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Second Growth Forest as Potential Marten Habitat in Western Newfoundland: An Examination of Forest Habitat Structure and Microtine Abundance

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SECOND GROWTH FOREST AS POTENTIAL MARTEN HABITAT IN WESTERN NEWFOUNDLAND: AN EXAMINATION OF FOREST HABITAT STRUCTURE AND MICROTINE ABUNDANCE

by

Brian R. Sturtevant

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Fisheries and Wildlife Ecology

Approved:

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Logan, Utah

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ABSTRACT

Second Growth Forest as Potential Marten Habitat in Western
Newfoundland: An Examination of Forest Habitat
Structure and Microtine Abundance

by

Brian R. Sturtevant, Master of Science

Utah State University, 1996

Major Professor: Dr. John A. Bissonette
Department: Fisheries and Wildlife

The American marten (Martes americana) is associated with large tracts of relatively undisturbed, mature coniferous forests. I examined coarse woody debris (CWD) structure and small mammal abundance with respect to forest age and stem structure within second-growth forests, in comparison with old-growth stands in western Newfoundland. Results suggest that a critical change in marten habitat quality may occur at stand senescence, due to decreased tree competition, more complex subcanopy structure, and increased meadow vole (Microtus pennsylvanicus) abundance.

Analysis of stem structure within a chronosequence of 19 second-growth stands indicated high intertree competition, with dense canopy closure and active self-thinning, until stand senescence at 80 years. Old-growth stands were less dense, offering more canopy openings. CWD volume observed within the chronosequence demonstrated the typical U-shaped temporal relationship observed in other forested systems. Lowest CWD volumes were observed within semimature to mature second growth. Highest levels of both CWD volume and structural complexity corresponded with stand senescence and old growth.

Small mammals were sampled within immature, semimature, mature, and silviculturally overmature coniferous stands in western Newfoundland during 1993 and 1994. Meadow voles were most abundant within overmature stands ($\underline{P}<0.05$). Vole abundance was negatively correlated with relative density ($\underline{P}<0.01$) and positively correlated with CWD ($\underline{P}<0.01$). I address the applicability of mainland marten habitat generalizations to the unique depauperate condition of Newfoundland.

Results from this study suggest that the critical elements of marten foraging habitat currently are found within a senescent forest stand structure. Further review of the literature and Newfoundland harvest records indicated that anthropogenic disturbance transformed a historically heterogeneous forested landscape into a more contiguous, even-aged, second-growth environment. Using the stand density management diagram, I designed a silvicultural approach to marten habitat management that simulates the structure of older forests within younger stages of forest development.

(135 pages)

DEDICATION

To my parents, Robert and Carol Sturtevant. You have given me a deep respect for life and all things wild. Your positive attitude and strong work ethic have always served as models for my own. This document would not have been possible without your unwavering faith, and your loving support.

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I also thank the many individuals at the WNMF for their effort in facilitating this project. Special thanks to Tina Newbury, Bill Dennis, and Keith Chaulk for their hard work in the field. Similarly, I thank the Newfoundland Division of Wildlife (NDW), the Newfoundland Forest Service (NFS), and Forestry Canada (FC) for their logistic support. I am grateful to Lem Mayo (NDW) and Bill Greene (NDW) for their field guidance and experience, and their persistence in enlightening me in the ways of Newfoundlanders. I also thank Gary Drew for his valuable input on marten behavior, and Darren Fillier for his discussions on forest habitat manipulation. I am grateful to Peter Newton (FC) for providing the relative density equations for balsam fir in Newfoundland, based upon his own unpublished data. In addition, Mont Osmond (NFS) and Wayne Dey (NFS) provided permanent sample plot data, and Sara Jeffreys (WNMF) created the color map of the WNMF. Dr. Ray Dueser provided

valuable expertise in the interpretation of my small mammal data, and Sue Durham aided in the statistical analysis.

Brian R. Sturtevant

FOREWORD

This thesis is presented in six chapters. Chapter I is a general introduction and overview, and chapter VI is an overall review, both of which were formatted in the style of the Journal of Wildlife Management. My research was organized into the four middle chapters (II-V), each addressing an aspect of this project. These chapters have been formatted in the style of Ecological Applications (chapter II), the Journal of Wildlife Management (chapter III), the Northern Journal of Applied Forestry (chapter IV), and Forest Ecology and Management (chapter V). Literature citations, tables, and figures are organized within individual chapters.

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CHAPTER I

INTRODUCTION

The American marten (Martes americana) is one of the few mammalian predators that is most abundant within undisturbed coniferous and mixed coniferous forests of North America. Because these habitats also represent a valuable economic resource, the conservation of marten often conflicts with the interests of timber and pulpwood industries. The problem is especially acute in western Newfoundland, where a threatened subspecies of marten (M. a. atrata) faces an uncertain future due to large-scale habitat loss and degradation (Thompson 1991). A recent coalition of government resource agencies, private corporations, and public environmental groups formed an organization known as the Western Newfoundland Model Forest, Inc. (Fig I-1). The program's primary goal is to create an integrated resource management and sustainable forest development plan for western Newfoundland. As a prime indicator of the health of the region's mature and overmature forests, the recovery of marten is paramount to the Model Forest's objectives.

Multiple studies in Newfoundland and elsewhere have focused on the short-term effects of timber harvest on marten habitat (Soutiere 1979, Snyder and Bissonette 1987, Bissonette et al. 1989, Harrison et al. in press, Hargis and Bissonette in press). The results were clear: Marten populations cannot exist on landscapes dominated by open clearcuts. Furthermore, regenerating forests typically lack the structural complexity of old growth, apparently required by

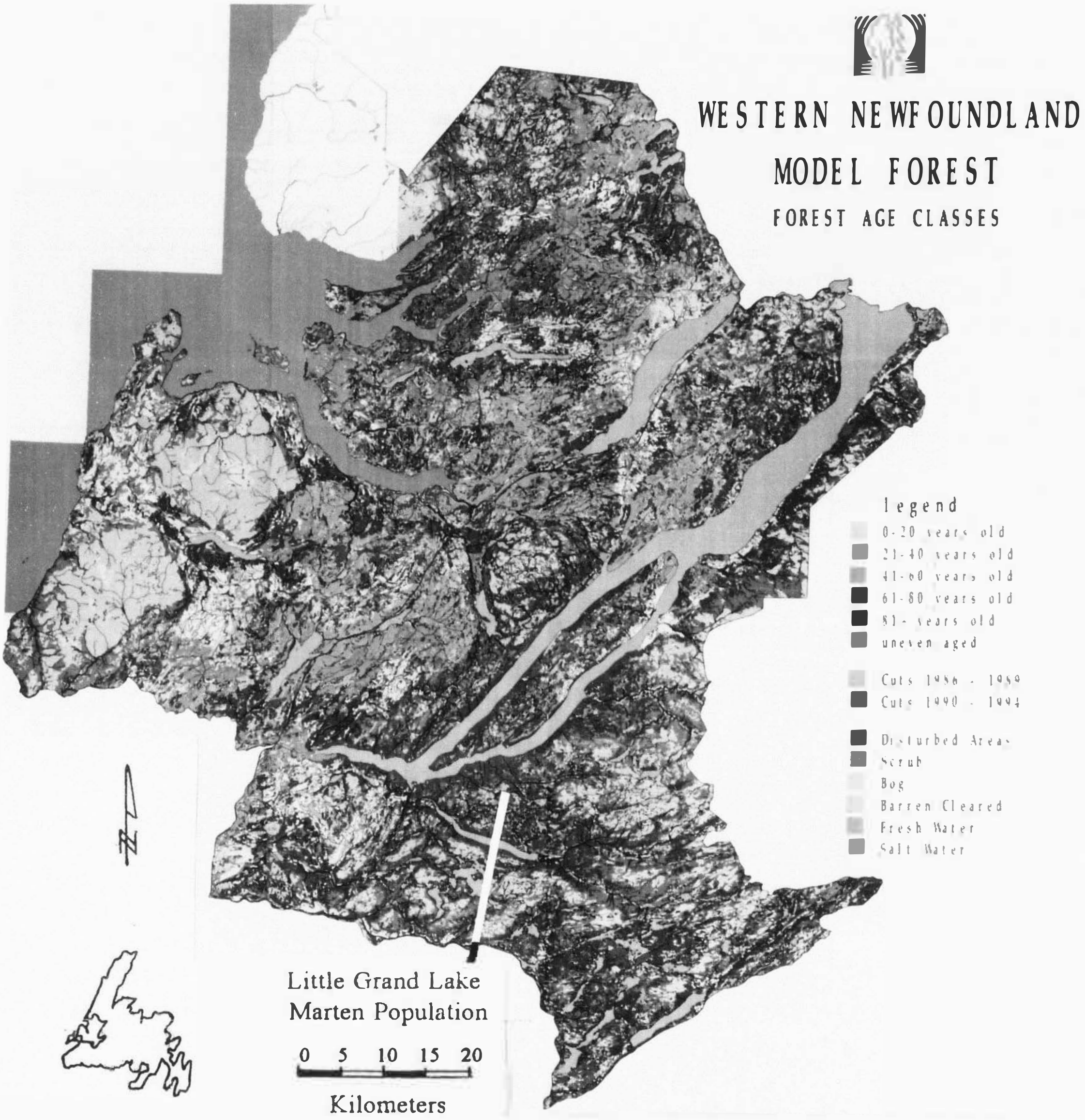

Fig. I-1. Landscape composition of the Western Newfoundland Model Forest, showing the distribution and extent of second-growth forest.[1] The marten population core currently resides in a region of old growth (indicated above).

[1] The majority of forests less than 80 years old are second growth.

marten (Thompson 1991, Thompson and Curran 1995). Conceptually, second growth should provide the structural elements necessary to sustain marten at some stage of development (Thompson and Harestad 1994). This information is critical to the formation of an integrated forest management plan that incorporates marten habitat as an objective. Indeed, the majority of Newfoundland is now characterized by different stages of second-growth forest, representing an enormous land base that may be used by marten in the future (e.g., Fig. I-1). Further, if we can understand some of the mechanisms influencing marten habitat quality in terms of forest structure, we may be able to improve the quality of younger forests for marten, using silvicultural techniques.

Marten remain active throughout the winter months, and must therefore find food, avoid predators, and keep relatively warm during this energetically demanding period. Coarse woody debris (CWD) is often cited as an important winter habitat component for marten, particularly as a vehicle for accessing a critical prey base beneath the snowpack (Campbell 1979, Corn and Raphael 1992, Sherburne and Bissonette 1993,1994, Bissonette and Sherburne 1994). An abundant feature within old forests, CWD is typically less available within a second-growth environment, and may limit marten use of these areas. Newfoundland marten may be additionally stressed due the lack of available prey species. As is typical of insular systems, Newfoundland supports a depauperate prey base (Tucker 1988, Bissonette et al. 1989), and the only available microtine species is the meadow vole (Microtus pennsylvanicus).

Because this important prey species is normally associated with open habitats, its availability within the forest cannot be assumed.

The goal of this project was to evaluate the relationship between forest age, CWD, and prey availability within second-growth forests in comparison with typical old-growth marten habitat. The following four chapters address different aspects of this goal. In chapter II, *"Coarse Woody Debris as a Function of Age, Stand Structure, and Disturbance in Boreal Newfoundland*," I examined a chronosequence of second-growth stands in comparison with old-growth stands. This chapter lends insight into some of the mechanisms that influence forest habitat structure (i.e., coarse woody debris, stem, and crown structure) following clear-cut disturbance in Newfoundland. Chapter III, *"Habitat Associations of Microtus pennsylvanicus Within Forests of Western Newfoundland as a Factor Influencing Marten Habitat Quality*," examined meadow vole abundance within different stages of forest development. Together, Chapters II and III suggest a link between food availability and stand development for marten in Newfoundland.

Stand structure may be easily manipulated using silvicultural techniques (e.g., thinning), however the consequences of these manipulations on marten habitat suitability are largely unknown. Yield-density relationships, when incorporated into density management diagrams, may be used to predict the consequences of various density manipulations on stem structure (Drew and Flewelling 1977). I constructed a diagram in Chapter IV, *"A Stand Density*

Management Diagram for Mixed Balsam Fir--Black Spruce Stands," as a tool to examine possible impacts and benefits of density management to marten habitat within second-growth forest.

In Chapter V, "*Temporal and Spatial Dynamics of Boreal Forest Structure in Western Newfoundland: Silvicultural Implications for Marten Habitat Management*," I combined the stand-level dynamics examined in Chapters II and III to create a conceptual model of stand development as it relates to marten habitat. I then compared the spatial distribution of forest stand development stages found on natural and second-growth landscapes, based on literature review and Newfoundland Forest Service inventory data, and applied my conceptual model to each landscape. Finally, I used the stand density management diagram constructed in Chapter IV to design a stand-level silvicultural prescription intended to enhance marten habitat within second growth stands. Together, Chapters II-V provide a comprehensive assessment of second-growth forest as potential marten habitat in Newfoundland based on forest structure and microtine abundance.

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CHAPTER II

COARSE WOODY DEBRIS AS A FUNCTION OF AGE, STAND STRUCTURE, AND DISTURBANCE IN BOREAL NEWFOUNDLAND[1]

Abstract. The volume and structural attributes of coarse woody debris (CWD) were examined in naturally thinned balsam fir and mixed balsam fir--black spruce forests of western and central Newfoundland. CWD within a chronosequence of second-growth stands following clear-cut disturbance demonstrated the typical "U-shaped" temporal pattern observed in other forested systems, and CWD abundance approached old-growth levels by approximately 80 years. Total volume of logs on the forest floor ranged from 15.2 m^3/ha in a 58-year-old stand to 78.1 m^3/ha in an 80-year-old stand. CWD was lowest within 50- to 70-year-old second-growth stands. The highest levels of CWD corresponded to the senescence of even-aged stands into a silviculturally overmature state. Defoliation disturbance increased both the volume and the structural diversity of CWD within silviculturally mature second-growth stands. Residual debris from the initial clear-cut disturbance, as well as residual standing trees, affected CWD abundance in second-growth stands during the early stages of forest development. Residual debris was rare within stands greater than 50-60 years of age. Factors affecting the rate of stem

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[1] Coauthored by Brian R. Sturtevant, John A. Bissonette, James N. Long, and David W. Roberts.

growth, such as site quality and initial stocking levels, should influence the accumulation and overall abundance of CWD within later stages of forest development. I therefore introduce the application of yield-density relationships as a method of examining stand-level dynamics of CWD.

INTRODUCTION

Coarse woody debris (CWD) is an important functional and structural component of forested ecosystems (Harmon et al. 1986). Often cited as an indication of "old-growth" status, CWD provides refugia for small mammals, salamanders, and fish (Tallmon and Mills 1994, Raphael 1984); cavities for den and nest sites; and foraging locations for insectivores (Raphael 1984). In cold climates, CWD may also provide important subnivean structure for non-hibernating mammals (Bissonette and Sherburne 1994, Sherburne and Bissonette 1993, Buskirk et al. 1989, Spencer 1984). Fallen tree boles also contribute significantly to nutrient cycling and energy flow in forested systems, and provide structure for regulating sediment displacement (Harmon et al. 1986). Insight into the dynamics of CWD will help land managers understand the impact of current management regimes on the CWD cycle, and incorporate this important resource into future plans for a more productive, diverse, and healthy forest ecosystem.

Several studies of CWD within forest chronosequences have described a general "U-shaped" temporal pattern, observed in northern hardwood (Tritton 1980), wave-regenerated balsam fir (Abies balsamea) (Lambert et al. 1980, Lang 1985), lodgepole pine (Pinus contorta) (Romme 1982), and Douglas-fir (Pseudotsuga menzeisii) forests (Spies et al. 1988) (Fig. II-1). In general, debris levels tend to be high following the initial stand disturbance. Residual debris then declines over time, with little additional input from the regenerating stand. As the stand matures, tree mortality due to competition and small scale disturbance (e.g., windthrow) contributes to the CWD reservoir. Debris levels usually reach a peak as the even-aged stand senesces into a silviculturally over-mature state, after which levels may decline due to the J-shaped diameter distribution of uneven-aged forests (Harmon et al. 1986, Spies et al. 1988).

