite variable. There were no significant differences between average annual radial growth rates of live dominant trees from 1991 – 2000 among age classes within all regions except in the UP-Raco region, where trees aged 40 – 59 yrs old had significantly higher average growth rates than trees that were 20 – 39 yrs old and trees that were 60+ yrs old ($F = 7.24$, $P = 0.0014$, d.f. = 2, 72) (Table 2-2). Significant correlations occurred between average radial growth rates and tree age in the NL-State ($r = -0.22$, $P = 0.0186$),

UP-East ($r = -0.24$, $P = 0.0141$), and UP-West ($r = -0.27$, $P = 0.0165$) regions. There were no correlations between tree age and average radial growth in the NL-HNF, UP-Raco, UP-ONF, and WI-State regions. Linear regression analysis indicated that tree age was a significant predictor of average annual growth rates in the NL-State ($F = 3.26$, $P = 0.0242$, $r^2 = 0.05$), UP-East ($F = 2.80$, $P = 0.0441$, $r^2 = 0.06$), and UP-West ($F = 3.07$, $P = 0.0328$, $r^2 = 0.08$) regions. However, the low r-square values suggested a high variability of annual growth patterns within these regions, indicating that these are potentially non-linear functions.

Within regions, average radial growth rates from 1991 – 2000 were generally greater on higher quality sites than on lower quality sites, except in the UP-East region. This comparison was significant only in the UP-ONF region ($t = 3.33$, $P = 0.0013$, d.f. = 1, 80) (Table 2-2). There was a significant correlation between average annual growth rates and site index in the UP-Raco ($r = 0.40$, $P = 0.0005$) and UP-ONF ($r = 0.29$, $P = 0.0070$) regions. Linear regression analysis indicated that the UP-Raco region was the only region where site index was a significant predictor of annual radial growth patterns during the 10-yr period ($F = 8.38$, $P < .0001$, $r^2 = 0.23$), however, the low r^2 value again suggests high variability and the possibility that it was a non-linear model.

Differences between basal area data calculated from permanent plots for live dominant jack pine trees and inventory database basal area data provided by cooperating agencies were significant only in the NL-HNF ($t = 2.24$, $P = 0.0275$, d.f. = 1, 98) and UP-West ($t = 4.43$, $P < .0001$, d.f. = 1, 96) regions. Within regions, permanent plot basal area data averaged 0.3 m²/ha, 0.5 m²/ha, and 2.2 m²/ha lower than inventory database basal area data in the UP-ONF, UP-Raco, and NL-State regions, while permanent plot basal

area data averaged 0.4 m²/ha, 2.6 m²/ha, 4.2 m²/ha, and 8.3 m²/ha higher than inventory database basal area data in the WI-State, UP-East, NL-HNF, and UP-West regions.

However, when all regions were combined, a Pearson's test of linear correlation resulted in a low r-value ($r = 0.35$), suggesting high variability and a lack of a linear relationship between permanent plot basal area data and inventory database basal area data used for stand category analysis.

Patterns between stand basal area and annual average growth rates from 1991 – 2000 among all regions were inconsistent. Among all regions combined, live dominant trees growing in over-stocked stands with basal area greater than 25.3 m²/ha had significantly higher growth rates than trees growing in under-stocked and well-stocked stands with basal area ≤ 25.3 m²/ha ($F = 8.89$, $P = 0.0002$, d.f. = 2, 658) (Table 2-2). However, significant interactions occurred between stand basal area and tree age ($F = 17.69$, $P < .0001$, d.f. = 5, 614), and between stand basal area and site index ($F = 51.26$, $P < .0001$, d.f. = 5, 614) when all regions were combined. Average radial growth patterns of trees between 20 and 39 yrs old increased with stocking levels until stands reached a density of approximately 25 m²/ha, then leveled off. However, trees older than 40 yrs continued to increase in annual growth as stocking levels increased, probably a result of heavier stocked stands growing on higher quality sites. Growth of dominant trees in well-stocked stands decreased as site quality increased, while annual growth of trees in under-stocked and over-stocked stands increased with site quality.

Among all regions, average annual growth patterns were significantly correlated with stand basal area ($r = 0.22$, $P < .0001$), likely due to the correlation between stand basal area and site index ($r = 0.31$, $P < .0001$). Linear regression analysis indicated that

stand basal area was a significant predictor of average annual radial growth patterns of live dominant jack pine trees ($F = 29.36$, $P < .0001$, $r^2 = 0.13$), however, the indications from correlation results imply that tree age and site index were more important predictors of annual radial growth of jack pine than stand basal area.

Within all regions except the NL-HNF and UP-West regions, live dominant trees in over-stocked stands with basal area greater than $25.3 \text{ m}^2/\text{ha}$ generally had greater average annual radial growth rates from 1991 – 2000 than dominant trees growing in well-stocked and under-stocked stands with basal area $\leq 25.3 \text{ m}^2/\text{ha}$, a potential result of the significant correlation between stand basal area and site index, except in the WI-State region where there was no correlation between the two stand variables. The UP-ONF ($F = 3.55$, $P = 0.0328$, d.f. = 2, 88) and WI-State ($F = 3.47$, $P = 0.0354$, d.f. = 2, 89) regions were the only areas where this comparison was significant. There was a significant correlation between average radial growth patterns and stand basal area in the UP-Raco ($r = 0.43$, $P = 0.0002$) and UP-ONF ($r = 0.28$, $P = 0.0075$) regions. Linear regression analysis indicated that in the UP-Raco region, stand basal area, along with site index, was a significant predictor of average annual growth rates of live dominant jack pine trees ($F = 8.38$, $P < .0001$, $r^2 = 0.23$).

Effects of jack pine budworm defoliation

Results did not show any clear or consistent annual losses of radial growth of dominant jack pine trees that were 55+ yrs old within all seven regions. Results of t-tests between average annual radial growth during outbreak and radial growth loss years and recovery years were not significant within all regions. This is likely due to inter and intra-stand variability of defoliation that occurs during a JPBW outbreak (Volney 1992; Wallin

and Raffa 1998). I was also unable to gather specific defoliation data for jack pine trees that were cored in most regions, so it was unclear whether or not sample trees had been significantly affected by defoliation.

Discussion

I wasn't expecting to find that older-aged trees had relatively higher growth rates than younger-aged trees in the UP-Raco, UP-East, UP-ONF, and WI-State regions, and that trees in well-stocked or over-stocked stands also had higher annual radial growth rates than trees in under-stocked stands in all regions except the NL-HNF region. There are a few explanations behind these unpredicted results. Higher average growth rates in older-aged trees in the UP-Raco and WI-State regions could have been a result of measured tree cores that were extracted from older trees growing on higher quality sites. Correlation results indicated that there was a significant linear association between tree age and site index in these two regions, indicating that older trees growing on higher quality sites could have relatively higher growth rates than younger trees in these regions. Relatively higher growth rates of dominant trees in heavier stocked stands could also be explained by the correlation results, which suggested that higher quality sites in all regions except the WI-State region contained denser stands of jack pine, and that these denser stands may have had better growth rates than under-stocked stands which occurred on lower quality sites.

Because of the large regional area covered and the fact that non-destructive sampling methods were used, tree core extraction was necessary instead of stem analysis. I also collected a very large sample size ($N = 1,147$) of tree cores, so a relatively rapid method of ring width measuring was necessary (used a digital scanner and computer software exclusively to measure ring widths of all cores). Consequently, ring widths of some cores may have been over-estimated because of the possible occurrence of light or missing rings following defoliation by JPBW (Conway et al. 1999b; Kulman et al. 1963;

O'Neil 1963), especially for jack pine trees growing in the intermediate and suppressed crown classes (Kozlowski 1971). Gross (1992) also noted that the use of tree cores to identify estimates of defoliation by JPBW can be negatively biased because growth impact along the bole of the tree can be variable, i.e. growth rings at 1.37 m height may not fully illustrate the impact to annual ring width patterns resulting from insect defoliation.

Total growth of jack pine from 1991 – 2000

Results indicated that growth rates of live jack pine trees from 1991 – 2000 were generally similar among most regions. Live dominant trees had higher growth rates in the UP-West region than in the other six surveyed regions. It has been well documented that jack pine can be relatively productive on better quality sites with higher moisture retention and nutrient-holding capacities than on lower quality sites with excessive moisture loss and nutrient leaching (Rudolf 1958; Rudolph and Laidly 1990). As indicated by the stand inventory data I received from regional managers, jack pine typically grew on relatively higher quality sites in the UP-West region than in most other regions, except the UP-ONF area, which had generally similar growing conditions. Mean and median site index values for jack pine in the UP-West region were generally 1.0 to 3.5 m higher than all other regions, where 1991 – 2000 growth rates were generally less.

There are a few reasons why growth rates of jack pine were generally similar in many of the regions. Dominant trees in the NL-State, NL-HNF, UP-Raco, and UP-East regions were generally growing in stands with similar site characteristics (Johnson 1990; Werlein 1998; Whitney 1992). These sites contained generally droughty to moderately drained sands with very little moisture holding capacity that are of lower site quality than

the UP-West and UP-ONF regions (Table 1-1), where annual tree growth was generally much higher.

As expected, overall growth of live dominant jack pine was higher than the growth of live jack pine in the intermediate and suppressed crown classes. Jack pine is a highly intolerant species and needs full sunlight in order to maintain adequate annual growth rates (Rudolph and Laidly 1990). Trees that are over-topped with a lack of sunlight or are growing with heavy crown competition, such as those occurring in the intermediate or suppressed crown level, generally have more difficulty capturing necessary light or mineral resources to gain sufficient annual growth (Kenkel et al. 1989). These results suggest that the effects of recurring disturbances in jack pine ecosystems such as JPBW or drought can act as natural thinning agents by stressing undesirable suppressed or intermediate trees. Heavy and persistent stress could then make intermediate and suppressed trees vulnerable to mortality, thus freeing up resources for merchantable trees growing in the dominant crown class (Conway 1998; Gross 1992).

Regional growth rates from 1991 – 2000

There are a few reasons why there were such high amounts of variation between the basal area data that I calculated from live dominant jack pine trees from permanent plots and basal area data received from cooperating forest manager's databases. The differences were likely due to the fact that my plot-level data was taken from jack pine trees only, while most stands were not complete monocultures of jack pine, e.g. plantations, and forest manager's likely included data on other companion species in stands while updating their stand inventory databases. On average, basal area data calculated from my plots were generally higher in four of the seven regions. These results

could reflect the potential that the stand inventory data I received from managers may not have reflected the density of the stand during this survey.

Within regions, relationships between annual radial growth patterns and stand inventory variables were inconsistent. Results of average radial growth rates for older-aged trees were higher than what previous studies have found. Brooks et al. (1998) found that 70+ yr old live jack pine trees in northern Saskatchewan and Manitoba grew at average rates of 1.0 mm per year, approximately 2.5 mm less than what my results of 70+ yr old dominant jack pine ($n = 66$) indicated. However, jack pine in the Great Lakes region generally have longer growing seasons and higher annual precipitation rates (Rudolph and Laidly 1990), which can contribute to higher annual radial growth increments.

As previously noted, jack pine trees growing on higher quality sites typically show higher growth rates than trees growing on lower quality sites (Rudolph and Laidly 1990). This is reflective of the growth of jack pine in all regions except the NL-State and UP-East regions, which had equal or lesser rates of annual growth on high quality sites than on low quality sites.

I was surprised to find that dominant jack pine trees in well-stocked or over-stocked stands generally grew an average of 0.1 to 0.9 mm more per year from 1991 – 2000 than trees growing in under-stocked stands in most regions. This could be explained by the possible over-estimates of annual ring widths as explained earlier because of our sampling procedure, or by a few biological factors. Recent studies have found high mortality rates of intermediate and suppressed jack pine trees in well-stocked and over-stocked stands (Klein et al. un-published data). It has also been recognized that if jack

pine stocking levels get too high, stagnation and excessive intra-stand mortality of suppressed, low vigor trees can occur (Benzie 1977; Rudolph and Laidly 1990). When this occurs, valuable light, water, and nutrient resources are released for the remaining, dominant trees. Therefore, radial increments could increase following this natural thinning stage in stands (Kenkel et al. 1989). Finally, higher growth rates of trees in heavier stocked stands could be explained by the previously explained relationship between stand basal area and site index within most of the regions.