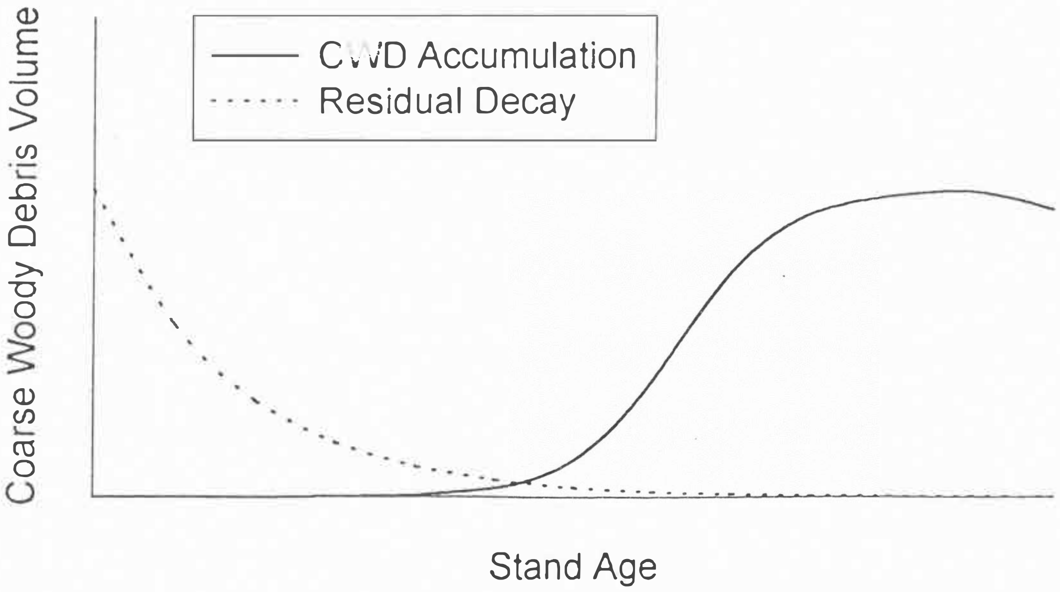

Fig. II-1. Conceptual relationship between coarse woody debris and stand age, graphically illustrating the decay of residual debris following harvest disturbance, followed by the accumulation of debris from the regenerating stand. Debris levels may begin to decline after stand senescence.

CWD is closely associated with the growth and mortality of stem structure within the stand, particularly after the majority of predisturbance debris has decayed (Harmon et al. 1986). Still, previous attempts to relate standing tree structure to CWD often have yielded poor results. For example, Muller and Liu (1991) found only a slight correlation between CWD abundance and basal area in old-growth hardwood stands. However, basal area gives limited information on the size and density of trees within a stand. In contrast, yield-density relationships provide this information, while also evaluating the state of competition between trees within a stand. Such quantitative measures may be useful tools for assessing forest stand structure as it relates to CWD.

Relative density relates the mean volume of trees to the density of stems, as a function of the self-thinning rule (Drew and Flewelling 1977). Three relative density thresholds serve as benchmarks for competition pressure. The crown closure line (CC) indicates the onset of intertree competition. The lower limit to the zone of imminent competition mortality (ZICM) indicates the relative density where limited resources cause mortality in suppressed trees. A relative density value of 1.0 (maximum) is defined approximately by the -3/2 rule of self-thinning (Yoda et al. 1963). Newton and Weetman (1993) defined the CC line and the lower limit to the ZICM at relative density index values of 0.13 and 0.5, respectively, for black spruce (Picea mariana).

Figure II-2 illustrates a hypothetical trajectory of an even-aged, unmanaged stand as it regenerates and matures following a disturbance event.

In the earliest stages of succession (Fig. II-2a), seedlings will increase in stem volume while maintaining a constant (or increasing) stem density, until the stand reaches the ZICM (Westoby 1984, White and Harper 1970, Newton and Weetman 1993). The stand will then parallel the self-thinning line, maintaining a constant relative density within the ZICM (Fig. II-2b). Some debris will accumulate during this stage, but stem mortality is typically restricted to small, suppressed individuals (Lang 1985), and the rate of CWD accumulation should remain relatively low. CWD studies often have a lower size limit in defining fallen logs, thus many of these small, self-thinned stems may not be recorded as CWD. However, as mean stem size increases, the ability of the stand to produce CWD volume also increases. Additionally, maturing trees will become more susceptible to windthrow and disease (Saville 1983). The accumulation of CWD should increase as large dominants and codominants fall to the forest floor. The rate of CWD input should raise to a maximum as the even-aged trees approach their longevity, and the stand senesces into the overmature state (Fig II-2c).

Site quality influences forest biomass production, affecting both the rate and volumetric accumulation of debris (Spies et al. 1988). However, site quality will not alter the hypothetical trajectory shown in Figure II-2. Instead, stands on better quality sites progress along the trajectory at a faster rate than stands growing in poorer conditions (Yoda et. al 1963, Westoby 1984, Newton and Weetman 1993). Thus, I would expect the CWD accumulation curve in Figure

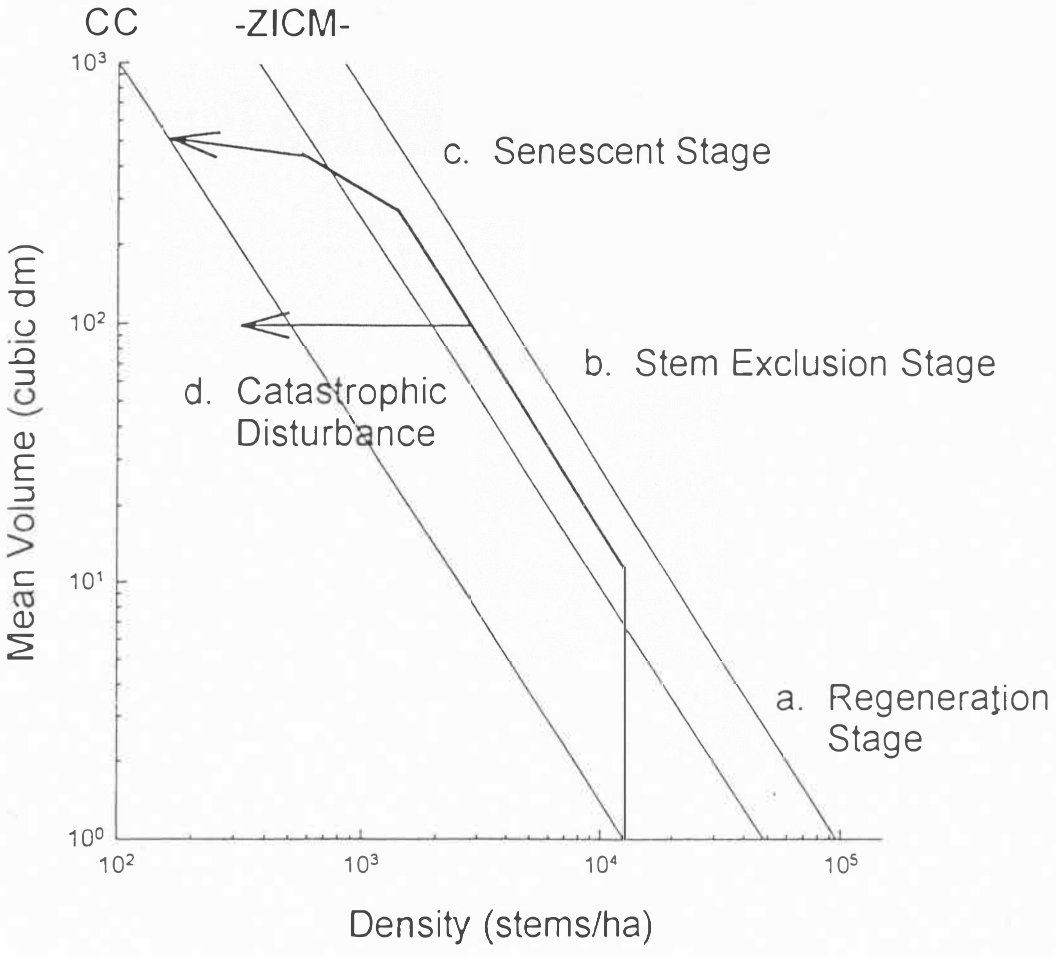

Fig. II-2. Conceptual trajectory of a typical, naturally thinned stand following clear-cut disturbance. a) Regeneration: Stem density remains constant while mean stem volume increases. b) Stem Exclusion: Stand maintains a constant relative density upon entering the zone of imminent competition mortality (ZICM), parallelling the self-thinning line. c) Senescence: Relative density decreases, and the stand falls out of the ZICM. d) Catastrophic Disturbance (e.g., defoliation): Mortality from disturbance causes a dramatic reduction in the density of live stems, while creating a subsequent pulse of CWD (not shown).

II-1 to shift to the left with an increase in site quality, as sizable logs become available more quickly. In contrast, a severe disturbance event (e.g., insect epidemic) will alter the stand's trajectory, causing a rapid decrease in stem density (Fig. II-2d) and a subsequent pulse of accumulated debris.

The combination of hypothetical models shown in Figure II-1 and Figure II-2 provides a reasonable mechanistic explanation for observed CWD temporal patterns in even-aged systems. However, parameters for the model will vary widely between different regions. Maximum debris levels range from as high as 174 Mg/ha in Douglas-fir forests of the northwestern U.S. (Spies et al. 1988) to 49 Mg/ha in northern deciduous forests (Tritton 1980). The combination of climate and species decay rates affects the persistence time of predisturbance and disturbance-generated debris, and consequently the relative importance of residual debris structure within future stages of stand development (Muller and Liu 1991). In addition, the longevity of individual tree species influences the temporal scale of the model. Other variables that affect CWD accumulation, e.g., disturbance regimes and soil conditions, are also highly site-specific.

The objective of this research was to examine the structural and temporal dynamics of CWD in second-growth balsam fir--black spruce stands following clear-cutting disturbance in western Newfoundland and to compare these sites with "old-growth" stands of natural origin. My goal was to determine the stage of forest stand development at which second-growth stands began to assume the characteristics of old-growth forests in terms of CWD abundance and structural diversity. Based upon CWD patterns observed in eastern hardwoods (Tritton 1980), and the Pacific Northwest (Spies et al. 1988), I hypothesized that debris should follow a U-shaped trajectory, followed by an asymptote. However, the critical parameter values of the model were unknown. For example, at what time does debris become the most limiting, and when does the stand begin to generate its own debris? When do levels of debris begin to approximate that of old growth?

My examination of CWD dynamics in balsam fir-dominated forests of Newfoundland incorporated three distinct phases: (a) analysis of CWD volume and structure in relation to a chronosequence of naturally thinned stands following clear-cut disturbance, in comparison with old-growth stands; (b) relating downed woody debris to standing tree structure; and (c) development of a theoretical CWD model fit to observed levels of debris, followed by a qualitative description of outliers to provide context relative to defoliation disturbance, site quality, and stand history. The theoretical model will serve as both a working hypothesis and a framework for future debris research in Newfoundland. This research was part of a larger effort to characterize the habitat quality of different ages of forest for the threatened Newfoundland marten (Martes americana atrata).

STUDY AREAS AND BACKGROUND

CWD and stand structure information was collected from western and central regions of Newfoundland (Forest Section B28b and B28a, respectively, of the Canadian Boreal Forest Region [Rowe 1972]). Each region was characterized by a wet, cool climate, with annual temperatures averaging 4°C, though study sites in central Newfoundland were influenced by a slightly more continental climate, with relatively colder winters and warmer summers (Banfield 1983). Western Newfoundland also had a longer frost-free period than central Newfoundland, and potential evapotranspiration (PET) values were slightly higher (350-400 mm for western sites and 300-350 mm for central sites, respectively). Mean precipitation ranged from 1200-1300 mm annually for western sites, and 1300-1500 mm for central sites, while average snowfall for both regions was approximately 4 m (Banfield 1983).

Damman (1983) subdivided the island of Newfoundland into ecoregions based upon climate, soil characteristics, and vegetative communities. Study sites in western Newfoundland were within the Corner Brook subregion of the Western Newfoundland Ecoregion. The hilly to relatively rugged terrain of this subregion is underlain by slates and limestone till, with relatively shallow, nutrient-rich soils (Damman 1983, Meades and Moores 1994). Elevation for my study sites ranged from 120-450 m. The absence of prolonged dry periods nearly prohibits fire disturbance; consequently, balsam fir dominates the forested landscape, and although black spruce is present, pure black spruce stands are generally restricted to rocky outcrops and poorly drained locations (Damman 1983). White birch (Betula papyrifera) was common throughout the area, and white spruce (Picea glauca) was locally abundant. Rubus-balsam fir and *Dryopteris-Hylocomium-balsam* fir (Meades and Moores 1994) were the most common forest ecosystem types associated with my study sites.

Study sites from central Newfoundland were located within the Red Indian Lake subregion of the Central Newfoundland Ecoregion. The undulating topography of this subregion was characterized by relatively nutrient-rich soils, although limestone was absent within the area. This subregion contained the most productive forest of the central region, and its relatively cool summers and wet climate have also diminished the impact of fire disturbance. Tree species composition was similar to that described for the western sites, and *Rubus-*balsam fir, *Dryopteris-Lycopodium-balsam* fir, and *Hylocomium-balsam* fir (Meades and Moores 1994) were the most common forest ecosystem associations.

Natural disturbance regimes for both study locations were dominated by periodic insect defoliation by spruce budworm (*Choristoneura fumiferana*) (Raske 1986) and more recently hemlock looper (*Lambidina fiscellaria*) (Thompson 1991). Defoliation events within balsam fir sites typically act to remove the mature and silviculturally overmature overstory to release new growth (Baskerville 1975). The shallow soils and maritime climate of Newfoundland also predispose the forests to chronic windthrow disturbance. Balsam fir is a relatively short-lived species, and stands older than 120 years were rare in Newfoundland (Thompson 1991). While I considered unharvested stands greater than 80 years "old growth," old stands appear to be largely even-aged.

The Corner Brook mill began logging in the South Brook valley (western Newfoundland) as early as 1924, with the greatest portion harvested in the 1940's (Horwood 1986). Although clear-cutting was the primary harvesting method used, small coniferous trees (<10 cm dbh) and all birch typically were left standing. Thus all second-growth stands contain some residual trees. The least accessible sites commonly were left as residual stands. I established additional study sites just southwest of Corner Brook, which were harvested around 1950. Pulpwood harvest began in the vicinity of Victoria Lake (central Newfoundand) in the late 1950's, and all wood accessible by major waterways was harvested within approximately a 10-year period, ending by the late 1960's (Abitibi-Price historical files).

METHODS

Study sites were selected to encompass both a range of second-growth age classes and a sample of "older-growth" sites, which were defined as uncut stands greater than 80 years of age (Bissonette et al. 1989). I focused my effort on stands greater than 40 years of age; however, younger stands also were sampled to gain insight on the impact of residual CWD (i.e., CWD generated before or during the initial disturbance). Study sites were defined by stand boundaries interpreted from air photos (Nfld. Dept. For. 1990). Approximately 15-20 sample plots were placed at 50-m intervals along a predetermined transect within each site, for a total of 454 plots within 26 sites.

Downed logs were measured using a modified version of Brown's (1976) plane intersect method for estimating fuel loading. A 20-m tape was placed along a random direction, centered on the sample point. Logs intersecting the vertical plane defined by the tape were measured for diameter at the point of intersection. Logs greater than 7.6 cm were measured to the nearest cm. CWD was classified as rotten if the outer layer could be fragmented by hand, and branches could be pulled free from the bole, indicating heartrot (Brown 1976). Logs were classified according to species wherever possible. Finally, intersected logs were categorized into four different height classes (<0.5 m, >0.5-1.0 m, >1.0-1.5 m, and >1.5 m), defined as the height the log was suspended above the ground at the point of plane intersection.

A measure of standing tree structure was taken at each CWD sample plot. Basal area was measured using a prism, and diameters of tallied trees were measured to the nearest cm. At alternating plots along the transect, two trees were randomly chosen during the basal sweep and aged at breast height using an increment borer. Sample ages were averaged as an estimate of overall stand age. An additional dominant tree was aged and measured for height (± 0.25 m) using a clinometer. Each plot was classified into forest ecosystem types (based upon plant indicators, topography, and soil type) as a measure of site potential (Meades and Moores 1994).

Relative density was calculated by the following method. Using dominant heights measured at individual plots, I calculated individual tree heights using Page and van Nostrand's (1973) height-diameter regression functions: $Ht = b_0 - b_1 \cdot D \cdot Ht_d - b_2 \cdot D^2$, where Ht is the estimated height, D is the diameter at breast height, Ht_d is the dominant height, and b_0, b_1, and b_2 are species-specific regression coefficients. Plots without recorded dominant heights were assigned heights as a function of adjacency and similarity of forest ecosystem type to other plots within the stand. Volumes were then calculated using Warren and Meades' (1986) taper equations. Stem density and volume estimates were calculated for each plot using Husch et al.'s (1972) methodology for variable radius sample plots. I then employed a preliminary relative density index equation provided by Newton (Forestry Canada, unpublished data) for balsam fir--black spruce stands in Newfoundland: $\underline{Pr} = N_o/(\underline{v}/10^{7.452})^{-0.49}$, where $\underline{Pr}$ = relative density index, N_o= number of trees per hectare, and $\underline{v}$ = mean stem volume in dm^3.

For the purpose of this chapter, CWD was defined as downed woody debris greater than 7.6 cm in diameter, based upon Brown's (1976) definition of logs. Snags were considered separately as standing dead wood. Furthermore, because the focus of this study was to examine the structural characteristics of CWD, I chose to focus on volume rather than mass. Finally, age was defined as the age taken at breast height, plus 8 years. Shade-tolerant species often exhibit erratic growth patterns below breast height (Griffin and Johnson 1980), and breast height ages were used to reduce the variability of my samples. Within western Newfoundland, regeneration typically takes eight years to reach breast height (D. Harris, personal communication). Table II-1 describes the mensurational characteristics of each site.

RESULTS AND DISCUSSION

Chronosequence data

Total volume of CWD ranged from 78.1 to 15.2 m^3/ha (Fig. II-3a), while sound volumes of CWD ranged from 48.8 to 4.0 m^3/ha (Fig. II-3b). In general, CWD volume decreased with stand age to a low at 55 years. The accumulation period followed for a relatively short, 30- to 40-year period and plaited at 80 years. Decayed CWD was highly variable and showed no detectable trend besides a slight deficiency at 60-70 years (Fig. II-3c). In the early to mid successional stages of the chronosequence, decayed wood is likely to be a function of the amount of residual trees and CWD remaining after disturbance, and may be quite variable. Additionally, rotten wood is often fragmented along its length, and could have contributed to significant volumetric sampling error.

The amount of CWD in earlier successional stages was strongly influenced by the presence of residual birch CWD (Fig. II-3d). In Newfoundland, birch is left standing during harvesting. Most of the standing birch dies soon after harvest due to the rapid change in site water balance, and vulnerability to windthrow. I observed residual birch CWD within stands as long as 60 years after disturbance, suggesting birch may serve as an important reservoir of CWD during earlier stages of succession, depending on the initial

Table II-1. Stand age and structure within the chronosequence.

Site	Location[a]	Stand Age	Basal Area	Trees/ Hectare	D_q[b]	Site Index[c]	Relative Density[d]
12[e]	VL	33	—	—	—	11.8	—
14	VL	35	22.12	11371.6	5.53	12.0	0.33
15	VL	36	36.73	22210.0	7.67	13.2	0.56
30	CBL	49	44.38	3377.8	15.62	15.3	0.53
32	CBL	58	44.38	5087.5	11.96	15.3	0.63
33	CBL	58	37.65	5978.9	12.36	15.4	0.51
3	SB	61	49.13	5002.2	13.26	14.1	0.62
4	SB	62	38.57	4742.8	12.96	14.8	0.52
18	SB	62	32.25	1046.1	25.15	15.4	0.34
10	SB	64	32.33	6307.2	11.17	11.8	0.48
11	SB	66	35.81	3777.2	12.87	13.4	0.50
7	SB	67	40.75	3417.6	15.95	14.1	0.53
22	SB	68	40.86	3298.5	16.95	15.0	0.52
16	SB	73	41.32	5204.1	11.45	12.2	0.54
5	SB	74	50.51	2887.1	17.27	15.4	0.62
6	SB	75	38.91	2754.2	13.18	13.5	0.51
21	SB	75	40.86	3380.7	14.22	13.4	0.55
23	SB	75	33.98	1539.1	19.68	14.8	0.43
8	SB	80	32.97	1484.4	19.27	14.8	0.43
17	SB	87	31.48	1661.7	18.82	14.7	0.42
13	VL	88	23.72	1011.1	20.24	13.5	0.28
81	SB	91	42.85	2483.1	20.42	14.6	0.55
9	SB	96	36.00	3904.8	15.37	12.8	0.48
1	VL	99	17.95	1066.1	17.20	13.2	0.22
20	VL	100	33.52	3043.5	14.24	11.7	0.45
2	VL	110	26.40	2666.7	14.96	12.5	0.34

[a] VL = Victoria Lake, CBL = Corner Brook Lakes, SB = South Brook

[b] Quadratic Mean Diameter

[c] Site Potential, (Meades and Moores 1994).

[d] Relative density index values > 0.5 within ZICM (Drew and Flewelling 1977)

[e] Stand structure information was not collected for this site.

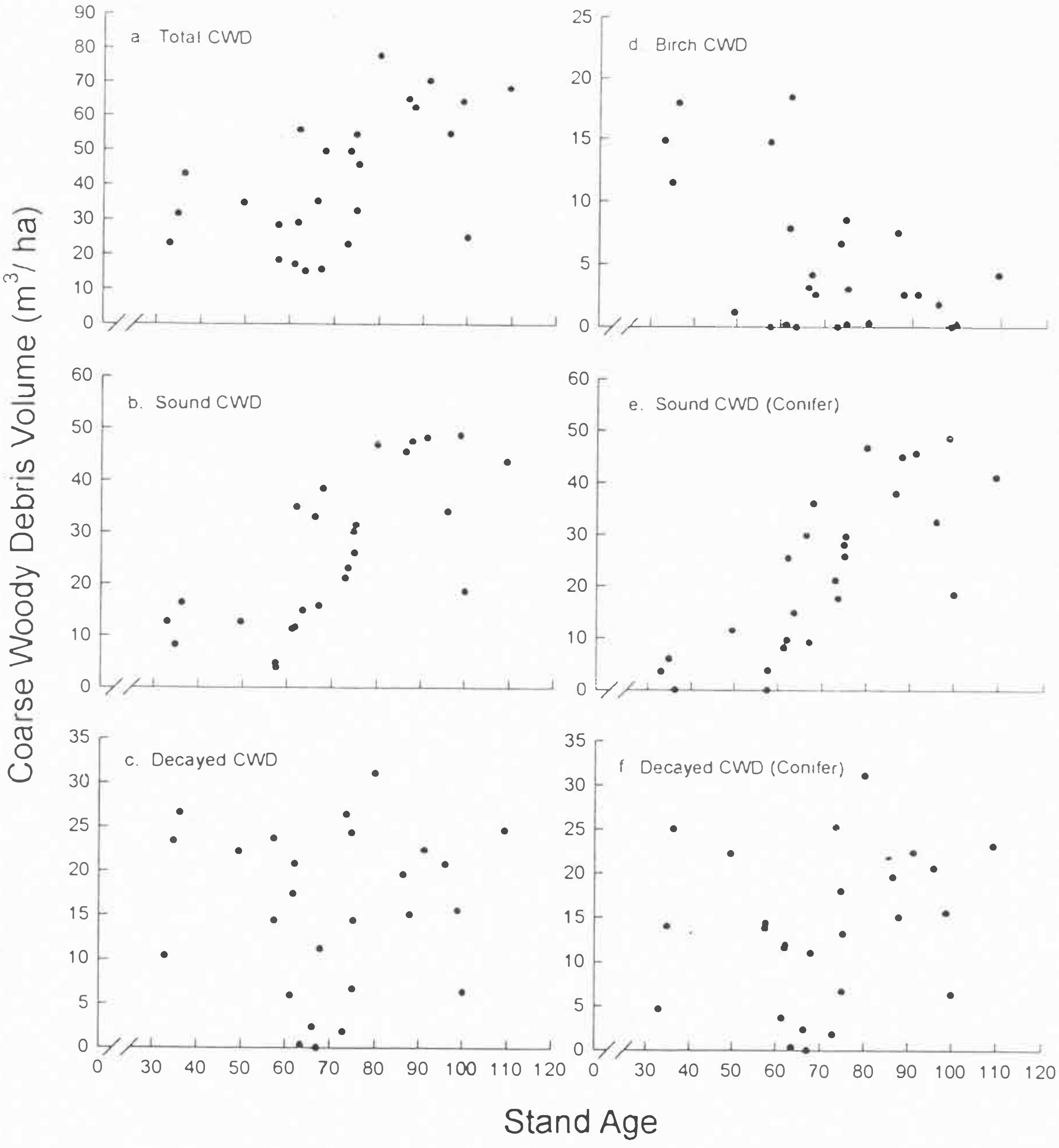

Fig. II-3. Coarse woody debris as a function of stand age, based upon chronosequence data.

birch component. The removal of birch data from the chronosequence shows a more clear representation of the contribution of new (sound) CWD from maturing stands (Fig. II-3e). Similarly, the removal of birch from the decayed CWD data shows a more pronounced deficiency in rotten CWD, centering on about 65 years (Fig. II-3f).

Using the volume of CWD suspended greater than 0.5 m above the ground surface as an index of structural diversity, I observed a similar U-shaped temporal pattern (Fig. II-4a,b). Very little structural diversity was observed during the semimature stages of forest succession (i.e., 40- to 60-year second growth). While some diversity was observed in the youngest stands, most debris over 0.5 m high was contributed by fallen birch snags. The majority of CWD in the young stands was composed of residual debris. Without additional input from the regenerating stand, the decomposition process lowers logs to the ground over time. In contrast, the highest structural diversity was clearly present in the overmature stage.

Standing dead wood generally was rare within young stands, but snag density increased dramatically after 60 years (Fig. II-5a). Similarly, the basal area of standing dead wood increased substantially after 60 years. However, snag basal area in older second-growth was much more similar to old-growth stands (Fig. II-5b), indicating a relatively high proportion of small diameter snags within second-growth stands. High numbers of small snags are typical of stands in the stem exclusion stage of development (Lang 1985).

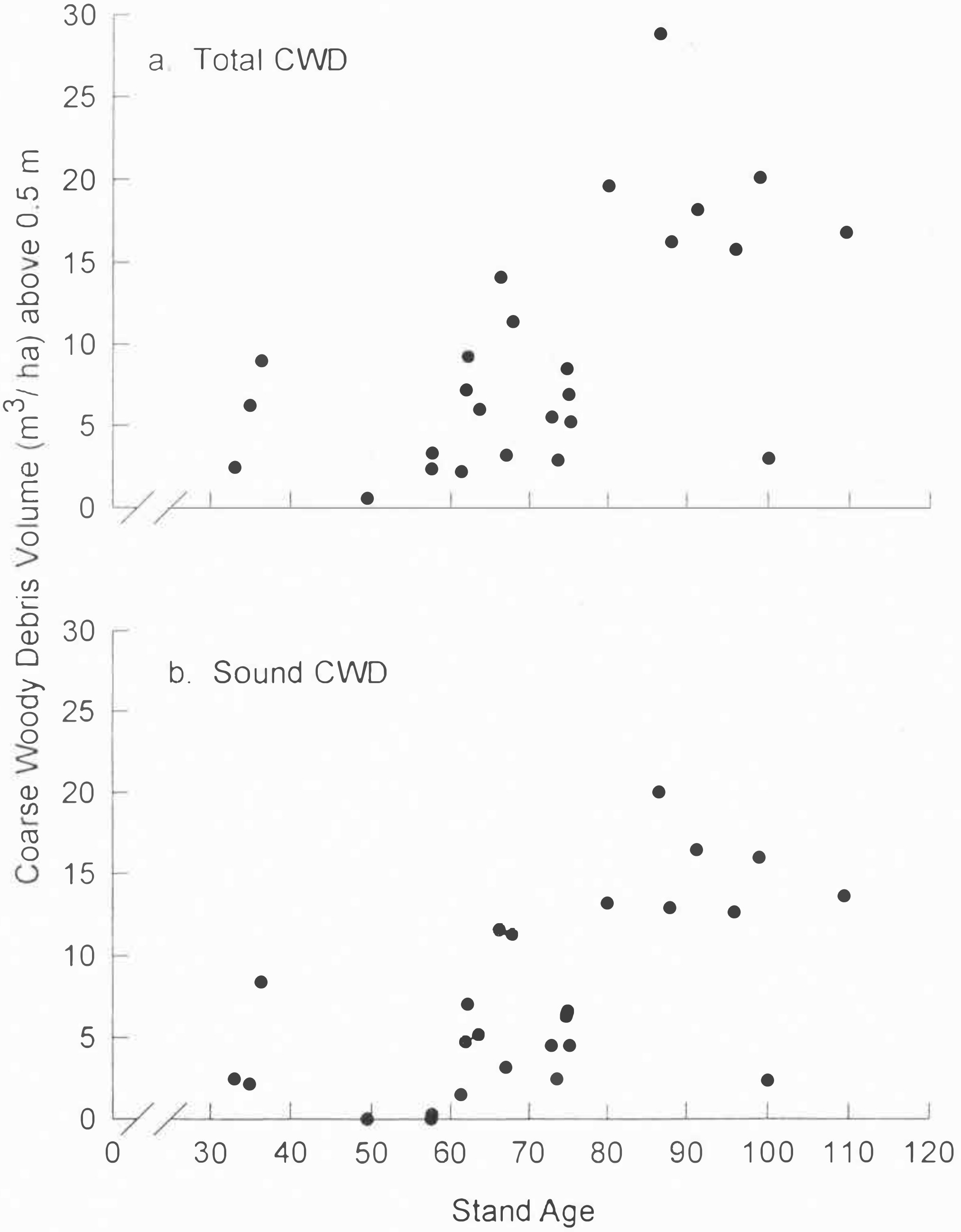

Fig. II-4. Structural diversity of coarse woody debris as a function of stand age. Vertical diversity is defined as the volume of logs encountered that were a minimum of 0.5 m above the ground surface. (See text for explanation).