Summary and conclusions

Some apparent inconsistencies in the results could have potentially been avoided by using different procedures. Previous research has noted that missing or light rings occur in annual growth rings of jack pine (Kulman et al. 1963; O' Neil 1963). Methods attempting to identify growth losses caused by JPBW defoliation among all regions could have also been modified or corrected by standardizing growth years by identifying one annual growth ring which was affected by one year of growth loss (i.e. identifying a widespread drought year, etc.). Results may also have been more consistent if annual growth patterns would have been analyzed with a binocular dissecting microscope to account for light or missing rings in a subset of tree cores.

This study is part of a larger research project to describe the current state of the jack pine resource in Michigan and Wisconsin. Regional growth patterns of jack pine have been quantified, and have compared the effects of within stand, crown level competition on the annual growth of trees. This baseline data could be used to build more specific future studies on the regional variation of annual radial growth rates of this economically important sub-boreal species.

Table 2-1. Comparison of average total growth rates (mm) from 1991 - 2000 ($\pm$ SE) between live dominant, and live intermediate and suppressed trees among all regions, and within each region. Regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Different letters indicate significant differences among regions within crown class categories (Fisher's LSD) ($p < 0.05$).

Region	Live Dominant		Live Intermediate & Suppressed	
NL-State	22.0 $\pm$ 0.90 <i>n</i> =118	d	18.4 $\pm$ 2.64 <i>n</i> =82	c
NL-HNF	26.7 $\pm$ 1.20 <i>n</i> =76	c	21.8 $\pm$ 1.66 <i>n</i> =21	abc
UP-Raco	25.8 $\pm$ 0.88 <i>n</i> =100	c	29.9 $\pm$ 2.33 <i>n</i> =30	bc
UP-East	26.7 $\pm$ 1.17 <i>n</i> =105	c	20.8 $\pm$ 1.57 <i>n</i> =7	abc
UP-West	35.0 $\pm$ 1.28 <i>n</i> =79	a	44.3 $\pm$ 5.30 <i>n</i> =16	a
UP-ONF	31.8 $\pm$ 0.86 <i>n</i> =90	b	26.2 $\pm$ 2.87 <i>n</i> =8	a
WI-State	26.7 $\pm$ 1.04 <i>n</i> =91	c	22.9 $\pm$ 2.23 <i>n</i> =11	ab
TOTAL¹	27.4 $\pm$ 0.42 <i>n</i> =659	a	28.4 $\pm$ 1.48 <i>n</i> =177	b

¹Different letters indicate significant differences between crown class categories (Fisher's LSD) ($p < 0.05$).

Table 2-2. Comparison of mean average growth rates (mm) from 1991 - 2000 ($\pm$ SE) for live dominant jack pine trees by tree age (yrs), site index (m), and stand basal area (m^2/ha) categories among all regions, and within regions. Regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), two regions of state land in the Upper Peninsula of Michigan (UP-East & UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Different letters indicate significant differences among categories within regions (Fisher's LSD) ($p < 0.05$).

Region	ALL	NL-State	NL-HNF	UP-Raco	UP-East	UP-West	UP-ONF	WI-State
Tree Age (yrs)								
20 - 39	2.7 $\pm$ 0.08 <i>n</i> =173	2.6 $\pm$ 0.17 <i>a</i> <i>n</i> =40	2.9 $\pm$ 0.27 <i>a</i> <i>n</i> =16	2.2 $\pm$ 0.21 <i>b</i> <i>n</i> =21	2.3 $\pm$ 0.19 <i>a</i> <i>n</i> =28	3.8 $\pm$ 0.26 <i>a</i> <i>n</i> =19	3.0 $\pm$ 0.21 <i>a</i> <i>n</i> =13	2.5 $\pm$ 0.15 <i>a</i> <i>n</i> =36
40 - 59	2.8 $\pm$ 0.07 <i>n</i> =272	2.4 $\pm$ 0.14 <i>a</i> <i>n</i> =52	2.6 $\pm$ 0.17 <i>a</i> <i>n</i> =36	3.1 $\pm$ 0.19 <i>a</i> <i>n</i> =31	2.5 $\pm$ 0.20 <i>a</i> <i>n</i> =26	3.5 $\pm$ 0.21 <i>a</i> <i>n</i> =38	3.3 $\pm$ 0.12 <i>a</i> <i>n</i> =50	2.4 $\pm$ 0.16 <i>a</i> <i>n</i> =39
60+	2.6 $\pm$ 0.09 <i>n</i> =176	2.0 $\pm$ 0.26 <i>a</i> <i>n</i> =26	2.6 $\pm$ 0.22 <i>a</i> <i>n</i> =24	2.2 $\pm$ 0.16 <i>b</i> <i>n</i> =23	2.7 $\pm$ 0.21 <i>a</i> <i>n</i> =46	3.3 $\pm$ 0.28 <i>a</i> <i>n</i> =22	2.9 $\pm$ 0.17 <i>a</i> <i>n</i> =25	3.1 $\pm$ 0.33 <i>a</i> <i>n</i> =10
Site Index (m)¹								
Low	2.7 $\pm$ 0.06 <i>n</i> =354	2.2 $\pm$ 0.12 <i>a</i> <i>n</i> =68	2.5 $\pm$ 0.17 <i>a</i> <i>n</i> =26	2.3 $\pm$ 0.11 <i>a</i> <i>n</i> =50	2.8 $\pm$ 0.19 <i>a</i> <i>n</i> =42	3.4 $\pm$ 0.17 <i>a</i> <i>n</i> =49	3.0 $\pm$ 0.11 <i>a</i> <i>n</i> =54	2.6 $\pm$ 0.13 <i>b</i> <i>n</i> =65
High	2.8 $\pm$ 0.06 <i>n</i> =307	2.2 $\pm$ 0.14 <i>a</i> <i>n</i> =50	2.7 $\pm$ 0.16 <i>a</i> <i>n</i> =50	2.9 $\pm$ 0.13 <i>a</i> <i>n</i> =49	2.6 $\pm$ 0.15 <i>a</i> <i>n</i> =64	3.6 $\pm$ 0.12 <i>a</i> <i>n</i> =30	3.5 $\pm$ 0.13 <i>a</i> <i>n</i> =37	2.8 $\pm$ 0.17 <i>a</i> <i>n</i> =27
Basal Area								
< 16.1 m^2/ha	2.6 $\pm$ 0.06 <i>n</i> =297	2.1 $\pm$ 0.14 <i>a</i> <i>n</i> =53	2.8 $\pm$ 0.18 <i>a</i> <i>n</i> =38	2.4 $\pm$ 0.11 <i>a</i> <i>n</i> =60	2.7 $\pm$ 0.18 <i>a</i> <i>n</i> =45	3.0 $\pm$ 0.26 <i>a</i> <i>n</i> =18	3.0 $\pm$ 0.15 <i>b</i> <i>n</i> =31	2.6 $\pm$ 0.14 <i>b</i> <i>n</i> =52
16.1 - 25.3 m^2/ha	2.8 $\pm$ 0.07 <i>n</i> =269	2.2 $\pm$ 0.13 <i>b</i> <i>n</i> =45	2.5 $\pm$ 0.20 <i>a</i> <i>n</i> =30	2.6 $\pm$ 0.16 <i>a</i> <i>n</i> =27	2.6 $\pm$ 0.18 <i>a</i> <i>n</i> =46	3.7 $\pm$ 0.16 <i>a</i> <i>n</i> =50	3.1 $\pm$ 0.14 <i>a</i> <i>n</i> =37	2.6 $\pm$ 0.15 <i>b</i> <i>n</i> =34
> 25.3 m^2/ha	3.1 $\pm$ 0.11 <i>n</i> =95	2.4 $\pm$ 0.24 <i>c</i> <i>n</i> =20	2.6 $\pm$ 0.14 <i>a</i> <i>n</i> =8	3.3 $\pm$ 0.28 <i>a</i> <i>n</i> =12	2.9 $\pm$ 0.31 <i>a</i> <i>n</i> =15	3.6 $\pm$ 0.29 <i>a</i> <i>n</i> =11	3.6 $\pm$ 0.15 <i>a</i> <i>n</i> =23	3.7 $\pm$ 0.45 <i>a</i> <i>n</i> =6

¹ Site index was stratified differently among regions: the Ottawa National Forest in the west Upper Peninsula and state land in west-central Wisconsin (low SI $\leq$ 16.8 m < high SI), state land in the western Upper Peninsula (low SI $\leq$ 18.3 m < high SI), other four regions (low SI $\leq$ 14.9 m < high SI).

CHAPTER 3

ACCUMULATION OF COARSE WOODY DEBRIS IN MICHIGAN AND WISCONSIN JACK PINE STANDS IN RELATION TO STAND AND SITE VARIABLES

Introduction

Coarse woody debris (CWD) is an important component of forest ecosystem dynamics. It functions as a source and sink of nutrients (Harmon et al. 1986; Jurgensen et al. 1987; Krankina et al. 1999; Laiho and Prescott 1999), provides habitat for vertebrate and invertebrate organisms (Bowman et al. 1999; Carey and Johnson 1995; Edmonds and Eglitis 1989; Graham 1925; Loeb 1999), serves as a seedbed for understory herbs and tree seedlings (Harmon et al. 1986; Thompson 1980), enhances soil organic matter, and regulates soil temperature levels (Marra and Edmonds 1994 and 1998; McFee and Stone 1966). Susceptibility of forests to catastrophic wildfires, however, can be greatly affected by the accumulation and composition of CWD (Loomis 1977; Tinker and Knight 2001).

Jack pine (*Pinus banksiana* Lambert) ecosystems are ecologically and economically important in the Great Lakes region of the U.S. and throughout much of Canada. In Michigan and Wisconsin, jack pine forests occur on nearly 485,000 ha (1.2 million acres) (Piva 1997). Jack pine is a rapid colonizer in early forest succession, tolerates relatively poor, sandy soils, and provides habitat for game and non-game species, including the endangered Kirtland's Warbler (*Dendroica kirtlandii*) (Benzie 1977). More than 270,000 cords of jack pine are annually harvested for wood fiber, amounting to a stumpage value of nearly \$10.1 million (USDA-Forest Service 2002). Management intensity in jack pine forests has escalated because of the enhanced economic value of jack pine pulp, which sold at roughly \$4/cord in 1991 and \$35/cord in

2002 (McCullough and Leefers 2000; USDA-Forest Service 2002), leading to more emphasis on shortening harvest rotations. Effects of management activities on CWD accumulation in jack pine stands, however, have not been previously addressed.

Jack pine forests in northern Michigan and Wisconsin experience multiple natural disturbances, such as wind, ice, and heavy snow that can affect the accumulation of CWD. Strong wind events occur stochastically and may be localized or occur across large areas (Zhang et al. 1999). While return intervals for catastrophic winds in north-temperate forests can be measured in centuries, storms with winds sufficient to cause damage to canopy trees in individual stands occur at frequencies measured in decades or less (Canham et al. 2001; Foster and Boose 1992). Strong winds can snap the boles of jack pine, or uproot trees, thus adding significant amounts of large diameter CWD to stands. Susceptibility of jack pine stands to damage from windstorms is affected by stand age and structure, slope, and soil type and depth (Attiwill 1994).

Biotic disturbances, including insect outbreaks, can also affect CWD accumulation and distribution in jack pine stands by killing trees or branches, or predisposing trees to attack and mortality caused by secondary pests. Outbreaks of jack pine budworm (*Choristoneura pinus pinus* Free.) (JPBW), a prominent native defoliator, occur at six to ten year intervals, and typically persist two to four years (McCullough 2000). Heavy defoliation can result in radial growth reduction, death of the terminal leader (top-kill), and tree mortality (Graham 1935; Gross 1992; Kulman et al. 1963). Mortality typically accumulates for two to three years following JPBW population collapse, and roughly 16% of trees can die following an outbreak (Conway et al. 1999a, 1999b; Gross and Meating 1994; McCullough et al. 1996).