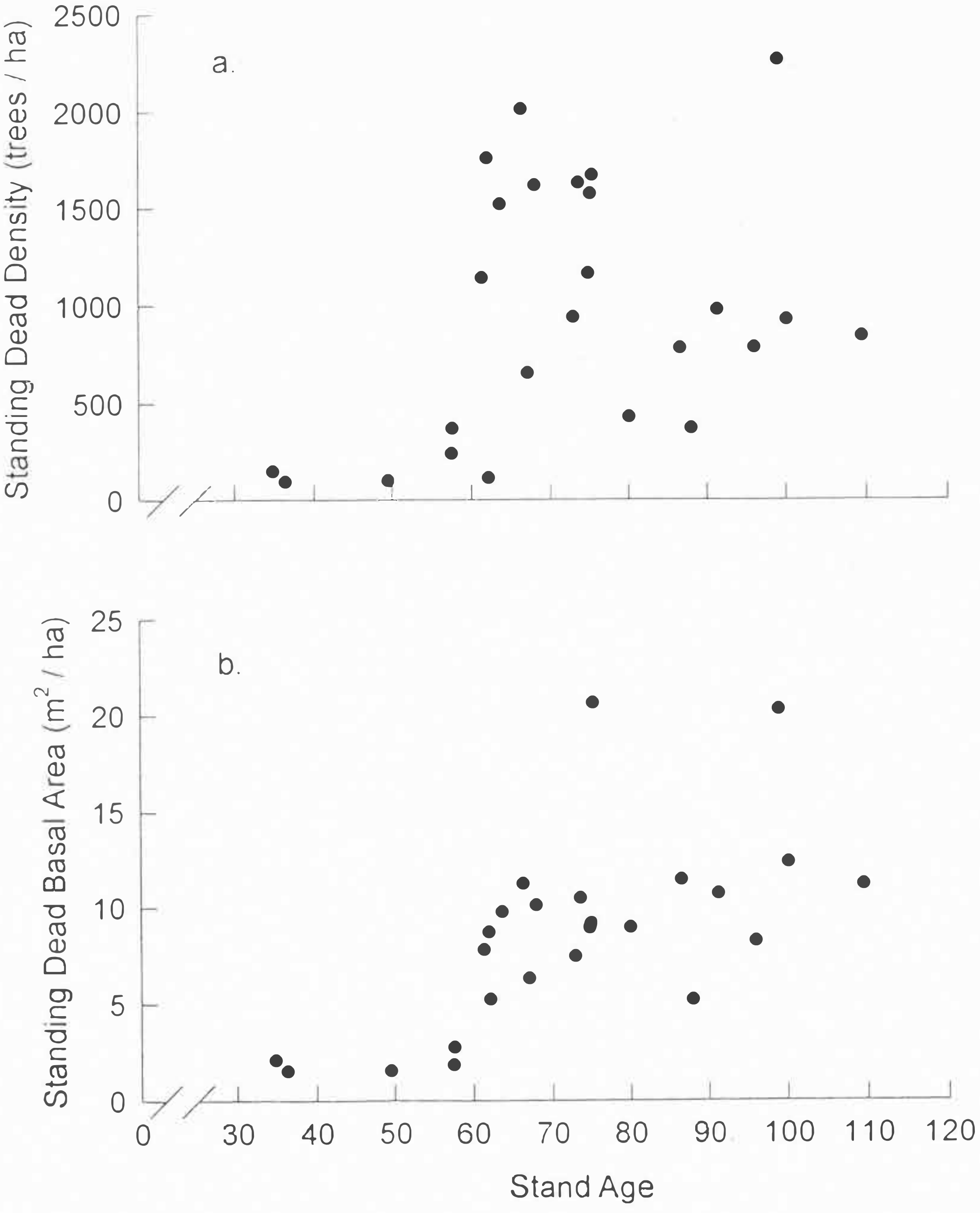

Fig. II-5. Standing dead wood a) trees per hectare and b) basal area, as a function of stand age.

CWD relationship to stand structure

Mean relative densities in measured stands ranged from a high of 0.63 in a young second-growth stand to a low of 0.22 in an old-growth stand (Table II-1). All stands sampled were naturally thinned, and relative densities reflected the degree of competition within each stand. The majority of second-growth stands had relative density index values greater than 0.5, indicating competition pressure and active self-thinning, while most old-growth stands fell outside the estimated ZICM (see Table II-1). A notable exception was site 18, a 61-year-old second-growth stand with a high percentage of birch. Hardwood species generally have lower density thresholds for self-thinning (Westoby 1984), and the actual relative density of the stand was probably underestimated. The decrease in relative density observed in older stands indicates the eventual senescence of mature even-aged stands into the overmature state. This transition corresponds to the high CWD volume observed within stands greater than 80 years of age, and indicates a critical change in both standing tree and subcanopy structure.

Conceptually, by examining standing tree structure within a stand, one can begin to assess when the stand can potentially generate CWD. For example, I analyzed stem structure using a stand density management diagram (see Chapter IV), employing site index curves provided by Page (1968) to predict the time necessary to generate stems of a specified size. Graphic analysis indicated that a stand within the ZICM (e.g., relative density = 0.7) will reach a quadratic mean diameter (D_q) of 8 cm at a dominant height of 8 m. However, I expect self-thinned stems to be considerably smaller than the average stem size (Lang 1985). Assuming that the D_q of 12 cm would be necessary to generate self-thinned stems averaging 8 cm in diameter at breast height, the stand should reach a dominant height of 14 m before self-thinned debris could be recorded. By employing Page's (1968) site index curves, a high-quality site (i.e., 16 m at a breast height age of 50 years) would be able to generate CWD at approximately 26 years, though self-thinned material greater than 8 cm in diameter would not be available until 48 years after disturbance. Similarly, a poor quality site (i.e., 12 m at a breast height age of 50 years) would not be able to generate CWD until 36 years post-disturbance, and self-thinned CWD greater than 8 cm in diameter (breast height) would not be available until 78 years post-disturbance. The impact of site quality on a stand's ability to produce CWD becomes evident when CWD dynamics are viewed in this context.

However, the question remains on whether the age of stand senescence will vary according to site quality. Two hypotheses are pertinent. If senescence were related to a size threshold, I would expect a high-quality site to senesce earlier than a stand on poorer site conditions. For example, large trees may be rare because the probability of windthrow mortality is very high for large stems (Saville 1983). Newton (1992) suggests that the shallow rooting strategy of both balsam fir and black spruce might limit stem size in Newfoundland's maritime climate. Conversely, senescence may be attributed to age-limiting factors. For example, old balsam fir is prone to heart rot, which increases its vulnerability to windthrow mortality, and may limit the fir's longevity (Seymour 1994). Vulnerability of stands to defoliation mortality may be associated with age and the structural characteristics of the host trees (Ostaff and MacLean 1989). It is likely that the above hypotheses are not mutually exclusive in Newfoundland, and both size and age-limiting factors are operating within the system.

Figure II-6 shows yield-density relationships of individual plot data, categorized into three site quality classes. The pattern of stand senescence appears similar: Few plots with mean volumes greater than 300 dm^3 exist within the ZICM, regardless of site quality. However, because my data were not stratified to address the hypotheses suggested above, I only suggest that the mechanisms governing stand senescence will lend valuable insight into the role of site quality in the dynamics of CWD.

Theoretical model for CWD

Temporal dynamics of CWD can be summarized in two phases: the decay of predisturbance and disturbance-generated debris, and the accumulation of debris from the regenerating stand (Harmon et al. 1986, Spies et al. 1988). I developed a two-stage theoretical model for sound CWD volume from collected chronosequence data. The utility of this model is not as a predictive model *per se*, but rather as a mechanistic working hypothesis to be

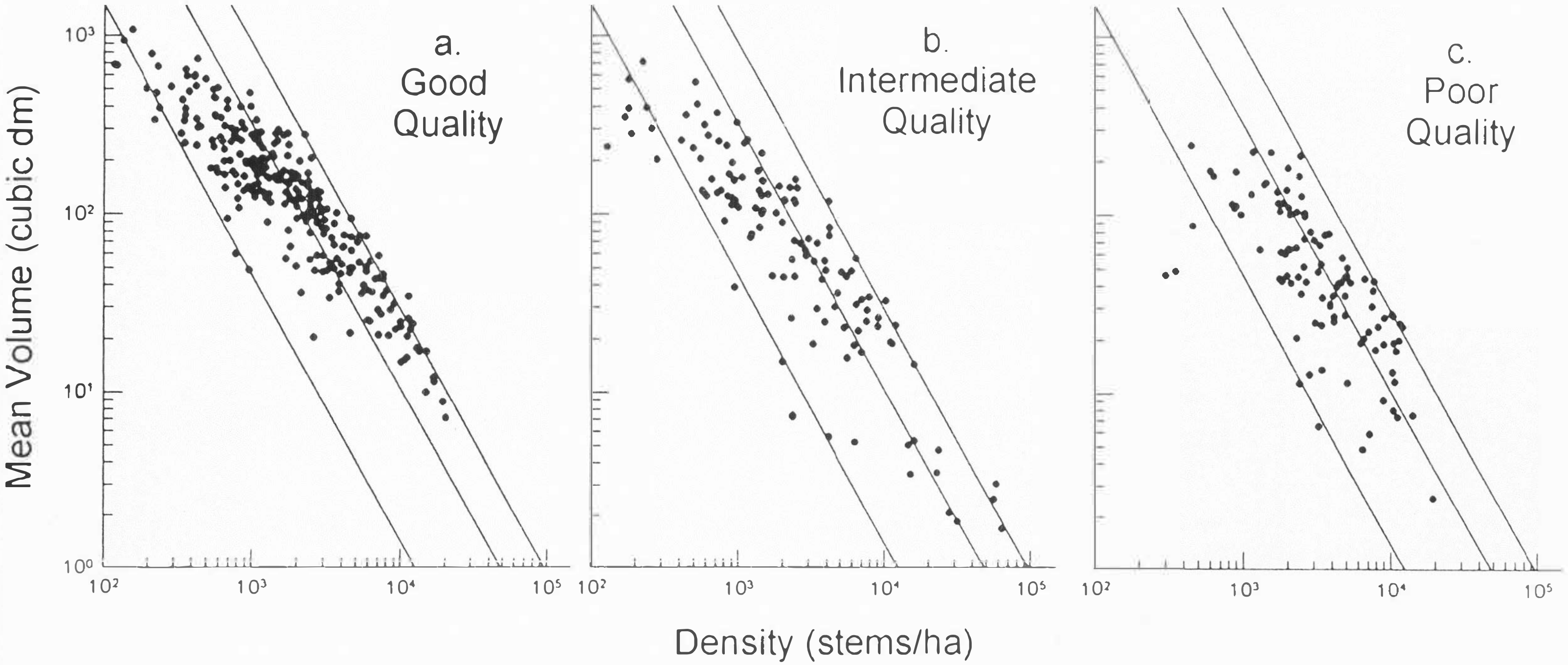

Fig. II-6. Size-density relationships of individual plot data, stratified by site quality. The pattern observed suggests the conceptual stand trajectory shown in Figure II-2 is followed regardless of site quality, and the difference is the time necessary to trace the trajectory. Plots located on poor soils (c) were primarily naturally open spruce fens, and were only included as a comparison.

tested.

The decay phase of the model is characterized by exponential decay (Lang 1985). Based upon my field observations, I assumed a 95% loss of sound CWD volume by 55 years. Decayed wood will lag behind the sound volume model, although my data indicate that much of the decayed residual wood structure is gone by 65-70 years. After that point, the majority of residual debris will be overtaken by mosses and incorporated into the forest floor (unpublished data). Residual birch adds an additional component of sound CWD to stands in the immature stages of development.

The shape of the CWD accumulation curve is sigmoidal, following Spies et al. (1988), and applies to naturally thinned, intermediate-good quality, balsam fir-dominated stands. Based upon my observed low point in sound CWD volume, sites younger than 50 years were excluded from the accumulation analysis. I assumed that the majority of sound birch debris within second-growth stands was residual debris, and removed the birch component for analysis. Four additional sites showing obvious differences in structural characteristics were dropped from the analysis, and are explained below. The logistic growth equation (Ratkowski 1990) defines the accumulation curve, with the form $V = b_0/(\exp(b_1-(b_2{*}A)))$, where V = sound volume of CWD in m^3/ha and A = stand age. Parameter b_0 (asymptote) was assumed at 48 m^3/ha based on observed values. Parameters b_1 and b_2 were assessed using least squares, nonlinear regression (corrected $\underline{R}^2 = 0.909$) and were estimated at 10.64 and

0.15, respectively.

The completed model is shown in Figure II-7. Points falling above the accumulation line during earlier stages of development indicate additional residual CWD. The sound CWD model (Fig. II-7a) overlaid on the total CWD plot (Fig. II-7b) graphically represents the sound debris base within the total available downed woody structure. While the inclusion of decayed wood in the model introduces more variance, the same general trends of decay and sigmoidal accumulation are observed.

Defoliation disturbance increased both CWD volume and structural diversity (Fig. II-8a,b). Defoliators affected stands in a patchy spatial pattern, with a typical patch size of about 0.5-2.0 ha. In semimature and mature second-growth stands, defoliated patches created locally abundant CWD within a matrix of more typical second growth (i.e., within the ZICM, personal observation). As shown in Figure II-8b, second-growth sites that were influenced by defoliation disturbance were the only stands that approached the structural diversity of old-growth sites.

The effect of site quality and stand history on CWD, reflected by differences in stand structure, is also apparent within the data (Fig. II-9a,b). Sites 30 and 18 (ages 49 and 63, respectively), both good-quality sites, were characterized by widely spaced, large diameter trees (see Table II-1) with high live-crown ratios. Both sites were beginning to generate new CWD. Additionally, site 30 was young enough to contain some residual sound debris,

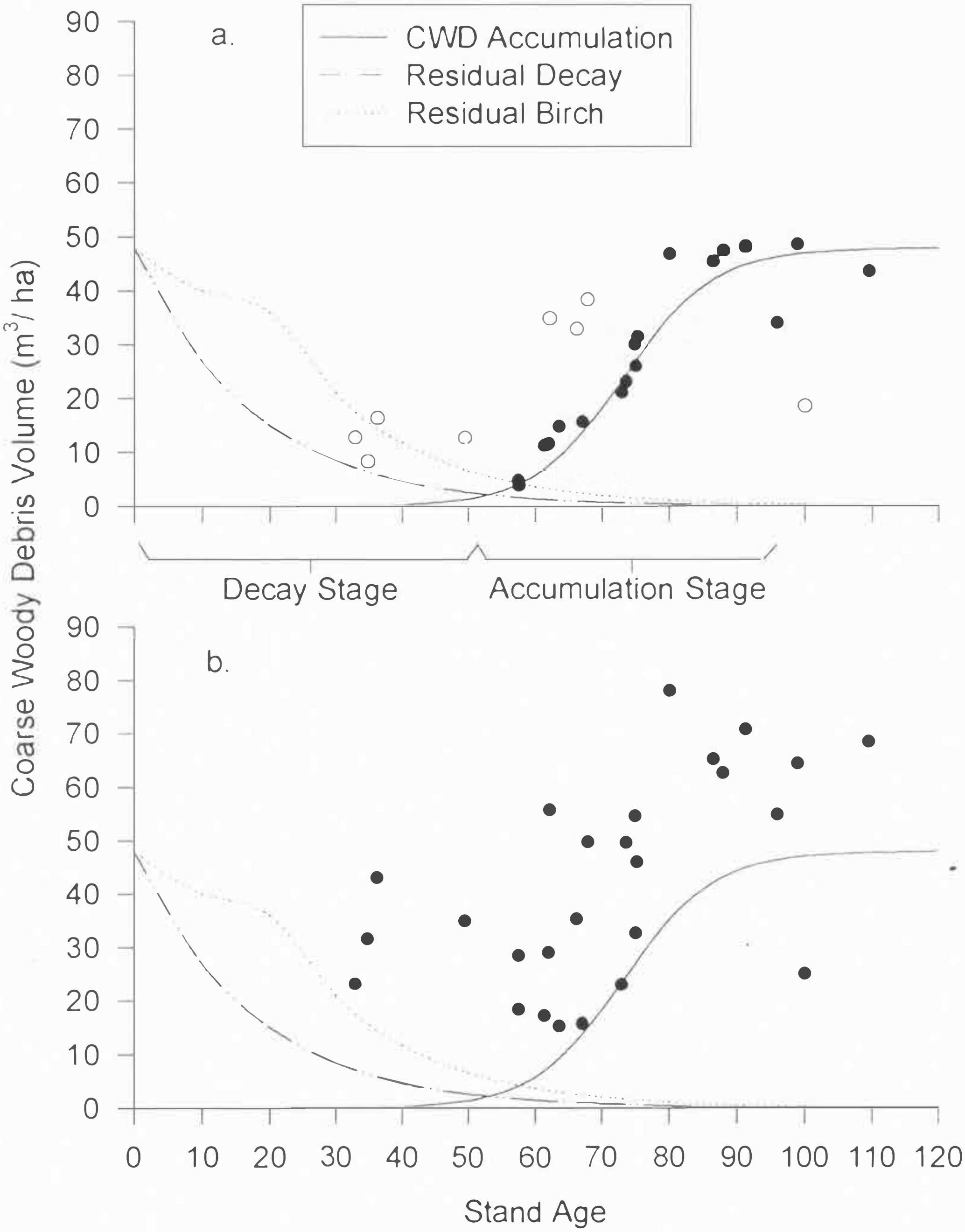

Fig. II-7. a) Theoretical model of coarse woody debris decay and accumulation. Open circles represent stands not used in creating the model (see text for explanation). b) Data points showing total CWD volume overlaid on the "sound" CWD model, graphically representing the sound CWD base underlying the total available debris in the chronosequence.