Coarse woody debris has received relatively little attention in jack pine stands, particularly in the sub-boreal region which includes Michigan, Wisconsin, and Minnesota. Previous studies addressed decomposition rates and changes in chemical composition of jack pine CWD compared with other sub-boreal species in Minnesota (Alban and Pastor 1993) and assessed the contribution of CWD to fuel densities in Michigan and Minnesota (Brown 1966). Pedlar et al. (2002) described the structure of CWD in jack pine and other boreal forest types in northwestern Ontario, Canada. Potential associations between CWD accumulation in managed sub-boreal jack pine forests in relation to site or stand characteristics have not been previously evaluated.

A study was initiated in 2001 to assess the current jack pine resource and to quantify long-term impacts of JPBW defoliation in six regions of northern Michigan and one region of Wisconsin. Objectives of this study were to: (1) quantify accumulation, size, and decay level of CWD in a network of permanent plots recently established to monitor impacts of JPBW defoliation, and (2) evaluate relationships between site and stand variables and the volume of CWD in the seven regions. Specifically, I hypothesized that accumulation of CWD would differ among the seven regions, because of variation in frequency and severity of disturbance, and management guidelines. Within a given region, I hypothesized that accumulation of CWD would be positively related to stand age and stocking level.

Methods

Study sites

I established permanent plots from May to August from 2001 – 2003 in six regions of northern Michigan and one region in Wisconsin to assess the current state of jack pine, including CWD accumulation, and to monitor long-term impacts of JPBW. These seven regions were selected based upon the relative abundance of jack pine in the area and the frequency of JPBW outbreaks. These regions included state land in the north-central Lower Peninsula of Michigan (NL-State), the Huron-Manistee National Forest in the northeastern Lower Peninsula (NL-HNF), the Raco Plains area of the Hiawatha National Forest in the eastern Upper Peninsula of Michigan (UP-Raco), two regions of state land in the Upper Peninsula (UP-East and UP-West), the Ottawa National Forest in the western Upper Peninsula (UP-ONF), and state land in west-central Wisconsin (WI-State) (Figure 1-1). Soils were generally moderately drained to droughty, except for two regions (UP-East and WI-State), which contained areas of poorly drained peat soils (Table 1-1). The terrain was generally level to gently sloping, with moderately steep areas in the UP-West and UP-ONF regions. The WI-State region had scattered sandstone mounds (Table 1-1).

Stand selection

A stratified random sampling approach was used to select jack pine stands in each of the seven regions. Stratification was based on stand age and basal area (Table 3-1), because of their documented relationship with tree mortality and jack pine volume (Conway et al. 1999a, 1999b; McCullough et al. 1996), and because these variables are

routinely collected and used operationally by forest managers. These variables were acquired for all jack pine stands from each respective forest management agency's database. After stands were grouped by age and basal area, I randomly selected jack pine stands from each group, based on the percentage of the total number of stands that were assigned to each stand category. Number of stands per region ranged from 35 stands in the NL-State region to 78 stands in the UP-Raco region. If stands had been recently harvested or were not accessible, I randomly selected a replacement stand from the same group.

Permanent plots were established from 2001 to 2003 in a total of 356 jack pine stands that encompassed 6,374 ha (15,750 acres) in northern Michigan and Wisconsin (Table 1-3). Stand age ranged from 10 yr in the UP-ONF region to 117 yr in the UP-Raco region. Site index ranged from 9.2 m (30 ft) in the UP-East region to 22.3 m (73.2 ft) in the UP-ONF region, and stand basal area ranged from 2.3 m²/ha (10 ft²/ac) in the NL-State, NL-HNF, UP-East, and WI-State regions to 50.6 m²/ha (220 ft²/ac) in the UP-Raco region (Table 1-3).

Measurement of coarse woody debris

One circular, 0.01 ha (0.025 acre) fixed-radius plot was randomly located in each stand using compartment maps overlaid with a transparent grid. Grid cells were selected at random for plot center location, and a compass and pacing was used to establish the permanent plot center in the field. Within each plot, variables measured included jack pine tree height, diameter at breast height (DBH; 1.37 m above ground), and dominance class. Area of CWD, including stems and branches or logs ≥ 7.6 cm (3.0 in) in diameter on the ground or leaning at less than or equal to 45° from the ground, was quantified

along three evenly spaced linear transects (5.6 m by 1 m) in each circular plot (FIA Monitoring Manual, USDA-Forest Service 2001). An unbiased estimator of the volume of CWD per unit area was calculated using summed transect data for each stand and the equation:

$$V = (\pi^2/8L)\sum d_i^2$$

where V is volume in m^3/ha ; L is transect length in m; and d_i refers to the diameter of the debris in cm (Van Wagner 1968). Average volume of CWD in m^3/ha by region was then estimated.

A decay level of each piece of CWD was modified from Sollins (1982). Coarse woody debris was classified as light decay: recently down with fine twigs, bark fully intact; moderate decay: little or no bark, and presence of older aged twigs or branches, no fine twigs; and high decay: no bark or twigs, and significant woody deterioration.

Statistical analysis

Stand level estimates of CWD volume were grouped for analysis based on categories or threshold values for age and basal area typically used for jack pine management in the Lake States (Table 3-1) (Benzie 1977), and previous studies that related these variables to JPBW impact (Conway et al. 1999a, 1999b; McCullough et al. 1996). Stands were divided into two categories based on age (< 50 yrs, 50+ yrs), and three categories based on basal area (< 16.1 m^2/ha (< 70 ft^2/ac), 16.1 – 25.3 m^2/ha (70 – 110 ft^2/ac), > 25.3 m^2/ha (> 110 ft^2/ac)) (Benzie 1977; Conway 1999a; McCullough 1996). Comparisons of CWD volume among basal area categories were made using data acquired from each forest manager's inventory database. Basal area values were then

calculated using jack pine data from live dominant trees, which were collected from my permanent plots and compared with the basal area data used for CWD volume comparisons to check for accuracy of the manager's inventory databases using a standard t-test ($p < 0.05$). Basal area values from stand inventory data were used for analyses.

Normality of variables was tested with the Shapiro-Wilk test (Kuehl 2000). Log transformations did not normalize CWD data, so I used a non-parametric ranked F test to assess differences in CWD volume among regions and among categories of basal area across all regions and within regions (Neter et al. 1996). If the F test was significant, treatment means were separated using a non-parametric multiple comparison procedure ($p < 0.05$) (Zar 1984). Interactions among CWD volume and stand age and basal area categories within regions were tested using a two-way ranked F test (Neter et al. 1996). Pairwise comparisons between age categories across all regions and within each region were analyzed using a non-parametric t-test. Linear associations between volume of CWD and stand age and basal area were estimated across all regions, and within regions, using Spearman's nonparametric correlation coefficient (r_s). Data were analyzed using SAS statistical software (SAS Institute, Inc. 2000) at $p < 0.05$ level of significance.

Results

Abundance and volume of coarse woody debris

I encountered a total of 449 pieces (44,900 pieces/ha) of CWD in 128 of 356 of the jack pine stands we surveyed in the seven regions. Stands with CWD were significantly older (57.2 ± 1.21 years) than stands where no CWD occurred along plot transects (48.2 ± 1.41 years) ($t = 4.78$, $P < 0.0001$, $df = 1, 354$). Stands with CWD also had significantly higher stocking levels (17.6 ± 0.64 m²/ha basal area) than stands where no CWD occurred along transects (14.2 ± 0.67 m²/ha basal area) ($t = 3.54$, $P = 0.0005$, $df = 1, 354$). Overall, volume of CWD in the 356 jack pine stands averaged 38.1 ± 3.36 m³/ha. Over 50% of the CWD pieces were in 7.6 – 11.4 cm in diameter, which included mostly twigs and small branches (Figure 3-2). Only 3% of the pieces were in the ≥ 21.8 cm diameter class, which included fallen trees and large limbs (Figure 3-2). Overall, nearly 70% of the CWD was lightly to moderately decayed (Figure 3-3).

The UP-ONF region had significantly more pieces of CWD (198 ± 32.80 pieces/ha) than the UP-Raco, UP-East, and UP-West regions ($F = 4.54$, $P = 0.0002$, $df = 6, 349$). The UP-Raco region had the fewest number of CWD pieces, averaging only 63 ± 13.49 pieces/ha, and had the lowest percentage of stands with CWD at 36%, while the UP-ONF region had the highest percentage of stands with CWD at 66%. Volumes of CWD in the UP-ONF (64.2 ± 12.80 m³/ha) and NL-HNF (60.1 ± 10.14 m³/ha) regions were significantly higher than in the UP-Raco (21.2 ± 4.81 m³/ha) and UP-East (22.5 ± 5.75 m³/ha) regions ($F = 4.73$, $P = 0.0001$, $df = 6, 349$) (Figure 3-4). Overall, the percentage of older stands (50+ yrs) with the highest average CWD volume (≥ 50 m³/ha),

ranged from 17% and 22% at the UP-East and UP-Raco regions, to 44% and 66% at the UP-ONF and HL-HNF regions.

More than 60% of the CWD was in the smallest diameter class in four regions (NL-State, UP-Raco, UP-ONF & WI-State). Based on personal observation, these pieces were likely a result of branch breakage from high winds or heavy snow or ice. The NL-HNF and UP-West regions had greater proportions of CWD that were ≥ 15.5 cm (Figure 3-2). Based on observations, these larger pieces of CWD were likely a result of bole snap, wind-throw, or leftover snags (standing dead trees) following a clearcut harvest. Among all regions, the UP-Raco and UP-ONF regions had relatively higher proportions of lightly decayed CWD, while most of the CWD in the NL-State, NL-HNF, UP-East, UP-West, and WI-State regions was moderately to heavily decayed (Figure 3-3).

Stand inventory variables and CWD accumulation

Basal area data calculated from permanent plots for live dominant jack pine trees was significantly different from inventory database basal area data provided by cooperating agencies only in the NL-HNF ($t = 2.24$, $P = 0.0275$, d.f. = 1, 98) and UP-West ($t = 4.43$, $P < .0001$, d.f. = 1, 96) regions. Within regions, plot basal area data averaged 0.3 m²/ha, 0.5 m²/ha, and 2.2 m²/ha lower than stand inventory basal area data in the UP-ONF, UP-Raco, and NL-State regions, while plot basal area data averaged 0.4 m²/ha, 2.6 m²/ha, 4.2 m²/ha, and 8.3 m²/ha higher than stand inventory basal area data in the WI-State, UP-East, NL-HNF, and UP-West regions. When all regions were combined, a Pearson's test of linear correlation resulted in a low r-value ($r = 0.35$, $P < .001$) suggesting high variability, and likely a non-linear relationship between plot basal area data and stand inventory basal area data used for stand category analysis.

Overall, stands ≥ 50 years old had significantly higher average CWD volume ($51.6 \pm 0.62 \text{ m}^3/\text{ha}$) than younger stands ($17.3 \pm 0.90 \text{ m}^3/\text{ha}$) ($t = 5.56$, $P < .0001$, $df = 1$, 354). Well-stocked ($45.7 \pm 1.03 \text{ m}^3/\text{ha}$) to over-stocked stands ($47.0 \pm 2.67 \text{ m}^3/\text{ha}$) with basal area $\geq 16.1 \text{ m}^2/\text{ha}$ ($70 \text{ ft}^2/\text{ac}$) also had significantly higher amounts of CWD than under-stocked stands ($28.5 \pm 1.72 \text{ m}^3/\text{ha}$) when all regions were combined ($F = 3.95$, $P = 0.0201$, $df = 2$, 353). However, there was a significant interaction between stand age and basal area ($F = 8.22$, $P < .0001$, $df = 5$, 350), suggesting a possible relationship between the two variables. When all regions were combined, stand age ($p < .0001$, $r_s = 0.27$) and basal area ($p = 0.007$, $r_s = 0.18$) were significantly correlated with CWD volume in jack pine stands ($n = 356$) (Table 3-3). However, the small r_s values suggest high levels of variability among stands and are likely non-linear functions.