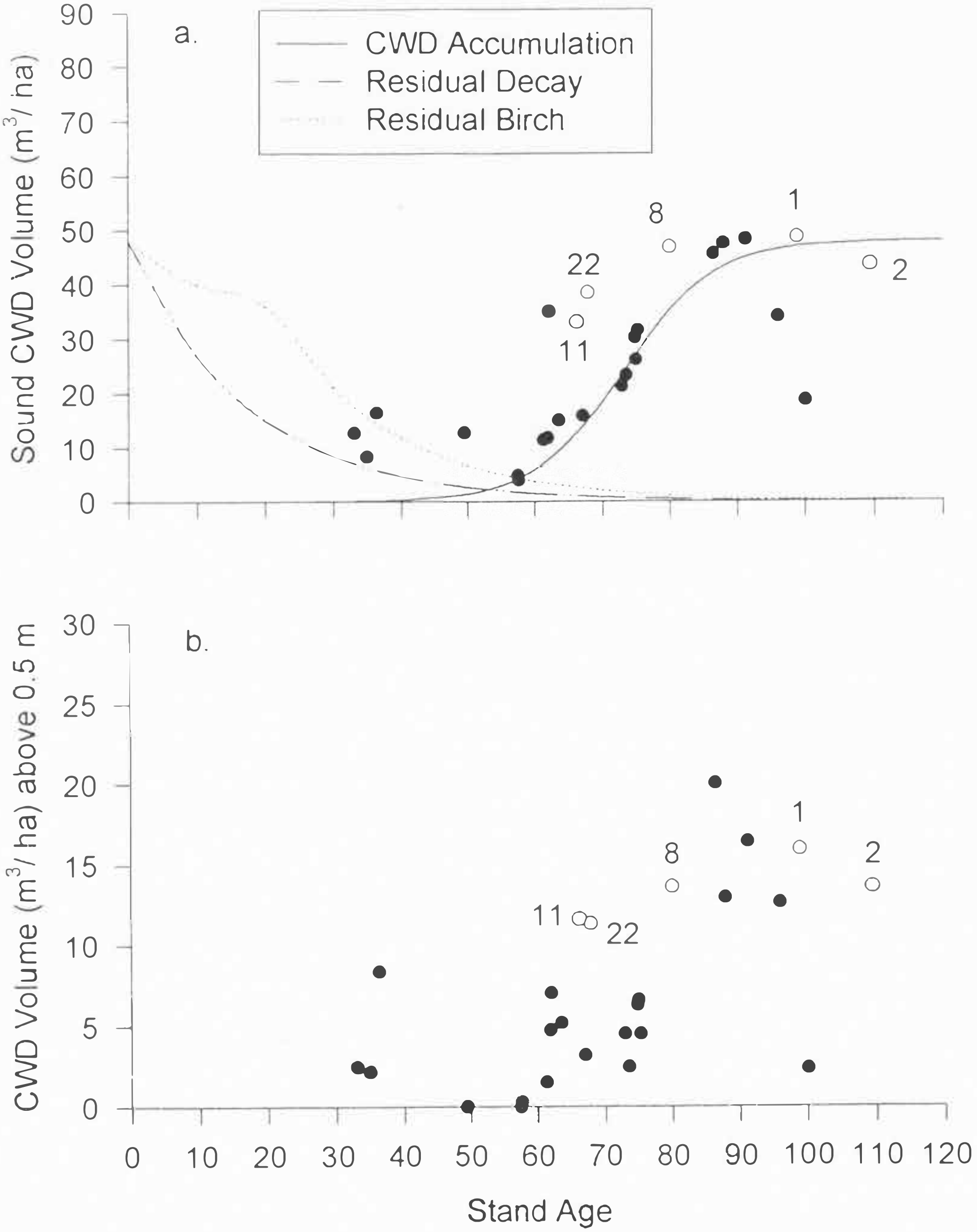

Fig. Ii-8. The effect of defoliation on a) CWD volume and b) structural diversity. Open circles represent sites where greater than twenty percent of the plots were affected by insect defoliation. Notice that the only second-growth stands that approached the structural diversity of old-growth stands were those affected by defoliation.

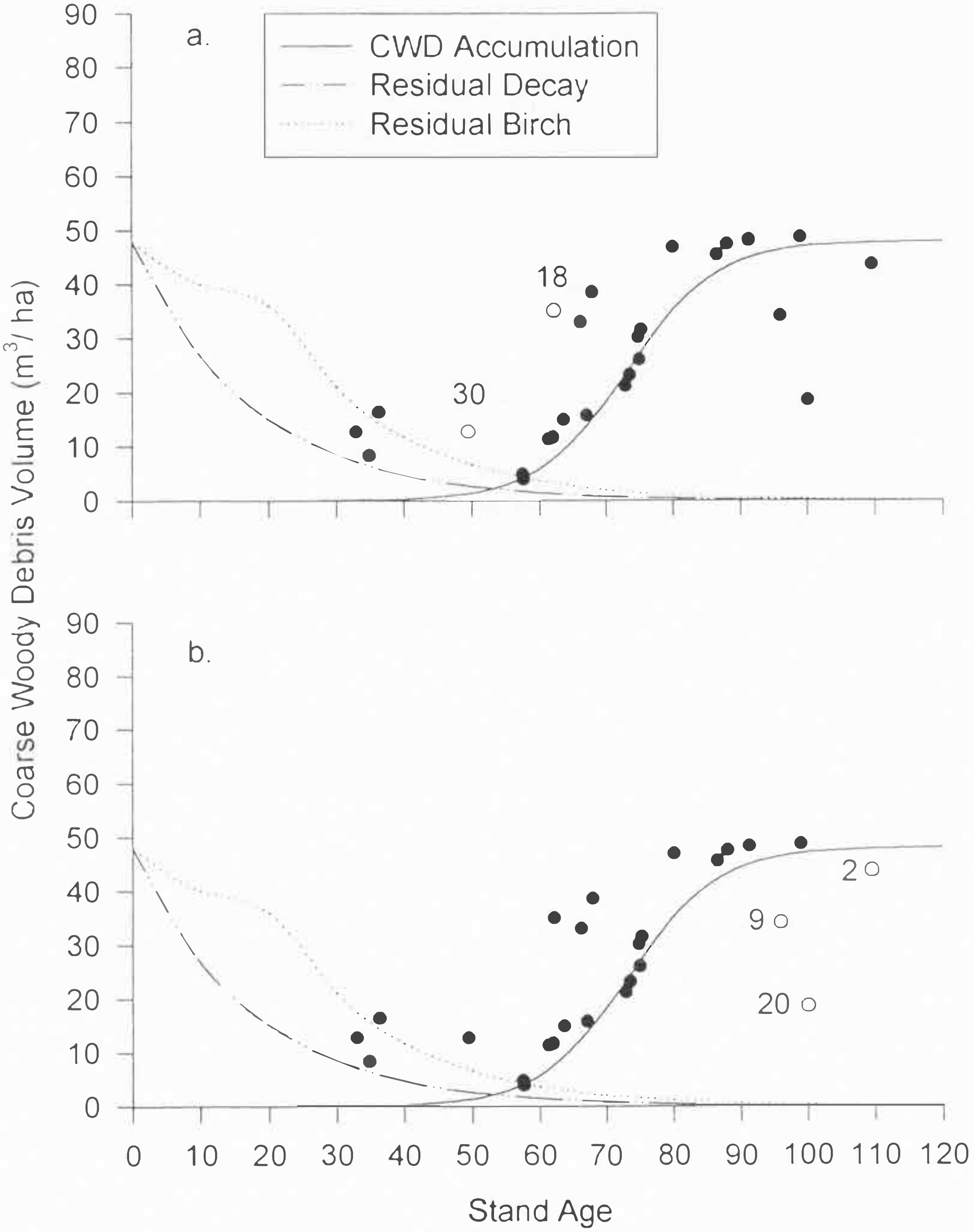

Fig. II-9. The effect of site quality and stand history on CWD volume. a) Open circles represent relatively good sites that were characterized by relatively large, widely spaced trees. b) Open circles represent relatively poor sites. (See text for explanation).

while site 18 contained a high proportion of residual birch that increased overall sound debris levels. Site 9, an old-growth site located on relatively poor soils, contained two distinct age classes. Old patches (>80 years) were dispersed among areas of 50-year regeneration, and probably originated from an earlier defoliation event. Occasional residual dominants were present throughout. The difference in structure probably lowered overall levels of debris. Site 2 was also located on relatively poor soils; however, patches of defoliation increased levels of CWD. Finally, site 20 is an old-growth stand on a poor site, and was characterized by small, widely spaced trees (see Table II-1) and a relatively open canopy. This site showed extremely low CWD for its age. The *Carex*-balsam fir ecosystem type of this stand was atypical of the rest of the study, but was included as a comparison.

CONCLUSIONS

The examination of CWD within the boreal forest system of Newfoundland demonstrates the typical "U-shaped" temporal CWD pattern observed elsewhere within the temperate zone (Lambert et al. 1980, Romme 1982, Lang 1985, Spies et al. 1988). Sound CWD volume exhibited a relatively predictable trajectory, with a decay stage ending near 58 years, and an accumulation stage between approximately 50 and 90 years, reaching an asymptote at approximately 48 m^3/ha. Total CWD volume exhibited a similar relationship, reaching a maximum observed volume of 78.1 m^3/ha. Residual birch affected CWD volumes as long as 60 years post-logging disturbance.

Both CWD volume and structural diversity were greatest in overmature stages of development, which was approached at approximately 80-90 years.

The availability of CWD within early stages of forest development is almost entirely dependent on individual stand history (Spies et al. 1988), i.e., predisturbance debris, disturbance generated debris, and residual standing trees. In contrast, CWD within the accumulation stage must be generated by the present stand, and is therefore dependent on the standing forest structure. Thus, factors influencing forest structure will likewise affect the structure of logs on the forest floor.

I expect that time is the variable driving the dynamics of downed woody material, directing all three major processes that influence CWD. Stand age directly affects stand structure as stems increase in volume. Similarly, critical stem size, stem suppression, and species longevity are all functions of time. Age also strongly influences decomposition of fallen logs within the stand (Lambert et al. 1980). The temporal pattern observed within my study is the result of CWD decay without significant input during early stages of forest development, followed by a rapid accumulation of sound wood due to a low degree of decomposition compared with a high input. The asymptote is reached as decomposition rates begin to equal the input rates of the senescing stand.

Age also indirectly influences CWD, because the cumulative probability of disturbance increases over time. The major forms of natural disturbance within the study sites were windthrow and insect defoliation. Wind-generated disturbance will interact with stand structure, because the size and relative density of standing trees is likely to affect the susceptibility of individual trees to windthrow (Saville 1983). Similarly, time will influence both the susceptibility (probability of attack) and vulnerability (probability of mortality) of a given stand to defoliation (MacLean 1990). This study demonstrates that defoliation may greatly increase both the volume and the structural diversity of CWD within second-growth stands.

Finally, site quality will influence stand structure in terms of volume potential and self-thinning rates (Westoby 1984). CWD similarly is influenced by the quality of a site, because the size of logs on the ground is a function of standing tree size. Certain outlier stands within my data set demonstrate the potential magnitude of this interaction. For this reason, I introduced the use of yield-density relationships as a mechanistic approach to examining stand-level dynamics of CWD. Traditionally, these relationships have been applied to even-aged stands, though they may be adapted to uneven-aged situations (Long 1985).

Because CWD within this system appears to be dependent on stand structure, the potential exists to manipulate stand structure to indirectly manipulate future CWD. The majority of my second-growth sites were within the ZICM. CWD generated during stem exclusion was small in size, and apparently remains for a period of time as standing dead wood. Though perhaps sufficient for other purposes (e.g., nutrient cycling), this type of debris is unlikely to provide adequate structure for wildlife. Conversely, a windthrown dominant or codominant is likely to provide a more beneficial structure, with a larger bole and substantially larger crown than a suppressed tree. Additionally, the gap created by the fallen tree or trees will increase light availability on the forest floor, increasing the potential for vegetation growth and diversity (Borman and Likens 1979). Two stands with naturally low relative densities and comparatively large diameter trees for their age were observed to be generating CWD at a faster rate than predicted by my model.

Yield-density relationships may be an appropriate tool for examining the interaction between stand structure and the generation of CWD, because the size and structure of standing trees may be predicted readily for stands of varying relative densities. However, the influence of both chronic and catastrophic disturbance within stands where stem density has been manipulated (e.g., thinning treatments) has not been well documented. Future research in CWD dynamics should include study of debris generated within managed stands to increase our understanding of size and structure-related disturbances, and the subsequent impact upon the CWD resource within managed systems.

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CHAPTER III

HABITAT ASSOCIATIONS OF MICROTUS PENNSYLVANICUS WITHIN FORESTS OF WESTERN NEWFOUNDLAND AS A FACTOR INFLUENCING MARTEN HABITAT QUALITY[2]

Abstract: The close similarity of marten (Martes americana) habitat associations across North America allows managers to use data gathered from various regions across the species' range in developing local management plans. Yet, local conditions often influence the utility of larger scale, non-regionally based information. The relatively depauperate and rapidly fluctuating abundance of the small mammal prey base on the island of Newfoundland provides a unique ecological situation for marten in North America. Microtus pennsylvanicus, normally associated with open habitats, is the only microtine found in Newfoundland, and one of the few prey items available within forested ecosystems of the island. Small mammals (M. pennsylvanicus and Sorex cinereus) were sampled within immature, semimature, mature, and silviculturally overmature coniferous stands in western Newfoundland during 1993 and 1994. My data indicate that although M. pennsylvanicus is found in forested habitats, it is most abundant in areas associated with openings in the forest canopy. I address the applicability of mainland marten habitat generalizations to the unique insular condition of Newfoundland.

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[2] Coauthored by Brian R. Sturtevant and John A. Bissonette.

The close association of marten (Martes americana) with older successional spruce-fir and mixed coniferous forest habitat is remarkably consistent across its entire range (Mech and Rogers 1977, Soutiere 1979, Spencer et al. 1983, Buskirk 1984, Bissonette et al. 1989, Thompson 1994). As a predator that requires large areas of relatively contiguous habitat, the marten is a reasonable indicator of the integrity of older coniferous forest systems. The similarity in marten behavior and requirements across regions allows land managers to develop local marten management plans based upon information from a wide variety of sources. However, managers must be cognizant of local ecological mechanisms that may influence marten response to different habitat management regimes.

Though marten are opportunistic foragers (Zielinski et al. 1983), they are also habitat specialists, restricted to areas within the forest matrix that offer, among other qualities, structural cover from predation (Thompson 1994, Drew 1995). The common management interpretation of this association is that large areas of dense, contiguous spruce-fir habitat must be available to maintain viable marten populations. A critical assumption inherent in this interpretation is that adequate prey will be available, provided that suitable cover is present (Allen 1982).

The depauperate prey base on the island of Newfoundland presents a unique ecological situation for marten. Of the seven potential mammalian prey species (Table III-1), six are available within forested habitats, and only three are distributed throughout the marten's range on the island (Tucker 1988). The notable absence of the red-backed vole (Clethrionomys gapperi) leaves the meadow vole (Microtus pennsylvanicus) as the sole microtine available to marten. However, while meadow voles are present within forested habitats, they are typically much more abundant within open, grassy habitats (Getz 1970, Grant 1971, Folinsbee et al. 1973).

The typical habitat associations of meadow voles on the mainland have been well documented, but their specific habitat requirements within forested systems are not well understood. I measured the relative abundance of small mammals during the summers of 1993 and 1994 within semimature, mature, and silviculturally overmature coniferous stands in western Newfoundland, and immature and overmature stands within central Newfoundland. I report on the age relationships and structural characteristics of microtine macro-habitat within these forested ecosystems, and discuss the management implications of my results to the management of marten on the island of Newfoundland.

STUDY AREAS

I collected small mammal data from two locations on the island. The South Brook study area was located approximately 20 km east of the town of Corner Brook, and falls within the western region of Newfoundland (Forest Section B28b of the Canadian Boreal Forest Region [Rowe 1972]). The Victoria Lake study area was located approximately 100 km east of the town of Stephenville, and falls in the western-most section of the central region of

Table III-1. Comparison of the Newfoundland small mammal prey base with its mainland counterpart in Labrador.