The NL-HNF and UP-Raco regions had significantly higher CWD volume in stands ≥ 50 yrs old than in younger stands < 50 yrs old (NL-HNF: $t = 4.03$, $P = 0.0002$, $df = 1$, 48; UP-Raco: $t = 3.66$, $P = 0.0005$, $df = 1$, 76). However, a significant interaction occurred between age and basal area in the NL-HNF region ($F = 4.97$, $P = 0.0047$, $df = 5$, 44). This trend was consistent in other regions, but not statistically significant (Figure 3-4A). All regions had more CWD volume in well or over-stocked stands (basal area $\geq 16.1 \text{ m}^2/\text{ha}$ ($70 \text{ ft}^2/\text{ac}$)), than in under-stocked stands (basal area $< 16.1 \text{ m}^2/\text{ha}$), but differences between well-stocked and under-stocked stands were significant only in the UP-Raco region ($F = 6.29$, $P = 0.0030$, $df = 2$, 75) (Figure 3-4B). Only three regions (NL-HNF, UP-West, WI-State) had significant correlations between age and CWD volume (Table 3-3). In the Raco Plains region, basal area was significantly correlated with CWD volume ($p = 0.004$, $r_s = 0.33$) (Table 3-3).

Discussion

Coarse woody debris volume in Michigan and Wisconsin

Jack pine stands in Michigan and Wisconsin had an average CWD volume of 38.1 m³/ha, which is relatively low compared to other coniferous forest types (Table 3-3). Several studies have found higher CWD levels in coniferous stands. For example, Butts and McComb (2000) found that managed stands of Douglas-fir (*Pseudotsuga menziesii* Mirb.) in the Pacific Northwest averaged 314.3 m³/ha of CWD, while Clark et al. (1998) measured an average of 100 m³/ha of CWD in fire-initiated lodgepole pine (*Pinus contorta* Dougl.) stands in the Canadian boreal forest. In managed southern yellow pine, Hess and Zimmerman (2001) recorded an average of 41.2 m³/ha of CWD volume per stand. Two studies have noted lesser amounts of CWD volume in coniferous ecosystems; black spruce (*Picea mariana* Mill.) (Pedlar et al. 2002) and ponderosa pine (*Pinus ponderosa* Dougl.)/ Douglas-fir (Robertson and Bowser 1999), which averaged 17.8 m³/ha and 15.9 m³/ha of CWD volume, respectively.

A possible explanation for the relatively lower volumes of CWD in jack pine ecosystems compared with other forest types could be the differences in maximum productivity between regions. Tree species in the Pacific Northwest region, such as Douglas-fir or Sitka spruce (*Picea sitchensis* Bong.) have much larger growth potentials than jack pine in the Lake States (Harlow et al. 1996), so when trees of their size die, much higher volumes of CWD are then produced.

Jack pine regions in Michigan and Wisconsin had different stand and density structures, along with variation in site characteristics. These regional variations could have affected the differences in the volume of CWD that we found. The variation of

CWD volume could also reflect differences in productivity levels, i.e. the more standing volume of jack pine an area is capable of growing, the greater potential that a higher volume of CWD could be left following a disturbance. The frequency and severity of disturbance may also contribute to variation in CWD volume. Canham et al. (2001) reported that localized disturbance events such as damaging thunderstorms can occur as frequently as less than every 10 years. Jack pine is relatively susceptible to wind damage (Everham and Brokaw 1996), and has generally weak wood structure, making it susceptible to bole snap during high wind events (Webb 1989). These results give support to the hypothesis that there is variation in the structure and condition of jack pine stands across the Lake States region and how they may be managed.

Coarse woody debris in relation to stand variables

There are a few reasons why there were such high amounts of variation between the basal area data that I calculated from live dominant jack pine trees from permanent plots and basal area data received from cooperating forest manager's databases. The differences were likely due to the fact that my plot-level data was taken from jack pine trees only, while most stands were not complete monocultures of jack pine, e.g. plantations, and forest manager's likely included data on other companion species in stands while updating their stand inventory databases. On average, basal area data calculated from my plots were generally higher in four of the seven regions. These results could reflect the potential that the stand inventory data I received from managers may not have reflected the density of the stand during this survey.

I hypothesized that the age and stocking level of jack pine stands would positively affect the accumulation of CWD volume. Our results show that older jack pine stands

contributed the highest levels of CWD volume. Similarly, in managed Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) forests in southern Finland, Siitonen et al. (2000) concluded that the oldest stands (129 – 198 yrs) had significantly higher average CWD volumes than relatively younger stands (95 – 118 yrs). Because of the significant correlation between stand age and basal area, we felt that basal area did not have as important of an effect on CWD volume as stand age.

Further evidence suggests that forest management and stand-initiating disturbance in the Lakes States region may play important roles in explaining variability of CWD accumulation among regions. Many of the old stands at the UP-ONF region were in designated riparian “buffer” zones where some windfall or stem breakage likely occurred, consequently adding larger diameter CWD (Mellstrom, USDA Forest Service, personal communication). In the NL-HNF region, a large percentage of the older aged jack pine stands were damaged or killed by fire in the 1940’s through the 1960’s and not salvaged, because of a lack of a jack pine market during that time period (McNichols, USDA Forest Service, personal communication). Mortality from fires, or from other disturbance events, may have added large diameter CWD in these stands, which could explain the relatively high CWD levels in the 50+ yr age class in this region.

The management intensity of jack pine stands may also play an important role in the size structure of CWD. Whole-tree harvesting or felling and bucking to a minimum diameter of 7.6 cm (3.0 in) DIB (diameter inside bark) have been used as the primary harvesting techniques among all regions (Beyer, Born, McNichols, Mellstrom, personal communication). This can result in very little to no large diameter slash left on-site. Duvall and Grigal (1999) concluded that the main structural component of CWD in

managed red pines stands in the Lakes States was smaller diameter logging slash. However, their results of logging slash apply mainly to younger stands that have regenerated following harvest. Logging slash is present in much fewer, if any, quantities in older jack pine stands, where the majority of CWD was measured in this study. Thus, logging may not be as important as first thought in adding sufficient amounts of CWD to jack pine stands. Benzie (1977) noted that jack pine stands can stagnate under certain conditions, and heavy competition among smaller diameter individuals can result in high levels of mortality, thus potentially adding higher amounts of smaller diameter CWD to stands. The fact that jack pine does not generally grow to be very large sizes (Rudolph and Laidly 1990) could then be an explanation of why there is generally little amounts of large diameter CWD in these jack pine regions. A better explanation may be natural disturbances, such as heavy snow, wind, or hail, which may damage jack pine trees by breaking off branches or dead terminal leaders from top-killed trees, which could account for the relatively high levels of smaller diameter CWD in older stands.

Within regions, older aged stands that were well-stocked or over-stocked, consistently had more CWD volume. Jack pine is a short-lived species, and quickly deteriorates beyond a threshold age, generally 50 to 60 yrs, depending upon site conditions (Benzie 1977; Rudolph and Laidly 1990). Consequently, an increase in CWD volume in old stands should be expected. Attiwill (1994) also noted that older aged jack pine is more susceptible to branch or bole damage from wind, ice, hail, or heavy snow.

Ecological importance of coarse woody debris

The role that the size and structure of CWD plays as a fire and wildlife habitat component in jack pine stands is unclear. However, jack pine is known as a pyrophilic

species (Rudolph and Laidly 1990), and lightning and human-caused ignition can add variation to the historic average fire return interval reported by Zhang et al. (1999). I propose that the persistence of large diameter CWD in older stands, perhaps caused by wind-throw or stem breakage, is an important component for fuel loads in jack pine. Alban and Pastor (1993) found that jack pine bolts 1.2 m in length with an average diameter of 14.7 cm in Minnesota had the slowest decay rates compared with quaking aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and red pine (*Pinus resinosa* Ait.) bolts of similar size. Jack pine boles decreased in density slower than the other species, thus potentially remaining as fuel for relatively longer periods of time. However, jack pine slash left following harvest practices which is in contact with mineral soil may decay at faster rates (Harmon et al. 1986). My results were similar to that study in that nearly 50% of the CWD pieces > 15.1 cm in diameter were in the low decay stage, while only 32% of the large diameter pieces were highly decayed.

The specific uses and habitat that jack pine CWD provides for wildlife species has not previously been addressed. Many insect species use all decay stages of CWD during their life cycles (Edmonds and Eglitis 1989; Graham 1925), and several species of salamanders and ground dwelling rodents (Bowman et al. 1999; Hayes and Cross 1987) use CWD as shelter. I made several observations of red squirrels (*Tamiasciurus hudsonicus* Erxleben) and black bears (*Ursus americanus* Pallas) that had apparently used downed logs for their respective feeding habits in several jack pine stands. Loeb (1999) found that larger quantities of CWD in managed longleaf pine (*Pinus palustris* Mill.) stands in South Carolina provided important habitat for cotton mice (*Peromyscus*

gossypinus) These results suggest that higher CWD volumes in managed jack pine forests could provide quality habitat for both small and large mammals.

Summary and conclusions

The results described here are part of a larger study focusing on the current state of the jack pine resource across Michigan and Wisconsin. This research is the first to quantitatively evaluate CWD in jack pine stands. Future research should focus on the structure and function of CWD within jack pine regions to understand what factors cause accumulation of CWD volume, and to further understand what ecological role that CWD has in jack pine ecosystems.

Table 3-1. Characteristics used to stratify jack pine stands for evaluation of coarse woody debris volume (m^3/ha) in six regions of Michigan and one region of Wisconsin.

Age (years)	Basal Area Class (m^2/ha) ¹	Number of Stands
Young (< 50)	Under	94
	Well	40
	Over	5
Old (50+)	Under	67
	Well	106
	Over	44
TOTAL		356

¹Basal area categories represent stands considered to be:

Under-stocked = (< 16.1 m^2/ha); Well-stocked = (16.1 - 25.3 m^2/ha); Over-stocked = (> 25.3 m^2/ha).

Table 3-2. Number of stands sampled and Spearman's non-parametric correlation coefficients (r_s) between coarse woody debris volume (m^3/ha) and stand characteristics among the seven regions. Regions surveyed included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Significant correlations are in bold and p-values are in parentheses ($P < 0.05$).

Region	N	Correlation with coarse woody debris (m^3/ha) (r_s)	
		Age (yrs.)	Basal Area (m^2/ha)
NL-State	35	0.12 (0.480)	-0.08 (0.666)
NL-HNF	50	0.49 (0.003)	0.23 (0.102)
UP-Raco	78	0.20 (0.077)	0.33 (0.004)
UP-East	50	0.18 (0.214)	0.11 (0.452)
UP-West	49	0.31 (0.028)	0.18 (0.203)
UP-ONF	50	0.17 (0.238)	0.08 (0.568)
WI-State	44	0.31 (0.040)	0.06 (0.669)
ALL	356	0.27 (<.001)	0.18 (0.007)

Table 3-3. Volume of coarse woody debris (m^3/ha) for selected forest types of North America. Coarse woody debris volume was calculated from an equation derived by Wagner (1968)^a.

Region	Forest Type	Managed/Un- managed	Mean CWD Volume (m^3/ha)	Reference	Comments
Rocky Mountain region	Ponderosa pine/ douglas fir	Unmanaged	15.9	Robertson and Bowser 1999	
Canada boreal-mixed	Black spruce	Managed	17.8	Pedlar et al. 2002	minimum diameter = 10 cm
Managed southern pine	Yellow pine type	Managed	41.2	Hess and Zimmerman 2001	minimum diameter = 10 cm
Canada boreal-mixed	Balsam fir/ black spruce	Managed	41.9	Sturtevant et al. 1997	
Canada boreal-mixed	Lodgepole pine; Spruce/fir	Unmanaged	100.0	Clark et al. 1998	all stands fire initiated
Pacific Northwest	White fir/ pine mix	Unmanaged	156.8	Harmon et al. 1987	minimum diameter = 15 cm
Canada boreal-mixed	Aspen/jack pine mix	Managed	160.8	Pedlar et al. 2002	minimum diameter = 10 cm
Pacific Northwest	Douglas fir	Unmanaged	217.8	Spies et al. 1988	
Pacific Northwest	Douglas fir	Managed	314.3	Butts and McComb 2000	
Pacific Northwest	Sequoia-mix	Unmanaged	722.3	Harmon et al. 1987	minimum diameter = 15 cm

^a38.1 m^3/ha CWD volume reported for jack pine stands in Michigan and Wisconsin.

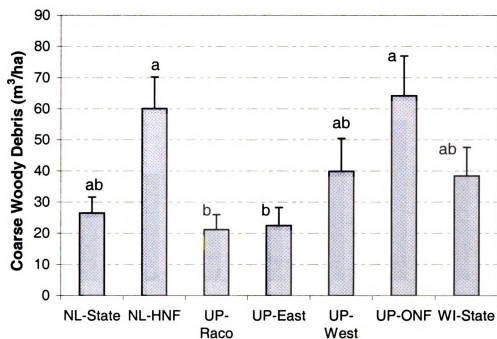


Figure 3-1. Mean ($\pm$ SE) volume (m^3/ha) of coarse woody debris in jack pine stands in seven regions in Michigan and Wisconsin. Regions surveyed included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Different letters indicate significant differences among regions ($p < 0.05$).

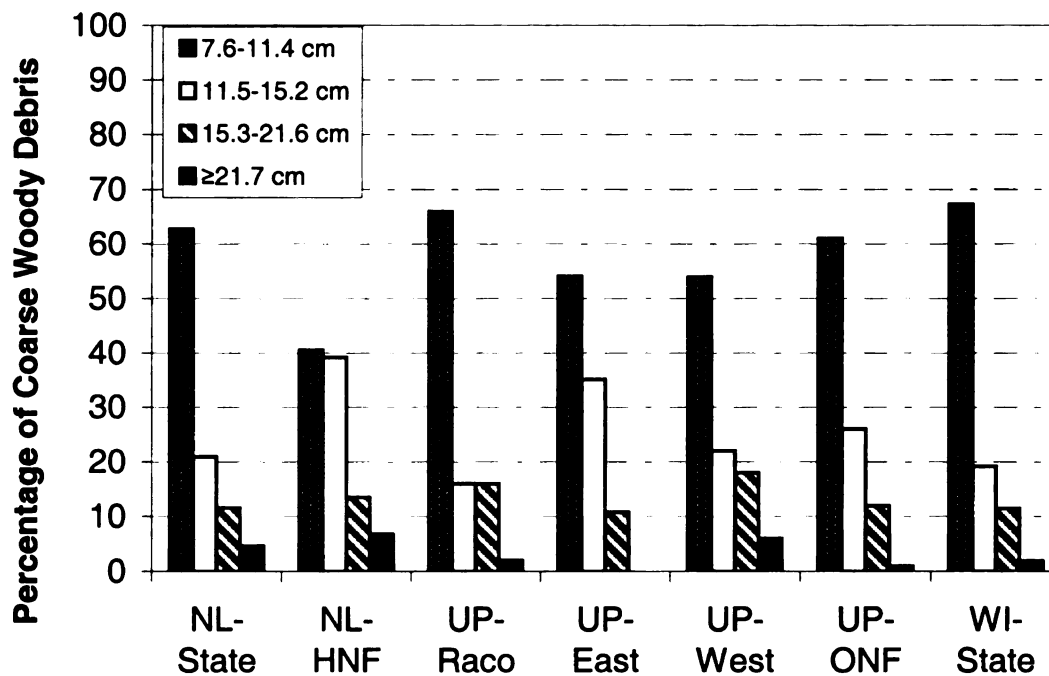


Figure 3-2. Distribution of coarse woody debris (m^3/ha) by diameter class (cm) in seven regions in Michigan and Wisconsin. Regions surveyed included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State).

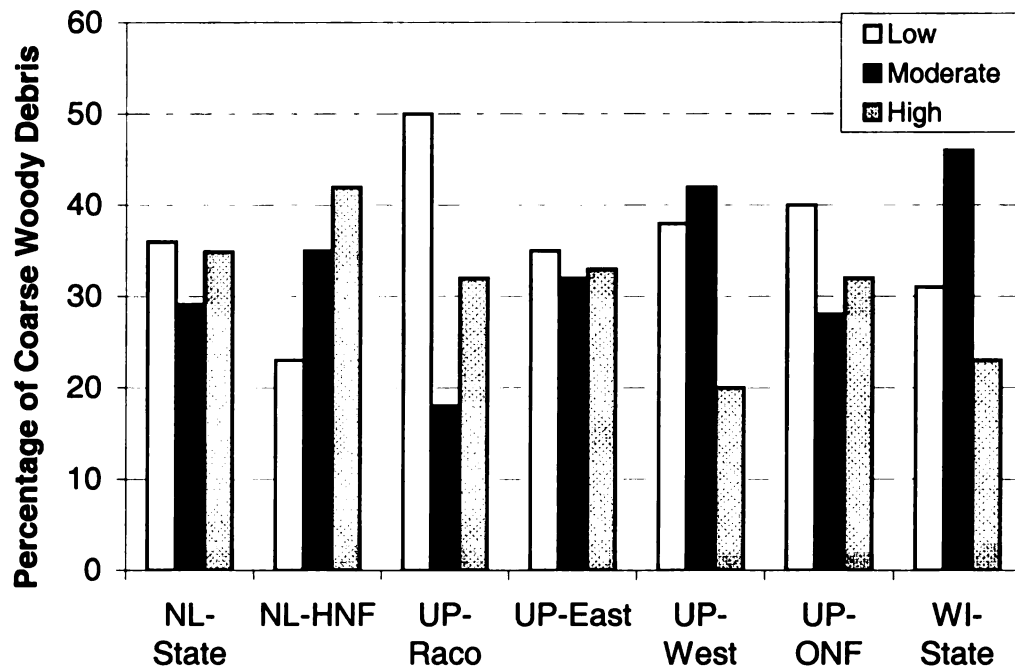


Figure 3-3. Distribution of coarse woody debris volume (m^3/ha) by decay class in the seven regions of Michigan and Wisconsin. Low decay refers to recently fallen pieces with fine twigs and bark fully intact; moderately decayed pieces had little or no bark or fine twigs; highly decayed pieces had obvious deterioration of woody tissue. Surveyed regions included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State).

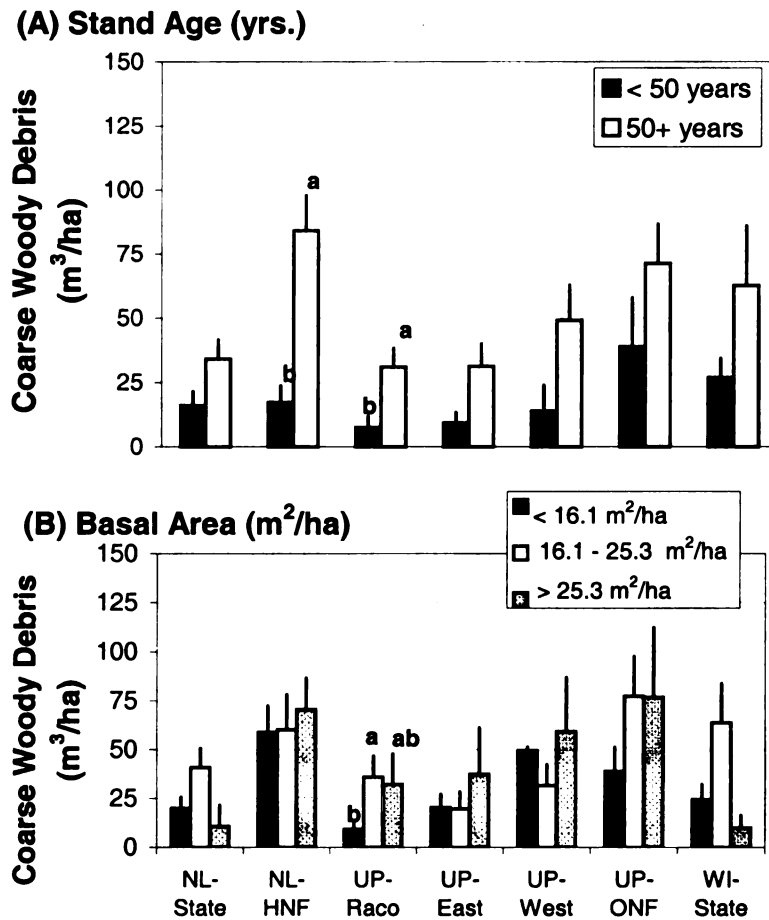


Figure 3-4. Mean ($\pm$ SE) volume (m^3/ha) of coarse woody debris in seven regions in Michigan and Wisconsin grouped by (A) stand age (yrs), and (B) basal area (m^2/ha). Regions surveyed included state land in northern lower Michigan (NL-State), the Huron-Manistee National Forest (NL-HNF), the Raco Plains area of the Hiawatha National Forest (UP-Raco), state land in the eastern Upper Peninsula of Michigan (UP-East), state land in the western Upper Peninsula (UP-West), the Ottawa National Forest (UP-ONF), and state land in west-central Wisconsin (WI-State). Different letters indicate significant differences among groups within regions ($p < 0.05$).

CONCLUSIONS, LIMITATIONS, AND FUTURE RESEARCH

Conclusions

Overall, standing volume and growth of jack pine was higher in the UP-West and UP-ONF regions than the other five regions. The NL-State, NL-HNF, UP-Raco, and UP-East regions generally had similar levels of standing jack pine volume and annual growth rates. Among all regions, CWD volume was higher in the UP-ONF and NL-HNF regions than the other five regions, but trends were more variable. Jack pine mortality was consistently higher in the intermediate and suppressed crown classes than in the dominant crown class, while the percentage of standing dead volume was higher in the dominant crown class than in the intermediate or suppressed classes.

Overall, stand age was most consistently related to mortality, dead volume, and accumulation of CWD volume. Stands that were under-stocked consistently had less mortality and dead volume, and had lower amounts of CWD volume, while well-stocked or over-stocked stands generally had higher levels of mortality, dead volume, and CWD volume. However, basal area was generally correlated with stand age, so results of differences among basal area categories should be interpreted with caution.

Management recommendations

One of the main objectives of this study was to collect baseline data about the current status of the structure of jack pine stands in northern Michigan and Wisconsin. A reason for collecting these data among several regions of jack pine was to validate the Jack Pine Budworm Decision Support System (JPBW DSS), a GIS-based extension which was developed from empirical data collected in the Raco Plains area of the

Hiawatha National Forest, one of the surveyed regions. Impact data were collected and analyzed from other regions, so that relationships between stand inventory variables and tree mortality, standing dead volume, and annual radial growth among different regions could be assessed to determine if the JPBW DSS could be applied to other managed jack pine regions. Overall results of this research indicated that the JPBW DSS could be used for management of jack pine in other regions other the UP-Raco region, where the model was developed. Those regions included the NL-State, NL-HNF, and the UP-East regions, where growing conditions for jack pine (i.e. site index and soil characteristics) seem to be relatively similar. However, updates or changes may be needed for the JPBW DSS for it to be validated for use in managing jack pine stands in the UP-West, UP-ONF, or WI-State regions, where site conditions seem to be different from the other regions.

Other management implications resulting from this study included maintenance of short rotation ages of jack pine for management in areas where the structure and growth potential of stands seems to deteriorate beyond a threshold age (generally 50 – 60 yrs). However, regions with the highest ratio of dead volume to live volume were in areas that had site characteristics which grew relatively productive jack pine stands. Harvest rotations may be longer in these regions, but my results tend to contradict that longer rotations of jack pine are economically viable on higher quality sites. Site index generally showed inconsistent trends in determining levels of mortality and standing dead volume. Research previously conducted in the UP-Raco region found that higher quality stands had more mortality and standing dead volume. Even though my results showed significantly higher mortality on higher quality sites than on lower quality sites in the UP-Raco region, none of the other regions showed statistical significance for that

comparison. However, trends among all other regions were counter-intuitive to how management guidelines for jack pine are instituted (Benzie 1977), suggesting that current guidelines in some regions may need to be re-evaluated. Because stand basal area was consistently correlated with stand and tree age, and the fact that age consistently had more powerful relationships with impact variables, implications should be interpreted with caution. Higher mortality in heavier stocked stands could be interpreted as a result of natural self-thinning in stands, but because correlations indicated that most heavily stocked stands were older, it could be concluded that the age of the stands was a more important factor than stand stocking levels.