Mainland Species (Labrador)	Present in Newfoundland	Available in Newfoundland Forests	Distributed Throughout Marten Range
Microtus pennsylvanicus	X	X	X
Clethrionomys gapperi			
Phenacomys intermedius			
Microtus chrotorrhinus			
Peromyscus maniculatus	X	X	
Zapus hudsonicus			
Lepus americanus	X	X	X
Lepus arcticus	X		
Tamiasciurus hudsonicus	X	X	
Glaucomys sabrinus			
Condylura cristata			
Synaptomys borealis			
Dicrostonyx hudsonicus			
Sorex cinereus	X	X	X
Sorex palustris			
Sorex hoyi			
Tamias striatus[a]	X	X	

[a] Present in Newfoundland, but not in Labrador.

Newfoundland (Forest Section B28a of the Canadian Boreal Forest Region [Rowe 1972]). Each region was characterized by a wet, cool climate, with annual temperatures averaging 4°C (Banfield 1983). Forest composition of each study area was similar. Balsam fir (Abies balsamea) dominated all study sites, while black spruce (Picea mariana), white spruce (P. glauca), and white birch (Betula papyrifera) were also common. Plant understory ranged from moss (e.g. Hylocolium splendens, Pleurozium schreberi) to herb dominated (e.g., Ribes spp., Viburnum spp., Streptopus spp.) communities (Meades and Moores 1994). Small spruce fens (0.1-0.5 ha) were interspersed throughout most forested stands. Additionally, periodic insect defoliation by spruce budworm (Choristoneura fumiferana) and hemlock looper (Lambidina fiscellaria) has opened the canopy of some of the more mature stands (Thompson 1991).

The Corner Brook mill began logging in the South Brook valley as early as 1924, with the greatest portion harvested in the 1940's (Corner Brook Pulp & Paper Ltd. historical files). The presence of residual stands provided three age classes of forest: semimature (40-60 years), mature (60-80 years), and overmature (80+ years). Conversely, tree harvest within the Victoria Lake study area occurred between the late 1950's and the late 1960's (Abitibi-Price historical files). A few inaccessible blocks remained unharvested. Thus, age classes available within the Victoria Lake study area were immature (20-40 years) and overmature. All sampled stands were naturally thinned.

Balsam fir is a relatively short-lived species, and stands older than 120 years are rare in Newfoundland (Thompson 1991). While I considered unharvested stands greater than 80 years "old growth," old stands appear to be largely even-aged. A more detailed description of site characteristics, disturbance regimes, and stand history is provided in Chapter II.

METHODS

Small Mammal Data

The 1993 trapping design was intended to determine differences in the relative abundance of small mammals between the two older second-growth age classes (semimature and mature) and unharvested, overmature stands. I selected three stands within each age class using forest inventory maps from the Newfoundland Department of Forestry. Standard 7x7 or 6x6 removal trapping grids were established according to Kirkland (1982), using a 15-m spacing between stations, and two Victor snap-traps per station. Traps were baited with peanut butter and set for four consecutive nights. The first trap session was conducted July 1993. All trapping grids were then moved 50-200 m from the first trap site to insure that the initial removal of animals did not influence population response during the second trap session, conducted from mid to late August.

Preliminary examination of 1993 data and observations from the field suggested that there was a fair degree of heterogeneity within stands due to small patches of residual trees, insect defoliation, and interspersion of spruce fens. To account for this variability, I altered my study design in 1994. I also included a younger age class (immature) in the 1994 trapping sessions. A minimum of two stands was selected for each age class available within each study area. Six "mini-grids" (2x8) were placed within each site, spaced uniformly along a predetermined transect established for collecting forest structure data (see Chapter II). Grids were spaced a minimum of 50 m apart. Three grids per site were set during each trap session, and I followed the same protocol for baiting and trapping duration as in 1993. Figure III-1 illustrates the difference in study design between years. Small mammal abundance was reported as the number of animals trapped per 100 trap nights (Getz 1982).

Habitat Data

Measurements of standing tree structure, downed logs, and understory were taken at four uniformly spaced plots within 1993 trap grid locations, while the same measurements were taken at two points within each 1994 mini-grid location (Fig. III-1). Standing trees were assessed using a variable-radius plot methodology (Husch et al. 1972). Two random trees per plot were aged at breast height with an increment borer. Overhead cover was estimated ocularly and classified into one of four classes (0-25, >25-50, >50-75, and >75-100%). Downed logs were measured using a modified version of Brown's (1976) plane intersect method. Finally, each plot was classified into forest ecosystem types (based upon plant indicator species, topography, and soil type) as a measure of site potential (Meades and Moores 1994).

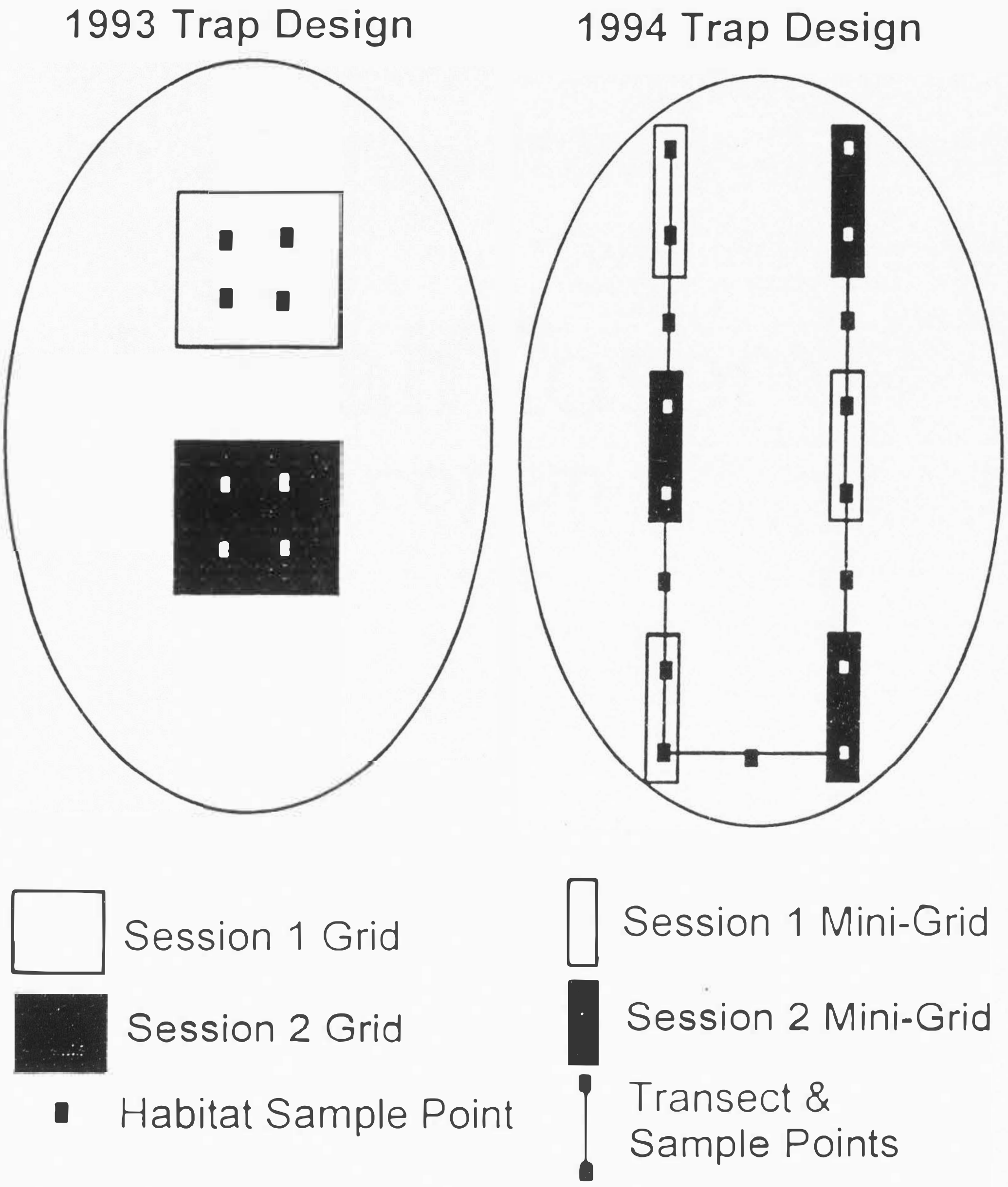

Fig. III-1. Study design changes from 1993 to 1994.

Tree structure was characterized using a preliminary relative density index equation derived by Newton (Forestry Canada, unpubl. data). Relative density relates mean stem volume to stem density as a function of the self-thinning rule (Drew and Flewelling 1977). Sample ages within each 1993 grid were averaged to assess individual ages for each grid location, while the average stand age was used for the 1994 trap sessions. I assumed that actual tree age was the age taken at breast height, plus 8 years, the estimated time for a tree to reach breast height (D. Harris, pers. commun.). A more detailed description of forest structure mensuration and calculations is provided in Chapter II.

Analysis

Due to potential population differences between study areas, I analyzed small mammal data from Victoria Lake and South Brook separately. Trapping grids from 1993 were purposely grouped into the a priori age classes according to actual grid age, not the stand age. Thus 1993 data reflect local conditions (1 ha), while 1994 data represent differences within (local) and between stands (20 ha). Relative abundance data were transformed for analysis using a log transformation (Sokal and Rohlf 1981). I used an analysis of variance (ANOVA) to test for differences between age classes and between sessions. A t-test was used for planned comparisons between individual second-growth age classes and the overmature age class (Sokal and Rohlf 1981). Pearson's product-moment coefficient (ρ) was used to determine the extent of correlation between vole abundance and habitat variables (Sokal and Rohlf 1981).

RESULTS

Vole abundance within the forest was generally low; a trap effort of 14,864 trap nights over 2 years yielded a total of 211 voles. However, vole abundance varied greatly over both time and space. Trap success in older-growth sites within the Victoria Lake study area remained relatively constant during the 2 years of trapping (Table III-2). In contrast, the South Brook study site experienced a sharp decline from 37 voles captured in 1993 to only 2 vole captured in 1994. The difference in population trends suggests that vole populations may fluctuate asynchronously among different regions on the island.

Table III-2. Population trends of the meadow vole within each study area.

Location	Year	Trap Session	# Voles	Trap Effort[a]
		Mid-August	42	560
	1994	Late June	58	1536
		Mid-August	36	1536
South Brook	1993	Mid-July	21	2744
		Late August	16	2328
	1994	Early July	2	3072
		Late August	0	2304

[a] Increased trap effort in Victoria Lake during 1994 reflects the additional trapping within immature second growth.

Vole abundance differed significantly ($P<0.05$) between age classes; the majority of voles were captured in overmature locations (Fig. III-2). My results show that both semimature and mature stands had significantly ($P<0.05$) lower vole abundance than overmature stands (Figure III-2a). Abundance differences were even more profound between immature stands and overmature stands. Two trap sessions in overmature stands within the Victoria Lake study area yielded a total of 93 captured voles, whereas the same trap effort in immature stands captured only 1 vole (Fig. III-2b). While statistical analysis of this relationship would violate the homogeneity of variance assumption of the analysis of variance (Sokal and Rohlf 1981), the relationship is clearly significant.

Vole abundance was also examined with respect to forest structure, independently of age. In stands greater than 40 years of age (South Brook data), the relative density of standing trees appeared to have a negative influence on vole abundance ($\rho = -0.682$, $P<0.01$). Voles also seemed to be associated with the amount (volume) of dead and downed woody debris ($\rho = 0.783$, $P<0.01$).

DISCUSSION

Typical meadow vole habitat is characterized by open, mesic locations supporting abundant graminoid vegetation (Getz 1970, Grant 1971, Folinsbee et al. 1973). My data suggest that within the forest, voles were most abundant in areas with low relative tree density and high subcanopy structure. This

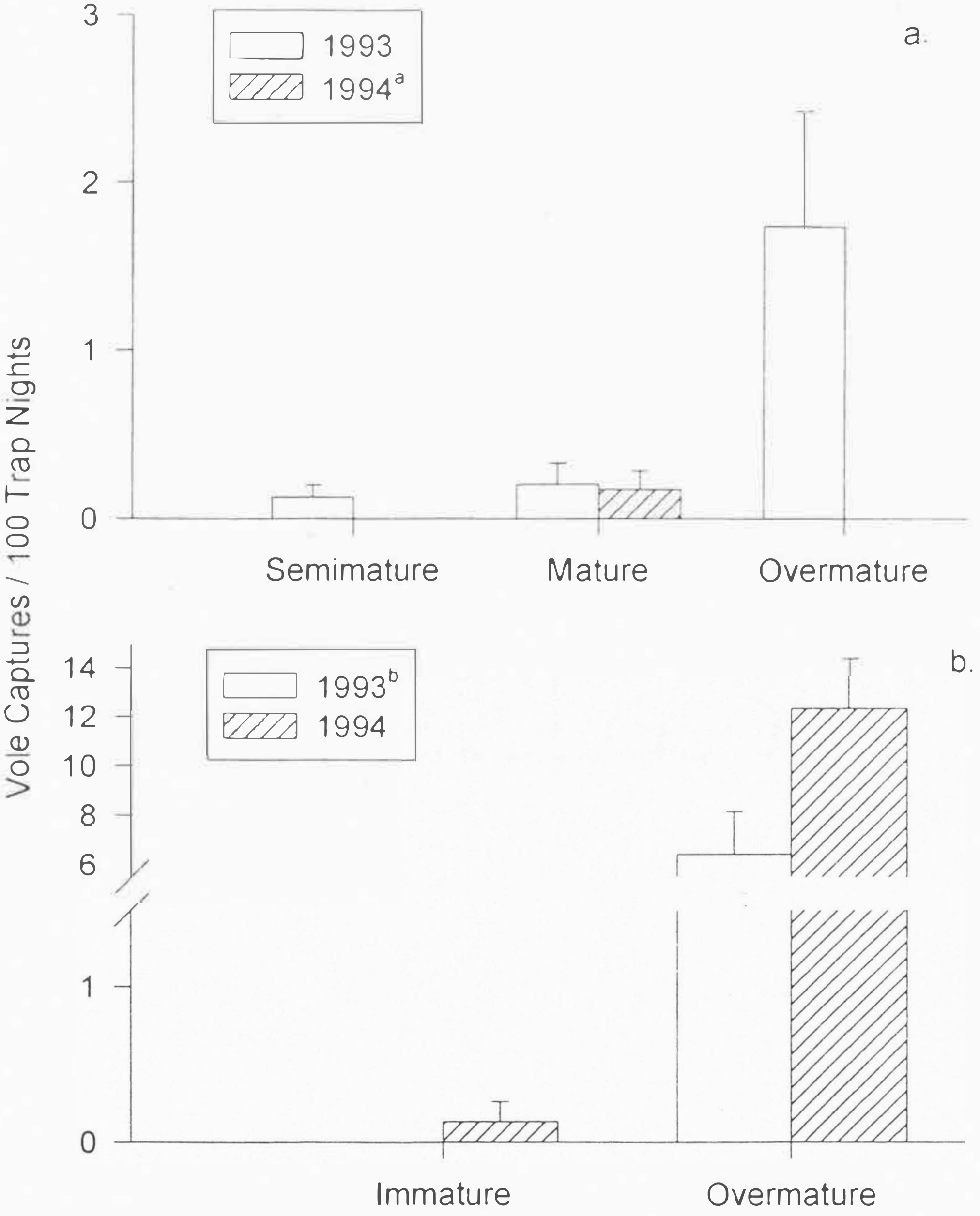

Fig. III-2. Meadow vole distribution among forest age classes: a) comparison of semimature, mature, and overmature classes at the South Brook study area, b) comparison of immature and overmature classes at the Victoria Lake study area.

[a] Population crash experienced at South Brook during 1994, only two voles captured.

[b] Immature stands were not sampled during 1993.

relationship is reflected in the distribution of voles among forest age classes; voles were significantly more abundant in overmature locations than all other forest age classes. A discussion of stand dynamics will further clarify this observation.