Limitations

One of the most highly limiting factors for this study was the availability of time and budget to either survey more stands within each region, or to survey other regions of jack pine. The range of jack pine extends into northern areas of both Wisconsin and Minnesota. Extending our survey into other jack pine areas would have provided important information on the current state of jack pine in other Lake States areas, and would have also provided results to other forest manager's on the availability and validity for the use of the JPBW DSS model. Further, I was also not able to obtain tree-specific information about defoliation by JPBW in all regions, which would have been valuable for my attempts to identify growth losses in merchantable trees resulting from defoliation by JPBW among regions.

Future Research

Future research should focus on the potential relationships between jack pine mortality and site index. My results indicated an inconsistent relationship between

mortality, dead volume, and site index among regions. However, because of the trends among regions that more mortality may occur on higher quality sites suggests that jack pine trees growing on these sites may be more susceptible to mortality by JPBW defoliation or other disturbances.

Further studies should also focus on exploring more specific growth patterns of jack pine by using stem analysis techniques in different regions to identify annual volume losses from impacts on growth by JPBW defoliation. Other studies should also focus on the ecological importance of CWD in jack pine stands by quantifying characteristics of downed wood and collecting empirical data about habitat use and importance of CWD for wildlife species in managed jack pine ecosystems.

APPENDICES

APPENDIX A

APPENDIX A

Long-term Impact Plot Locations

Table A-1. Locations and global positioning system (GPS) coordinate waypoints of permanent plot centers with identification of compartment numbers, stand numbers, and plot numbers within the seven surveyed regions in Michigan and Wisconsin.

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
Lower Peninsula -					
Michigan					
NL-State	44° 44' 07.0" N	84° 15' 01.6" W	9	4	1
	44° 44' 03.2" N	84° 15' 02.8" W	9	4	2
	44° 45' 59.3" N	84° 15' 03.7" W	9	20	1
	44° 45' 58.0" N	84° 15' 01.0" W	9	20	2
	44° 45' 54.9" N	84° 15' 04.7" W	9	20	3
	--	--	9	27	--
	44° 44' 29.8" N	84° 14' 55.6" W	9	46	1
	44° 44' 42.6" N	84° 15' 03.1" W	9	46	2
	44° 44' 46.0" N	84° 15' 01.7" W	9	46	3
	44° 44' 53.8" N	84° 14' 53.1" W	9	46	4
	44° 44' 41.0" N	84° 14' 32.0" W	9	46	5
	44° 16' 06.8" N	85° 19' 56.5" W	110	25	1
	44° 16' 01.4" N	85° 19' 59.9" W	110	25	2
	44° 16' 53.2" N	85° 19' 16.9" W	110	89	1
	44° 16' 49.5" N	84° 19' 20.3" W	110	89	2
	44° 16' 48.1" N	85° 19' 13.7" W	110	89	3
	44° 22' 39.5" N	85° 10' 40.7" W	115	78	1
	44° 22' 41.0" N	85° 40' 42.2" W	115	78	2
	44° 34' 20.4" N	85° 04' 59.1" W	135	20	1
	44° 34' 21.5" N	85° 04' 53.3" W	135	20	2
	44° 42' 41.0" N	85° 15' 44.2" W	161	3	1
	44° 42' 47.5" N	85° 15' 47.8" W	161	3	2
	44° 42' 45.4" N	85° 15' 36.9" W	161	3	3
	44° 43' 27.5" N	85° 13' 48.9" W	162	27	1
	44° 43' 23.9" N	85° 13' 42.5" W	162	27	2
	44° 43' 24.9" N	85° 13' 39.3" W	162	27	3
	44° 43' 08.3" N	85° 15' 36.1" W	162	42	1
	44° 42' 58.9" N	85° 15' 36.1" W	162	42	2
	44° 43' 01.8" N	85° 15' 54.0" W	162	47	1
	44° 43' 34.6" N	85° 16' 20.7" W	162	55	1
	44° 43' 29.0" N	85° 16' 19.3" W	162	55	2
	44° 43' 40.5" N	85° 16' 09.6" W	162	55	3
	44° 43' 45.2" N	85° 13' 53.1" W	164	58	1
	44° 43' 45.3" N	85° 13' 50.6" W	164	58	2
	44° 43' 48.1" N	85° 14' 56.9" W	164	69	1
	44° 44' 02.1" N	85° 15' 08.6" W	164	69	2

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
NL-State	44° 42' 42.8" N	84° 48' 40.1" W	179	8	1
	44° 42' 47.8" N	84° 48' 44.9" W	179	8	2
	44° 41' 37.4" N	84° 49' 56.3" W	180	7	1
	44° 41' 38.9" N	84° 49' 47.2" W	180	7	2
	44° 41' 43.7" N	84° 49' 47.6" W	180	7	3
	44° 41' 28.4" N	84° 49' 59.7" W	180	7	4
	44° 41' 55.8" N	84° 48' 53.8" W	180	14	1
	44° 41' 49.3" N	84° 48' 53.8" W	180	14	2
	44° 41' 45.1" N	84° 48' 45.1" W	180	14	3
	44° 41' 09.1" N	84° 49' 60.0" W	180	20	1
	44° 41' 11.4" N	84° 49' 54.2" W	180	20	2
	44° 41' 10.5" N	84° 49' 22.1" W	180	21	1
	44° 41' 08.9" N	84° 49' 16.3" W	180	21	2
	44° 28' 46.8" N	84° 12' 16.6" W	197	37	3
	44° 28' 22.0" N	84° 12' 25.9" W	197	65	1
	44° 28' 08.0" N	84° 12' 21.1" W	197	65	2
	44° 28' 15.0" N	84° 10' 07.0" W	197	126	1
	44° 28' 09.5" N	84° 10' 16.2" W	197	126	2
	44° 28' 06.2" N	84° 10' 18.2" W	197	126	3
	44° 28' 48.9" N	84° 12' 07.4" W	198	37	1
	44° 28' 50.7" N	84° 12' 10.8" W	198	37	2
	44° 34' 59.5" N	84° 38' 22.5" W	231	2	1
	44° 34' 58.1" N	84° 38' 26.9" W	231	2	2
	44° 34' 58.2" N	84° 38' 32.5" W	231	2	3
	44° 34' 53.7" N	84° 38' 40.9" W	231	2	4
	44° 34' 30.9" N	84° 37' 10.7" W	231	12	1
	44° 34' 18.3" N	84° 37' 20.4" W	231	12	2
	44° 34' 20.9" N	84° 37' 15.9" W	231	12	3
	44° 34' 21.9" N	84° 37' 36.0" W	231	12	4
	44° 48' 33.8" N	84° 39' 18.8" W	233	7	1
	44° 38' 30.3" N	84° 39' 09.2" W	233	7	2
	44° 37' 30.4" N	84° 39' 05.1" W	233	27	1
	44° 37' 27.3" N	84° 39' 16.6" W	233	27	2
	44° 37' 23.6" N	84° 39' 13.1" W	233	27	3
	44° 41' 10.2" N	84° 29' 03.6" W	280	30	1
	44° 41' 11.5" N	84° 28' 59.2" W	280	30	2
	44° 41' 13.5" N	84° 28' 57.2" W	280	30	3
	44° 41' 08.0" N	84° 28' 52.2" W	280	30	4
	44° 46' 36.0" N	84° 22' 35.2" W	288	55	1
	44° 46' 41.7" N	84° 22' 29.8" W	288	55	2
	44° 46' 45.5" N	84° 22' 29.1" W	288	55	3
	44° 46' 37.4" N	84° 22' 25.9" W	288	55	4
	44° 47' 24.1" N	84° 24' 49.3" W	290	32	1
	44° 47' 24.5" N	84° 24' 43.5" W	290	32	2
	44° 47' 32.0" N	84° 24' 45.5" W	290	32	3
	44° 49' 57.4" N	84° 24' 53.5" W	291	37	1
	44° 49' 49.9" N	84° 24' 54.1" W	291	37	2

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
NL-State	44° 49' 42.9" N	84° 24' 45.8" W	291	37	3
	44° 35' 48.3" N	84° 33' 28.6" W	297	2	1
	44° 35' 52.5" N	84° 33' 29.4" W	297	2	2
	44° 34' 37.9" N	84° 33' 51.2" W	297	22	1
	44° 34' 40.9" N	84° 33' 45.7" W	297	22	2
	44° 34' 42.0" N	84° 33' 42.9" W	297	22	3
	44° 34' 28.1" N	84° 32' 31.7" W	297	28	1
	44° 34' 25.0" N	84° 32' 28.9" W	297	28	2
	44° 34' 27.6" N	84° 32' 15.2" W	297	28	3
	44° 34' 04.7" N	84° 32' 52.6" W	297	43	1
	44° 34' 08.5" N	84° 32' 46.1" W	297	43	2
	44° 34' 05.2" N	84° 32' 57.2" W	297	43	3
NL-HNF	44° 38' 08.0" N	84° 35' 15.4" W	31	11	1
	44° 39' 07.6" N	84° 26' 24.4" W	61	5	2
	44° 39' 07.6" N	84° 25' 36.3" W	66	3	3
	44° 39' 25.1" N	84° 24' 10.5" W	67	4	4
	44° 38' 01.8" N	84° 23' 27.7" W	63	17	5
	44° 39' 28.7" N	84° 21' 20.4" W	83	38	6
	44° 38' 21.6" N	84° 19' 13.0" W	110	61	7
	44° 39' 08.1" N	84° 18' 00.2" W	110	77	8
	44° 44' 12.0" N	84° 17' 40.5" W	110	52	9
	44° 40' 16.4" N	84° 17' 08.9" W	111	17	10
	44° 38' 31.8" N	84° 17' 26.9" W	113	29	11
	44° 38' 13.9" N	84° 16' 32.4" W	115	4	12
	44° 38' 48.3" N	84° 31' 21.7" W	40	2	13
	44° 38' 55.8" N	84° 29' 33.2" W	41	84	14
	44° 35' 11.2" N	84° 15' 07.1" W	118	26	15
	44° 39' 52.8" N	84° 14' 54.8" W	134	4	16
	44° 39' 42.8" N	84° 12' 43.4" W	139	1	17
	44° 38' 58.5" N	84° 10' 48.0" W	166	27	18
	44° 40' 22.2" N	84° 06' 55.5" W	167	1	19
	44° 40' 25.4" N	84° 07' 27.7" W	167	2	20
	44° 39' 30.1" N	84° 06' 37.8" W	169	20	21
	44° 38' 44.3" N	84° 06' 12.3" W	170	5	22
	44° 39' 03.0" N	84° 04' 26.0" W	229	43	23
	44° 38' 57.0" N	84° 05' 15.0" W	229	25	24
	44° 39' 00.8" N	84° 02' 21.6" W	231	18	25
	44° 39' 01.7" N	84° 01' 22.7" W	228	17	26
	44° 38' 11.6" N	84° 01' 05.4" W	228	37	27
	44° 37' 50.1" N	84° 01' 10.5" W	227	54	28
	44° 38' 00.7" N	84° 16' 18.4" W	115	8	29
	44° 39' 40.1" N	84° 06' 56.9" W	169	33	30
	44° 36' 05.6" N	83° 52' 08.9" W	752	8	31
	44° 35' 29.2" N	83° 50' 44.3" W	753	13	32
	44° 32' 08.9" N	83° 49' 02.3" W	804	10	33
	44° 29' 46.9" N	83° 48' 34.8" W	324	2	34
	44° 27' 53.9" N	83° 48' 30.0" W	357	8	35

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
NL-HNF	44° 28' 22.5" N	83° 50' 35.8" W	323	12	36
	44° 29' 57.7" N	83° 43' 48.9" W	308	5	37
	44° 29' 26.2" N	83° 44' 32.8" W	309	12	38
	44° 28' 53.9" N	83° 42' 17.2" W	329	13	39
	44° 28' 28.8" N	83° 41' 16.3" W	329	8	40
	44° 21' 53.9" N	83° 40' 16.6" W	440	4	41
	44° 25' 09.5" N	83° 21' 28.9" W	375	11	42
	44° 24' 58.2" N	83° 21' 42.7" W	375	24	43
	44° 23' 12.9" N	83° 39' 52.5" W	429	7	44
	44° 25' 03.7" N	83° 38' 48.5" W	364	11	45
	44° 25' 30.6" N	83° 33' 50.5" W	367	29	46
	44° 25' 50.3" N	83° 32' 25.8" W	368	11	47
	44° 26' 15.1" N	83° 38' 30.6" W	365	4	48
	44° 35' 02.1" N	84° 15' 00.8" W	118	33	49
	44° 39' 19.4" N	84° 06' 44.6" W	169	21	50
Upper Peninsula -					
Michigan					
UP-Raco	46° 18' 46.0" N	84° 53' 59.2" W	78	72	1
	46° 18' 54.5" N	84° 51' 47.5" W	78	17	2
	46° 18' 57.1" N	84° 52' 40.5" W	78	16	3
	46° 18' 56.1" N	84° 51' 29.2" W	78	23	4
	46° 18' 37.2" N	84° 51' 56.9" W	78	27	5
	46° 18' 18.1" N	84° 52' 23.4" W	78	55	6
	46° 17' 50.5" N	84° 51' 47.5" W	78	80	7
	46° 17' 26.9" N	84° 51' 10.4" W	78	46	8
	46° 19' 07.6" N	84° 54' 00.1" W	78	69	9
	46° 17' 58.2" N	84° 53' 52.5" W	78	4	10
	46° 18' 51.7" N	84° 52' 50.1" W	78	18	11
	46° 17' 46.6" N	84° 52' 51.9" W	78	40	12
	46° 17' 39.9" N	84° 53' 23.8" W	78	39	13
	46° 18' 45.9" N	84° 50' 14.3" W	79	19	14
	46° 18' 48.9" N	84° 50' 18.2" W	79	18	15
	46° 19' 51.5" N	84° 49' 41.1" W	79	3	16
	46° 19' 42.8" N	84° 49' 58.5" W	79	9	17
	46° 18' 49.1" N	84° 51' 09.5" W	79	22	19
	46° 17' 33.2" N	84° 51' 09.5" W	79	25	20
	46° 19' 05.5" N	84° 51' 02.6" W	79	33	21
	46° 18' 35.9" N	84° 50' 57.3" W	79	45	22
	46° 21' 01.0" N	84° 54' 24.4" W	58	71	23
	46° 20' 18.2" N	84° 55' 28.7" W	58	68	24
	46° 19' 42.0" N	84° 54' 52.9" W	58	17	25
	46° 19' 51.5" N	84° 55' 40.3" W	58	27	26
	46° 21' 42.6" N	84° 47' 56.4" W	49	4	27
	46° 22' 03.2" N	84° 48' 03.2" W	49	61	28
	46° 22' 24.8" N	84° 48' 02.9" W	49	60	29
	46° 22' 27.2" N	84° 47' 40.7" W	49	5	30
	46° 22' 14.8" N	84° 47' 18.4" W	49	9	31

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
UP-Raco	46° 22' 01.1" N	84° 47' 23.8" W	49	11	32
	46° 21' 51.1" N	84° 47' 13.3" W	49	21	33
	46° 22' 01.6" N	84° 47' 11.0" W	49	29	34
	46° 22' 01.4" N	84° 46' 56.2" W	49	30	35
	46° 22' 02.3" N	84° 46' 44.4" W	49	36	36
	46° 22' 23.9" N	84° 46' 13.7" W	49	23	37
	46° 22' 06.2" N	84° 46' 21.7" W	49	35	38
	46° 22' 00.8" N	84° 46' 22.7" W	49	62	39
	46° 22' 19.1" N	84° 46' 09.8" W	49	34	40
	46° 22' 04.5" N	84° 46' 13.7" W	49	67	41
	46° 22' 02.6" N	84° 45' 23.1" W	49	71	42
	46° 21' 49.6" N	84° 46' 28.9" W	49	38	43
	46° 22' 23.7" N	84° 45' 45.8" W	49	70	44
	46° 22' 38.5" N	84° 46' 03.1" W	49	68	45
	46° 22' 33.9" N	84° 46' 07.9" W	49	33	46
	46° 23' 23.9" N	84° 46' 11.0" W	30	8	47
	46° 23' 18.5" N	84° 46' 07.0" W	30	30	48
	46° 23' 16.7" N	84° 46' 19.2" W	30	39	49
	46° 23' 55.3" N	84° 46' 48.2" W	30	5	50
	46° 23' 46.1" N	84° 46' 15.2" W	30	9	51
	46° 23' 13.3" N	84° 46' 27.5" W	30	32	52
	46° 23' 07.2" N	84° 47' 13.5" W	31	37	53
	46° 23' 17.9" N	84° 47' 28.4" W	31	24	54
	46° 23' 26.4" N	84° 47' 00.7" W	31	36	55
	46° 24' 04.9" N	84° 46' 55.7" W	31	30	56
	46° 24' 08.7" N	84° 47' 38.1" W	31	53	57
	46° 24' 29.6" N	84° 48' 04.8" W	31	18	58
	46° 22' 36.3" N	84° 48' 09.3" W	32	3	59
	46° 22' 36.1" N	84° 49' 20.6" W	32	84	60
	46° 24' 23.4" N	84° 48' 23.9" W	32	53	61
	46° 23' 02.8" N	84° 48' 18.5" W	32	21	62
	46° 23' 17.5" N	84° 50' 25.4" W	48	32	63
	46° 22' 33.4" N	84° 50' 50.4" W	48	26	64
	46° 22' 27.8" N	84° 48' 11.3" W	48	1	65
	46° 22' 07.0" N	84° 48' 24.2" W	48	15	66
	46° 22' 00.3" N	84° 48' 15.4" W	48	5	67
	46° 22' 01.7" N	84° 49' 16.9" W	48	18	68
	46° 19' 05.5" N	84° 53' 32.5" W	77	3	69
	46° 19' 04.6" N	84° 53' 27.3" W	77	61	70
	46° 19' 11.0" N	84° 52' 48.5" W	77	12	71
	46° 19' 03.2" N	84° 52' 43.9" W	77	58	72
	46° 19' 06.3" N	84° 51' 49.1" W	77	21	73
	46° 19' 14.2" N	84° 51' 12.8" W	77	69	74
	46° 21' 07.4" N	84° 54' 07.9" W	57	7	75
	46° 21' 14.8" N	84° 53' 47.2" W	57	6	76
	46° 21' 23.0" N	84° 52' 53.9" W	57	14	77
	46° 20' 31.2" N	84° 52' 59.9" W	57	3	78

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
UP-East	46° 20' 14.8" N	84° 52' 58.5" W	57	26	81
	46° 38' 05.0" N	85° 44' 31.1" W	8	1	1
	46° 39' 06.2" N	85° 37' 29.3" W	17	95	2
	46° 36' 53.6" N	85° 36' 48.3" W	19	7	3
	46° 40' 00.8" N	85° 34' 29.4" W	23	12	4
	46° 40' 18.4" N	85° 35' 35.3" W	23	14	5
	46° 39' 24.9" N	85° 33' 13.7" W	25	8	6
	46° 37' 31.8" N	85° 36' 08.8" W	26	61	7
	46° 40' 17.6" N	85° 30' 31.7" W	32	20	8
	46° 40' 03.1" N	85° 28' 36.8" W	33	44	9
	46° 40' 16.0" N	85° 27' 36.3" W	33	31	10
	46° 40' 13.9" N	85° 27' 18.4" W	33	30	11
	46° 41' 15.8" N	85° 26' 18.6" W	33	3	12
	46° 39' 31.2" N	85° 27' 02.4" W	34	3	13
	46° 49' 23.7" N	85° 28' 03.9" W	34	36	14
	46° 38' 40.3" N	85° 28' 12.0" W	34	25	15
	46° 35' 52.2" N	85° 28' 30.5" W	35	54	16
	46° 36' 42.2" N	85° 30' 06.6" W	35	62	17
	46° 36' 46.7" N	85° 29' 39.1" W	35	60	18
	46° 36' 25.2" N	85° 29' 48.8" W	35	58	19
	46° 39' 40.4" N	85° 26' 15.9" W	36	25	20
	46° 39' 46.8" N	85° 26' 25.5" W	36	24	21
	46° 39' 23.3" N	85° 26' 40.0" W	36	37	22
	46° 40' 30.5" N	85° 26' 23.7" W	36	13	23
	46° 40' 51.6" N	85° 28' 09.6" W	32	10	24
	46° 38' 44.5" N	85° 27' 15.6" W	36	87	25
	46° 41' 46.8" N	85° 23' 51.9" W	38	25	26
	46° 41' 56.6" N	85° 24' 51.1" W	38	39	27
	46° 39' 49.2" N	85° 25' 30.8" W	39	54	28
	46° 25' 37.5" N	85° 50' 07.5" W	93	105	29
	46° 42' 54.0" N	85° 08' 46.2" W	56	31	30
	46° 42' 45.3" N	85° 08' 48.3" W	56	30	31
	46° 38' 33.9" N	85° 07' 39.7" W	58	46	32
	46° 38' 52.7" N	85° 04' 43.0" W	63	20	33
	46° 44' 11.3" N	85° 01' 10.5" W	59	98	34
	46° 45' 06.7" N	85° 06' 03.9" W	59	234	35
	46° 35' 48.3" N	85° 06' 47.9" W	65	119	36
	46° 38' 27.1" N	85° 04' 12.8" W	63	34	37
	46° 38' 30.1" N	85° 04' 14.6" W	63	35	38
	46° 40' 30.8" N	85° 06' 24.0" W	62	16	39
	46° 41' 43.3" N	85° 05' 48.4" W	61	8	40
	46° 42' 55.7" N	85° 05' 51.6" W	60	2	41
	46° 43' 05.5" N	85° 05' 46.1" W	60	11	42
	46° 37' 43.1" N	85° 06' 23.2" W	65	55	43
	46° 37' 36.9" N	85° 07' 13.2" W	65	69	44
	46° 46' 07.9" N	84° 57' 40.0" W	59	2	45
	46° 38' 13.2" N	85° 06' 03.4" W	63	45	46