In stands with a high relative density index (Pr), trees compete for limited resources (e.g., light) (Drew and Flewelling 1977). Above a certain threshold density for a given average stem size, a stand can no longer support all trees present, and self-thinning results. The range of relative densities where self-thinning occurs is termed the zone of imminent competition mortality (ZICM) (Drew and Flewelling 1977). Newton and Weetman (1993) calculated the ZICM for black spruce in central Newfoundland as those stands falling between Pr values of 0.5 and 1.0, the latter being the maximum index value.

Stands within ZICM are typically very dense, with high canopy closure and, consequently, sparse understories. Conversely, as a stand begins to senesce into a silviculturally overmature state, mortality occurs at a faster rate than the remaining trees can use the released resources. Dominant and codominant trees die and fall to the ground, the canopy opens, and the subcanopy structure becomes much more diversified (see Chapter II). My data indicate that voles respond to this phenomenon, as the majority of voles were captured in locations where relative densities were less than 0.5 (Fig. III-3). Notice that the relationship is largely independent of age; overmature sites within the ZICM also have low vole abundance. The relationship between vole

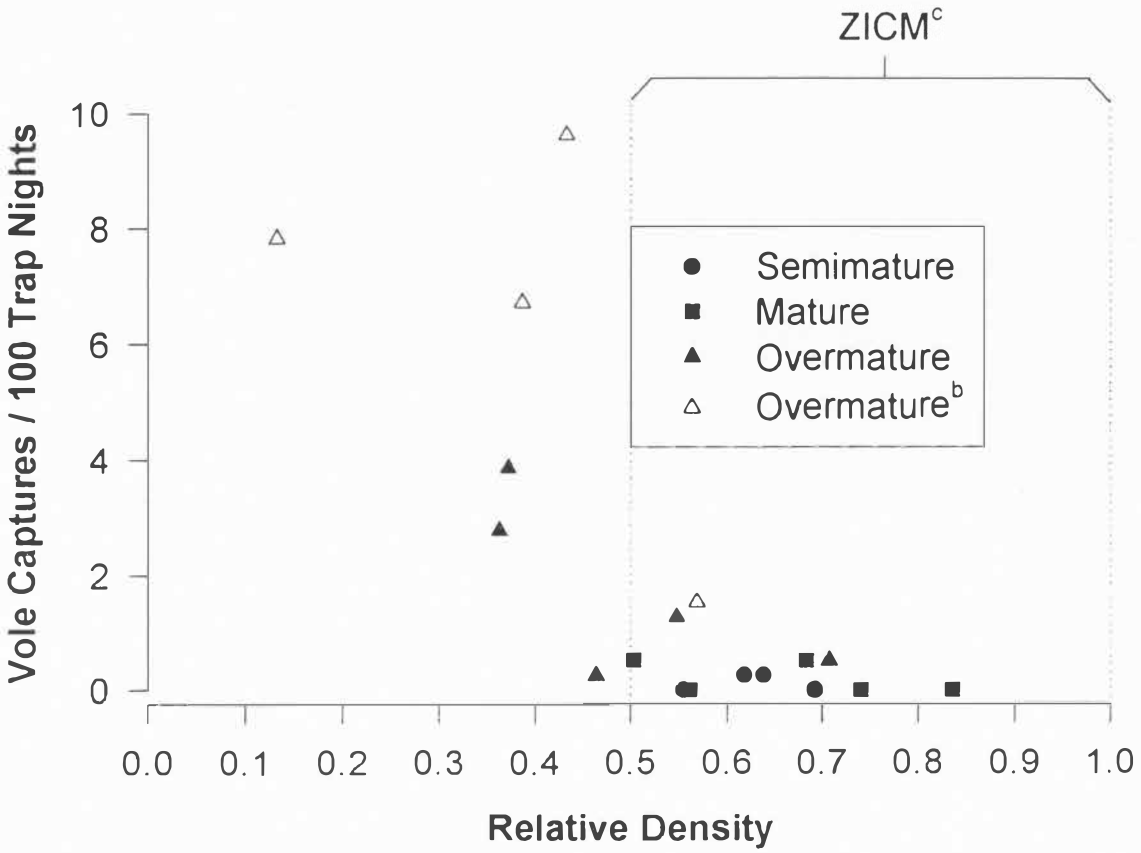

Fig. III-3. Meadow vole response to forest structure.[a]

[a] Trapping data from 1993.

[b] Victoria Lake sites not included in analysis (see text).

[c] Zone of imminent competition mortality.

abundance and forest age likely reflects the increased probability that older stands will contain locations in various stages of senescence (see Chapter II).

Meadow vole habitat associations are likely to affect marten habitat suitability on the island of Newfoundland. Newfoundland meadow voles appear to retain their affinity for open locations, even within forested areas. While marten cannot exploit the microtine resource beyond 150-200 m into open areas (Hargis and McCullough 1984, Drew 1995), overmature stands offer a form of structural "common ground," open enough to support vole populations while still maintaining sufficient cover for a foraging marten.

The observed relationships indicate that certain assumptions of marten habitat quality may not apply to the unique ecological situation on the island of Newfoundland. Overhead cover is commonly expressed in the literature as a major factor influencing marten habitat suitability (Hargis and McCullough 1984, McCallum 1992). Allen's (1982) Habitat Suitability Index model for marten assumes that overhead cover greater than 50% is optimal, and local marten habitat management plans stress the importance of high canopy closure (e.g., Beaudette 1991). My data indicate that meadow voles are virtually nonexistent within very dense stands, suggesting that the maintenance of contiguous, dense conifer forests could potentially be detrimental to Newfoundland marten. While many studies suggest that small openings may be beneficial to marten by increasing prey abundance (e.g., Koehler et al. 1975, Spencer et al. 1983), the relative importance of this phenomenon may be amplified in Newfoundland due to the rather specific habitat requirements of the main prey species.

Perhaps equally as dangerous, defoliation disturbance is often perceived as detrimental to marten habitat because of substantial canopy loss. Yet defoliated areas often retain a high degree of structure for over a decade after the initial disturbance (Ostaff and MacLean 1989). Defoliated patches may serve as short-term reservoirs for microtines within a forested environment. Observations by Drew (1995) and Sturtevant (unpubl. data) indicate that marten in Newfoundland may select defoliated areas as foraging sites.

Most marten biologists agree that marten habitat quality improves with forest succession (see McCallum 1992 for review). Several mechanisms have been implicated as the cause of this close association, including thermal constraints (Buskirk 1984, Buskirk et al. 1989), energetic requirements (Hargis and McCullough 1984, Bissonette and Sherburne 1994), and predator avoidance (Thompson 1994, Drew 1995). As a subspecies, the Newfoundland marten is probably not very different from its mainland counterpart, and must operate under the same physiological and psychological constraints. What makes Newfoundland unique is the low selection of prey species. My results indicate that voles become scarce at the time of canopy closure, and do not increase significantly in abundance until the stand begins to senesce into an overmature state. While other regions may also observe a general increase in the abundance of small mammals within overmature forests (e.g., Raphael 1984), the distinction between mature and overmature forests may not be as acute in areas with a full array of small mammal prey species.

Equally as important, marten on the mainland appear to have a much greater chance of surviving a prey crash by switching to alternate prey species. Observations from the present study and others on the island (Tucker 1988, Adair unpubl. data) suggest that microtine populations are volatile in Newfoundland. The effect on the resident marten population may be profound (Tucker 1988).

The assumption of available prey does not apply to the local conditions of Newfoundland. Marten on the island have few prey species available within their environment. One of the main prey species appears to be closely tied to the overmature stage of forest succession. The increased complexity of volatile vole population dynamics creates a fragile system that may be particularly sensitive to human disturbance. Consequently, any management plan that includes marten habitat as an objective must account for the constraints imposed by the available prey resource.

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CHAPTER IV

STAND DENSITY MANAGEMENT DIAGRAM FOR MIXED BALSAM FIR--BLACK SPRUCE STANDS[3]

ABSTRACT: A stand density management diagram for mixed balsam fir--black spruce stands was constructed using 129 plots from 24 stands and 17 measurements from 9 permanent sample plots, located in western and central Newfoundland. The diagram's applicability is discussed, and an example of its use is provided.

Introduction

The manipulation and control of tree density can effectively manage stand structure, yield, tree size, and rotation length between successive tree harvests (Kumar et al. 1995, Long 1985). Stand density management diagrams (SDMD) are empirically derived, ecologically based models that graphically illustrate yield-density relationships and density-dependent mortality at different stages of stand development (Newton and Weetman, 1993, 1994, Drew and Flewelling 1977, Kumar et al. 1995, Smith 1989). SDMDs allow generalized management objectives to be translated into planned thinning regimes, and effectively illustrate the advantages and consequences of alternative silvicultural prescriptions. They also may be used to adapt traditional timber management to incorporate the specific structural attributes necessary for wildlife habitat

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(Lilieholm et al. 1993, Smith and Long 1987, Chapter V).

SDMDs have been created for monospecific black spruce (Picea mariana) stands (Newton and Weetman 1993,1994). However, no models exist for balsam fir, another critical commercial species in eastern boreal forests. Furthermore, most models are created for monospecific conditions. In Newfoundland, balsam fir often grows in close association with black spruce, and mixed stands are common (Meades and Moores 1994). Additionally, current models for the region do not allow for reliable predictions beyond the typical 60-year rotation schedule used for commercial pulpwood harvest, yet long-term predictions are particularly useful for incorporating the management of wildlife species associated with later stages of stand development (e.g., Chapter V, Lilieholm et al. 1993). Hence, the objective of this chapter was to create a SDMD that a) may be applied to mixed balsam fir--black spruce stands in Newfoundland and b) allows predictions of stand structure within mid to late stages of stand development.

Methods

Study Area

I collected stand information from two locations in Newfoundland. Approximately two thirds of the plots were established within a 20-km radius of the town of Corner Brook, located within the western region of Newfoundland (Forest Section B28b of the Canadian Boreal Forest Region [Rowe 1972]).

The remainder were established in the western-most section of the central region of Newfoundland (Forest Section B28a of the Canadian Boreal Forest Region [Rowe 1972]) in the vicinity of Victoria Lake, located approximately 100 km east of the town of Stephenville. Each region was characterized by a wet, cool climate, with annual temperatures averaging 4°C (Banfield 1983).

Forest composition of each study area was similar. Balsam fir (Abies balsamea) dominated all study sites, though black spruce (Picea mariana) typically contributed to approximately 15% (± 26%) of the basal area. White spruce (P. glauca) and white birch (Betula papyrifera) were also present, but neither comprised more than 10% of the basal area. Plant understory ranged from moss (e.g., Hylocomium splendens, Pleurozium schreberi) to herb and shrub-dominated (e.g., Ribes spp., Viburnum spp., Streptopus spp.) communities (Meades and Moores 1994). Small spruce fens (0.1-0.5 ha) were interspersed throughout most forested stands. Additionally, periodic insect defoliation by spruce budworm (Choristoneura fumiferana) and hemlock looper (Lambidina fiscellaria) has opened the canopy of some of the more mature stands (Raske 1986, Thompson 1991, Chapter II).

Data Base

The majority of the data used in the construction of the SDMD consisted of plot measurements taken within 24 stands, with mean stand age ranging from 30 to 100 years. Stands less than 80 years of age were naturally regenerated from past harvest operations, while stands greater than 80 years of age were never harvested. Five to 10 sample plots were placed at 100 meter intervals along a predetermined transect for each stand. Only those plots characterized by even-aged structure and negligible mortality due to defoliation were used in the construction of the model, yielding a total of 129 plots.

Stand structure was measured using a variable radius sampling methodology. Basal area was estimated using a prism, and diameters (breast height) of tallied trees were measured to the nearest cm. Two trees were randomly chosen during the basal sweep and aged at breast height using an increment borer. An additional dominant tree was aged and measured for height using a clinometer. I then estimated individual tree heights using Page and van Nostrand's (1973) height-diameter regression functions: $HT = b_0 - b_1 \cdot D \cdot HT_d - b_2 \cdot D^2$, where HT is the estimated height, D is the diameter at breast height, HT_d is the dominant height and b_0, b_1, and b_2 are species-specific regression coefficients. Volumes were then calculated using Warren and Meades' (1986) taper equations. Stem density and volume estimates were calculated for each plot using Husch et al.'s (1972) methodology for variable radius sample plots. Finally, each plot was classified into forest ecosystem types (based upon plant indicator species, topography, and soil type) as a measure of site potential (Meades and Moores 1994). Site index (dominant height at a breast height age of 50) was estimated using the site index curves provided by Page (1968).

The above data lacked sufficient numbers of plots in the smaller height classes (<10 m) to allow extrapolation to the immature stage of forest development. I therefore incorporated permanent sample plot (PSP) data, provided by the Newfoundland Forest Service, to derive a more complete diagram. Initial measurements of eight PSPs were collected in 1987; these plots were remeasured in 1992. An additional PSP established in 1992 yielded a total of 17 measurements for analysis. The data include individual tree height (± 0.1 m) and breast height diameter (± 0.1 cm) within fixed-area plots ranging from 0.01 to 0.002 ha in size. Tree density was calculated directly, and volumes were obtained by using Warren and Meades' (1986) taper equations. All PSPs were from unmanaged stands located in the vicinity of Victoria Lake, described above. Table IV-1 describes the mensurational characteristics of the combined database.

Table IV-1. Mensurational characteristics of the database (n=146).

Parameter	Mean	SD	Range
Density (stems/ha)	8131.4	14217.7	287.1 - 71000.0
Mean Volume (dm^3)	117.5	130.1	0.5 - 640.9
D_q[1] (cm)	13.8	6.6	2.1 - 31.3
HT_d[2]	13.5	4.7	2.9 - 22.8
Age_{bh}[3]	61.7	27.7	16.8 - 165.0
Site Index[4]	14.2	1.8	7.0 - 16.8
Total Volume (m^3/ha)	208.6	99.6	10.8 - 527.3
Basal Area (m^2/ha)	40.7	16.4	5.7 - 82.6

[1] Quadratic mean diameter outside bark at breast height (1.37 meters).
[2] Dominant height
[3] Mean plot age at breast height
[4] Dominant height at base age 50 (Meades and Moores 1994, Page 1968)

Construction of the Diagram

The approach used in the construction of the SDMD follows Newton and Weetman (1993). P. Newton (unpubl. data) provided a relative density index equation for monospecific balsam fir stands in Newfoundland:

$$\underline{Pr} = N_o/(\underline{v}/10^{6.64})^{-0.37} \qquad (1)$$

where $\underline{Pr}$ = relative density index, N_o= number of trees per hectare, and $\underline{v}$ = mean stem volume in dm^3. The exponents in equation (1) were derived from a relatively limited sample of balsam fir stands (n = 11) in central Newfoundland, and should be considered as preliminary (P.F. Newton, pers. commun.). These exponents were averaged with those derived for black spruce (Newton and Smith 1990) to yield the following relative density function for mixed balsam fir--black spruce stands:

$$\underline{Pr} = N_o/(\underline{v}/10^{7.452})^{-0.49} \qquad (2)$$

While this equation should be considered approximate, it coincided well with my own data set. Relative densities corresponding to the lower limit of the zone of imminent competition mortality (ZICM) and the crown closure (CC) line (Drew and Flewelling 1977) for balsam fir could not be determined using the available data. Newton (1992) observed that balsam fir and black spruce occupied similar size class distributions within mixed stands. I therefore substituted black spruce relationships (Newton and Weetman 1993) as a tentative approximation, where the lower limit of the ZICM is delineated by a Pr of 0.50 and the CC line is defined at Pr = 0.13.

Quadratic mean diameter (D_q) and dominant height (HT_d) isolines were derived using plot data. Following methodology by Newton and Weetman (1993), D_q was related to mean volume by Eq. 3.

$$\log_{10}(D_q)=b_0+b_1\cdot\log_{10}(\underline{v})+b_2\cdot\log_{10}(\underline{N}) \qquad (3)$$

where b_0, b_1, and b_2 are parameter estimates obtained by least squares regression techniques. Parameter estimates and associated regression statistics were as follows: $b_0 = 0.540$; $b_1 = 0.361$; $b_2 = -0.025$; $r^2 = 0.995$; $SEE(\log_{10}) = 0.019$; F-ratio = 13856.13; $p \leq 0.05$; $n = 146$. D_q isolines were then obtained by rearranging Eq. 3 with respect to mean volume at specified D_q values.