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
UP-East	46° 42' 22.4" N	85° 02' 41.2" W	67	37	47
	46° 41' 13.0" N	85° 06' 27.5" W	61	25	48
	46° 43' 02.4" N	85° 01' 27.9" W	67	2	49
	46° 40' 13.0" N	85° 28' 40.7" W	33	43	50
UP-West	See Table C-2				
UP-ONF	46° 37' 08.0" N	88° 37' 50.8" W	5	6	1
	46° 36' 57.0" N	88° 39' 02.6" W	6	1	2
	46° 37' 03.4" N	88° 39' 16.5" W	6	7	3
	46° 36' 48.4" N	88° 38' 60.0" W	6	8	4
	46° 36' 17.5" N	88° 51' 11.2" W	13	9	5
	46° 35' 35.1" N	88° 51' 14.7" W	13	8	6
	46° 36' 46.6" N	88° 38' 49.9" W	19	8	7
	46° 36' 33.8" N	88° 37' 49.8" W	19	4	8
	46° 33' 59.4" N	88° 49' 46.4" W	26	20	9
	46° 35' 43.8" N	88° 50' 19.4" W	26	35	10
	46° 35' 00.7" N	88° 37' 09.7" W	20	2	11
	46° 34' 59.2" N	88° 50' 49.3" W	27	27	12
	46° 34' 07.7" N	88° 50' 27.5" W	27	11	13
	46° 34' 16.8" N	88° 51' 23.6" W	28	17	14
	46° 34' 52.0" N	88° 51' 53.9" W	28	47	15
	46° 34' 46.8" N	88° 52' 19.3" W	28	3	16
	46° 33' 32.6" N	88° 57' 45.1" W	65	24	17
	46° 33' 13.5" N	88° 58' 18.8" W	65	53	18
	46° 33' 14.5" N	88° 58' 13.5" W	25	27	19
	46° 32' 47.1" N	88° 57' 58.1" W	65	56	20
	46° 32' 24.8" N	88° 58' 54.4" W	73	51	21
	46° 31' 55.5" N	88° 58' 31.2" W	73	3	22
	46° 38' 34.1" N	88° 37' 44.2" W	111	43	23
	46° 33' 59.1" N	88° 49' 17.1" W	44	21	24
	46° 34' 24.9" N	88° 49' 11.5" W	44	8	25
	46° 31' 46.8" N	88° 56' 49.2" W	64	31	26
	46° 30' 48.2" N	88° 56' 11.3" W	76	15	27
	46° 34' 03.6" N	88° 50' 04.4" W	27	34	28
	46° 37' 24.9" N	88° 39' 34.3" W	112	57	29
	46° 37' 31.6" N	88° 39' 49.9" W	112	56	30
	46° 33' 07.5" N	88° 57' 27.9" W	65	10	31
	46° 31' 59.2" N	88° 58' 19.5" W	73	48	32
	46° 31' 49.3" N	88° 58' 32.5" W	73	32	33
	46° 32' 12.5" N	88° 59' 09.4" W	73	5	34
	46° 32' 33.5" N	88° 59' 00.1" W	66	22	35
	46° 38' 33.6" N	88° 40' 22.5" W	112	22	36
	46° 37' 47.9" N	88° 40' 03.8" W	112	53	37
	46° 37' 44.9" N	88° 39' 48.7" W	112	59	38
	46° 37' 15.8" N	88° 39' 24.7" W	6	2	39
	--	--	73	39	40
	46° 33' 11.7" N	88° 59' 21.8" W	38	13	41
	46° 38' 51.7" N	88° 38' 33.5" W	112	33	42

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
UP-ONF	46° 35' 29.3" N	88° 36' 59.2" W	19	22	43
	46° 38' 26.6" N	88° 37' 05.8" W	111	30	44
	46° 38' 33.6" N	88° 37' 10.7" W	111	55	45
	46° 37' 22.7" N	88° 39' 24.6" W	112	58	46
	46° 33' 46.0" N	88° 57' 02.1" W	65	1	47
	46° 36' 55.9" N	88° 37' 48.5" W	5	2	48
	46° 33' 55.5" N	88° 57' 26.4" W	39	25	49
	46° 32' 39.7" N	88° 49' 31.6" W	60	9	50
Wisconsin					
WI-State	44° 15' 22.1" N	90° 50' 34.0" W	5	8	1
	44° 21' 58.6" N	90° 41' 18.5" W	39	10	2
	44° 10' 45.5" N	90° 37' 04.5" W	93	2	3
	44° 11' 51.6" N	90° 38' 19.0" W	84	2	4
	44° 12' 40.2" N	90° 38' 09.8" W	79	7	5
	44° 14' 01.5" N	90° 39' 15.6" W	72	10	6
	44° 13' 35.8" N	90° 34' 09.9" W	76	4	7
	44° 16' 18.4" N	90° 38' 36.7" W	64	5	8
	44° 16' 11.6" N	90° 36' 58.7" W	69	15	9
	44° 15' 49.9" N	90° 37' 02.5" W	69	20	10
	44° 15' 53.8" N	90° 36' 19.9" W	69	9	11
	44° 20' 02.4" N	90° 40' 14.3" W	45	1	12
	44° 19' 48.8" N	90° 34' 01.9" W	50	3	13
	44° 20' 04.7" N	90° 39' 36.4" W	45	3	14
	44° 18' 28.0" N	90° 38' 57.2" W	56	10	15
	44° 23' 35.9" N	90° 44' 32.4" W	14	9	16
	44° 18' 13.1" N	90° 38' 15.1" W	56	13	17
	44° 17' 13.7" N	90° 38' 38.9" W	63	2	18
	44° 16' 53.4" N	90° 38' 25.4" W	62	5	19
	44° 20' 09.9" N	90° 41' 48.5" W	28	9	20
	44° 22' 04.1" N	90° 41' 26.9" W	17	5	21
	44° 19' 24.5" N	90° 38' 27.6" W	46	2	22
	44° 15' 47.1" N	90° 35' 49.4" W	69	22	23
	44° 21' 00.8" N	90° 44' 06.6" W	25	8	24
	44° 18' 22.0" N	90° 39' 07.1" W	56	12	25
	44° 24' 44.4" N	90° 39' 37.6" W	32	18	26
	44° 25' 30.7" N	90° 40' 05.1" W	32	12	27
	44° 24' 30.9" N	90° 39' 24.6" W	31	1	28
	44° 24' 25.8" N	90° 38' 25.1" W	33	1	29
	44° 24' 16.5" N	90° 38' 54.3" W	33	6	30
	44° 23' 48.9" N	90° 40' 39.5" W	34	6	31
	44° 23' 40.0" N	90° 42' 00.9" W	10	14	32
	44° 23' 32.3" N	90° 43' 08.1" W	12	1	33
	44° 23' 05.3" N	90° 43' 03.0" W	12	5	34
	44° 23' 07.8" N	90° 41' 30.0" W	11	7	35
	44° 21' 56.7" N	90° 42' 11.1" W	18	2	36
	44° 22' 59.5" N	90° 43' 18.7" W	13	2	37
	44° 23' 29.2" N	90° 44' 12.4" W	13	11	38

Table A-1 (cont.)

Region	GPS Coordinates		Compartment	Stand	Plot
	Latitude	Longitude			
WI-State	44° 23' 26.9" N	90° 43' 58.9" W	13	13	39
	44° 23' 17.6" N	90° 44' 02.3" W	13	4	40
	44° 22' 46.0" N	90° 40' 15.7" W	35	8	41
	44° 21' 53.7" N	90° 41' 54.5" W	18	1	42
	44° 20' 09.0" N	90° 45' 09.0" W	30	2	43
	44° 22' 04.1" N	90° 44' 53.7" W	21	2	44

Table A-2. Locations and ground-recorded directions to established permanent plot locations with compartment numbers, stand numbers, and plot numbers in state land in the western Upper Peninsula of Michigan (UP-West).

Directions	Compartment	Stand	Plot #
9 chains @ 64' from Perch Lk Rd./2-track intersection Starting Point: JP sapling w/ orange dot	227	12	1
4.5 chains @ 67' from 2-track intersections Starting Point: JP w/ orange dot	254	10	2
6 chains @ 47' from curve along County Rd CG Starting Point: JP w/ orange dot	254	12	3
9.5 chains @ 129' from stand 3/County Rd. CG intersection Starting Point: JP w/ orange dot	254	3	4
9.5 chains @ 200' from stand 5/4 border along 2-track Starting Point: JP w/ red and orange dots	254	5	5
10.5 chains @ 13' from stand 24/25 border along County Rd. CD Starting Point: 3 chains + 3 paces from small gravel pit	254	24	6
16.5 chains @ 45' from Plot 6 Starting Point: 1 chain backsite from Plot 6	254	7	7
3.5 chains @ 150' from stand 46/32 border along County Rd. CD Starting Point: JP w/ orange dot	254	46	8
6.5 chains @ 28' from County Rd. CD/2-track intersection Starting Point: JP w/ orange dot	254	29	9
7 chains @ 145' from stand 18/19 border along 2-track Starting Point: JP w/ orange dot	254	18	10
6.5 chains @ 109' from stand 15/1 border along 2-track Starting Point: RM saplings w/ orange spray	267	15	11

Table A-2 (cont.)

16.5 chains @ 347' from end of 2-track Starting Point: Birches w/ orange spray	267	13	12
20 chains @ 355' from plot 12 Starting Point: Plot 12	267	3	13
7.5 chains @ 5' from stand 2/3 border along County Rd. 553 Starting Point: JP w/ orange dot	274	2	14
12.5 chains @ 356' from stand 10/19/prvtlnd border along 2-track Starting Point: JP w/ orange dots	274	10	15
3.5 chains @ 325' from stand 26 along County Rd. 581 Starting Point: JP w/ orange dot	228	26	16
7 chains @ 24' from stand 14/44 border along 2-track Starting Point: Spruce w/ orange dot	228	14	17
11.5 chains @ 33' from AAA Rd./2-track intersection Starting Point: JP w/ orange dot	208	28	18
12 chains @ 114' from stand 23/14/15 border Starting Point: WP w/ orange dot	208	15	19
5 chains @ 307' from stand 27/2-track intersection Starting Point: JP w/ orange dot	298	27	20
4 chains @ 11' from 2-track intersection Starting Point: BC shrubs w/ orange dots	219	25	21
7 chains @ 41' from stand 2/9 border along 2-track Starting Point: JP w/ orange dot	229	2	22
3.5 chains @ 353' from stand 17/18 border along Flat Rock Rd. Starting Point: JP sapling w/ orange spray	229	17	23
3 chains @ 21' from stand 24/33 border along 2-track Starting Point: BC w/ orange spray	243	24	24

Table A-2 (cont.)

4 chains @ 95' from stand 32/53 border along 2-track Starting Point: JP w/ orange dot	243	32	25
16 chains @ 40' from stand 11/31 border along County Rd. FR Starting Point: JP w/ orange dot	253	11	26
3 chains @ 25' from County Rd. PRA/2-track intersection Starting Point: RP w/ orange dot	253	26	27
10 chains @ 101' from stand 19/25 border along 2-track Starting Point: JP saplings w/ orange spray	253	19	28
4.5 chains @ 109' from stand 9/72 border along County Rd. FFJ Starting Point: JP w/ orange dot	225	9	29
3 chains @ 146' from stand 5/6 border along 2-track Starting Point: JP w/ orange dot	268	5	30
6 chains @ 55' from Floodwood Rd./2-track intersection Starting Point: RP w/ orange dot	245	1	31
6.5 chains @ 212' from stand 17/408 border along 2-track Starting Point: ASP w/ orange dot	245	17	32
3 chains @ 16' from stand 50/65 border along 2-track Starting Point: JP w/ orange dot	245	50	33
7 chains @ 222' from stand 49/65 border along 2-track Starting Point: ASP w/ orange dot	245	49	34
8 chains @ 210' from stand 48/29/24 border along 2-track Starting Point: ASP w/ orange dot	245	48	35
5.5 chains @ 19' from stand 4/5/50 border Starting Point: JP w/ orange dot	221	4	36
6 chains @ 65' from County Rd. 553/2-track intersection Starting Point: JP dwarf w/ orange spray	280	13	37

Table A-2 (cont.)

3 chains @ 337' from Floodwood Rd./2-track intersection Starting Point: Blue reflector @ 2-track X	243	33	38
11 chains @ 139' from County Rd. 553/2-track intersection Starting Point: Seasonal road sign	280	10	39
13 chains @ 40' from stand 4/2 border along 2-track Starting Point: JP w/ orange dot	208	4	40
7 chains @ 75' from stand 35/34 border along 2-track .45 mi N of 5th St. Starting Point: RP w/ orange spray	280	23	41
7 chains @ 198' from stand 13/12 border along privateland line Starting Point: Cherry w/ orange spray	276	13	42
11.5 chains @ 145' from stand 40/50 border off 2-track Starting Point: JP w/ orange dot	280	40	43
8 chains @ 355' from stand 37/408 border along Delphi Rd. Starting Point: JP w/ orange dot	280	37	44
5 chains @ 151' from stand 3/privateland border along 2-track Starting Point: JP w/ orange dot	284	3	45
6 chains @ 237' from stand 23 corner along 2-track Starting Point: JP w/ orange dot	284	23	46
18 chains @ 235' from Plot 46 Starting Point: Plot 46	284	2	47
10 chains @ 134' from stand 1/privateland border along 2-track Starting Point: JP w/ orange dot	284	1	48
3 chains @ 323' from stand 7/privateland border along road Starting Point: JP w/ orange dot	274	7	49

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	
14.9 m	49 ft
16.8 m	55 ft
18.3 m	60 ft
Basal Area	
16.1 m ² /ha	70 ft ² /ac
25.3 m ² /ha	110 ft ² /ac

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