HT_d isolines were derived using the two-step regression procedure employed by Newton and Weetman (1993). First, the data were partitioned into height classes (4.0-20.0 by 1-m intervals). Data in each HT_d class were then fit to Kira et al.'s (1953) reciprocal equation of the competition-density (C-D) effect (Eq. 4).

$$1/\underline{v} = k_1 + k_2\cdot\underline{N} \qquad (4)$$

where parameters k_1 and k_2 were estimated using least squares regression. Results indicated that 10 of the relationships were significant. First-stage parameters estimates were then related to HT_d class using Eq. 5 and Eq. 6.

$$\log_{10}(k_1) = b_3 + b_4 \cdot HT_d \qquad (5)$$

$$\log_{10}(k_2) = b_5 + b_6 \cdot HT_d \qquad (6)$$

where parameters b_3, b_4, b_5, and b_6 were estimated using least squares regression. Parameter estimates and associated regression statistics for Eq. 5 were as follows: $b_3 = -0.194$, $b_4 = -0.150$, $r^2 = 0.915$; $SEE(\log_{10}) = 0.232$; F-ratio = 86.397; $p \leq 0.05$; $n = 10$. Similarly, for Eq. 6: $b_5 = -5.042$, $b_6 = -0.031$, $r^2 = 0.831$; $SEE(\log_{10}) = 0.071$; F-ratio = 39.199; $p \leq 0.05$; $n = 10$. Second-stage models were then incorporated back into Eq. 4 using predicted parameter estimates for each HT_d class.

An examination of residuals revealed that the resultant regression equations were unbiased with respect to the independent variables, dominant age, site index, and species composition (i.e., percentage of the basal area in black spruce). However, residual analysis for the D_q isoline equation showed a slight underestimation of mean volume over a dominant height of 18 m. Figure IV-1 shows the completed stand density management diagram.

Discussion

The manipulation of growing stock to reach optimum production goals can be a complex endeavor, particularly when other values, such as wildlife habitat, are included within an overall, multiple-use forest management strategy.

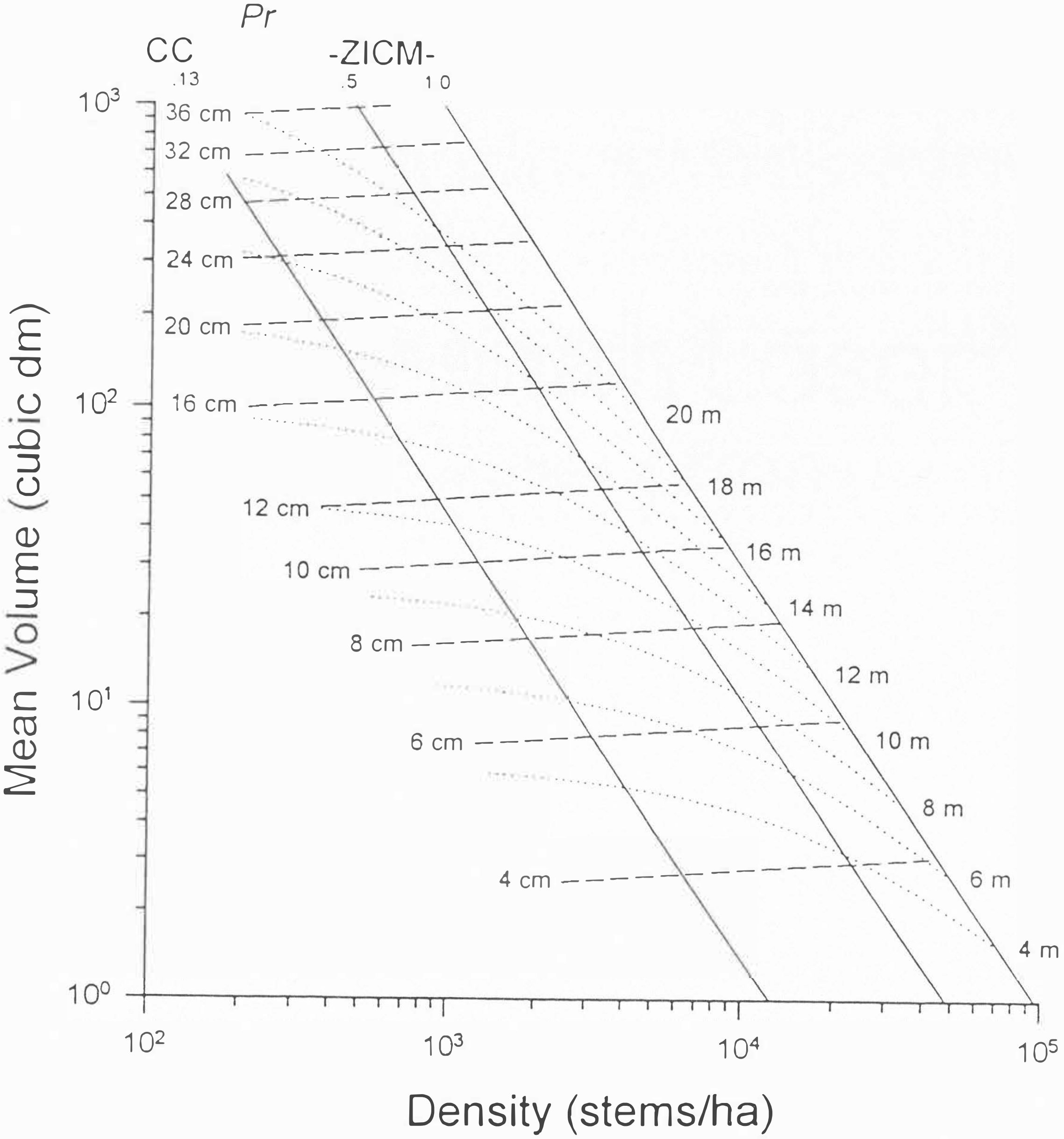

Fig. IV-1. Mixed balsam fir--black spruce stand density management diagram graphically illustrating: (1) the self-thinning rule at a relative density index (Pr) of 1.0; (2) lower limit of the zone of imminent competition-mortality (ZICM) at Pr = 0.50; (3) approximate crown closure line at Pr = 0.13; (4) reciprocal equation of the C-D effect at specified dominant heights (height isolines [.......]) and (5) quadratic mean diameter (D_q) isolines (--------).

Yield-density relationships, when incorporated into a SDMD, can simplify the process by graphically illustrating stand response to alternative silvicultural prescriptions (McCarter and Long 1986). Though SDMDs are empirically derived, the ecological processes of the self-thinning (Yoda et al. 1963) and intraspecific competition govern its construction (Newton and Weetman 1993). Size-density indices are particularly useful in characterizing stand structure because they are independent of stand age and site potential. However, time may be readily interpreted from the diagram using site index curves in conjunction with the dominant height (HT_d) isolines (Drew and Flewelling 1977).

Density management is characterized by trade-offs between individual stem growth and overall stand production (Long 1985, Kumar et al. 1995). Relative density benchmarks such as the crown closure (CC) line and the zone of imminent competition mortality (ZICM) serve as guidelines for density management strategies. The CC line indicates threshold above which trees begin to compete, while relative densities falling within the ZICM indicate active self-thinning due to intense intraspecific competition (Drew and Flewelling 1977). A common management strategy for fiber production would limit the maximum relative density to 0.5 to avoid self-thinning and insure stand vigor.

I illustrate the utility of the SDMD with a simple comparison of two alternative density management regimes: precommercial thinning versus no silvicultural treatment (Fig. IV-2). The thinning prescription described here reflects current density management regimes practiced in the western region of

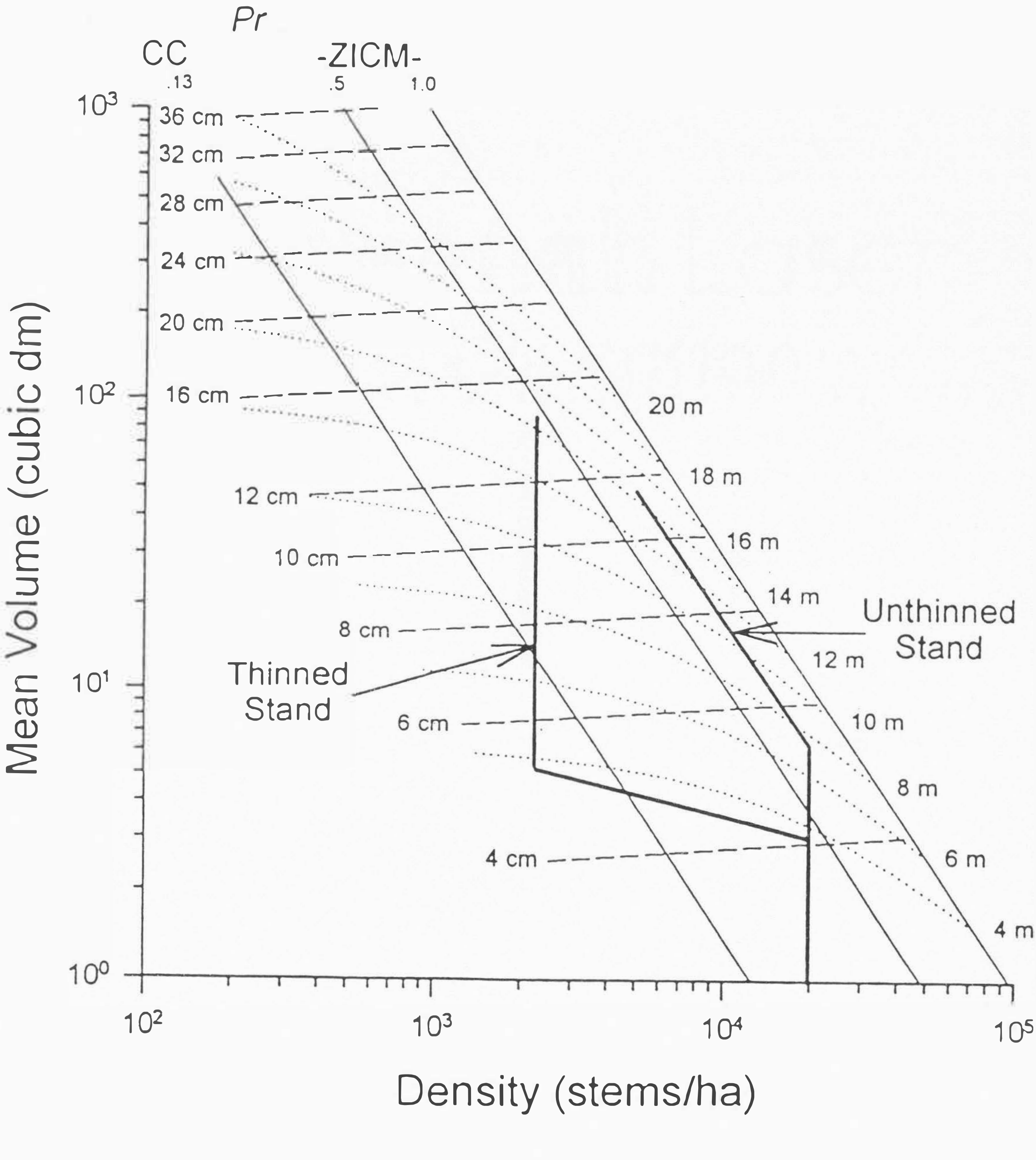

Fig. IV-2. Predicted trajectories of thinned and unthinned stands. (See text for description).

Newfoundland (D. Harris pers. commun.). The primary objective of thinning in this region is to shorten the rotation age of stands for fiber production.

For this example, I will use a relatively productive site (15 m at breast height age of 50 [Page 1968]), and assume that an unmanaged stand will maintain a fairly constant relative density of 0.7 through active self-thinning. Given that balsam fir typically reaches breast height by 7-8 years, the stand will attain a dominant height of 14.5 m within a 55-year rotation (Page 1968). A low-thinning treatment is simulated on the diagram by tracing the dominant height isoline to the target density, in this case 2200 stems per hectare (Fig. IV-2). This procedure assumes that cut stems are biased towards the small diameter trees; consequently, stand D_q increases and dominant height is retained (Newton and Weetman 1993). In this example, a thinned stand would reach a mean volume of 85 dm^3 at a density of 2200 stems per hectare at 55 years. Conversely, an unmanaged stand is more dense (5000 stems per hectare), but mean stem size is significantly reduced (50 dm^3). In Newfoundland, naturally thinned stands are typically harvested on a longer (65-year) rotation (D. Harris, pers. commun.).

This diagram was constructed using data from balsam fir and mixed balsam fir--black spruce forests on the western side of the island of Newfoundland. Though plots from the central Newfoundland were employed, these plots were located in a transition zone that is distinct from the typical upland, black spruce-dominated forests of central insular Newfoundland

(Meades and Moores 1994, D. Harris pers. commun.). The SDMD will need to be evaluated and used with caution if it is applied beyond the range of sites and stand structures represented in my data set (Table IV-1).

In the absence of a thinning, forest stands would be expected to enter and subsequently remain in the ZICM, parallelling the self-thinning line. However, White and Harper (1970) indicated that the gradient for oak and beech decreased from -1.5 to -1 after culmination of the mean annual increment. Graphical analysis of my plot data showed that the majority of unmanaged plots with mean volumes less than 100 dm^3 fell, as expected, within the ZICM. However, above a mean volume of 300 dm^3, very few plots fell within this zone (see Chapter II). The shallow rooting system typical of balsam fir and black spruce increases the susceptibility of large trees to windthrow, a prominent form of disturbance in Newfoundland's maritime climate (Newton 1992, Meades and Moores 1994). Balsam fir is also particularly prone to heart rot at later stages of stand development, increasing the probability of windthrow mortality (Seymour 1992). Finally, mature balsam fir and black spruce, to a lesser extent, are particularly vulnerable to defoliation disturbance. These size-dependent, but largely density independent mortality factors may effectively limit the attainable size of the growing stock. Managers should consider these factors when planning for stands with large stem sizes.

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CHAPTER V

TEMPORAL AND SPATIAL DYNAMICS OF BOREAL FOREST STRUCTURE IN WESTERN NEWFOUNDLAND: SILVICULTURAL IMPLICATIONS FOR MARTEN HABITAT MANAGEMENT[4]

Abstract

The conservation of marten (Martes americana) populations within managed forests will require planning at appropriately large temporal and spatial scales. A conceptual model of stand-level dynamics is constructed from empirical study of forests in western Newfoundland and related to the habitat requirements of resident marten. The model suggests that the critical elements of marten foraging habitat are currently found within a senescent forest stand structure. Implications of the model are discussed as they relate to landscape-level disturbance patterns. Changes in both stand-level dynamics and landscape-level phenomena indicate that intensive silviculture is necessary to promote marten habitat within managed forests in Newfoundland. I propose a density management regime designed to provide a marten habitat window within a reasonable pulpwood rotation period. The stand-level prescriptions are intended as a tool to be incorporated into an overall landscape management regime.

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[4] Coauthored by Brian R. Sturtevant, John A. Bissonette, and James N. Long.

1. Introduction

The American marten (Martes americana) typically is recognized for its close association with late successional coniferous forests (Mech and Rogers, 1977; Soutiere, 1979; Spencer et al., 1983; Buskirk, 1984; Bissonette et al., 1989; Thompson, 1994; Thompson and Curran, 1995) and epitomizes the conflict between a valuable economic resource and the preservation of core-sensitive wildlife species. Habitat structure required for healthy marten populations generally takes decades to develop, and individual home range requirements are typically very large for such a small carnivore (see Buskirk and MacDonald, 1989). Attempts to mitigate the conflict between timber harvest objectives and marten demand planning on similar temporal and spatial scales (Bissonette et al., 1989; Thompson and Harestad, 1994).

The clear-cut harvesting techniques typically practiced throughout the boreal region impact marten populations directly (Soutiere, 1979; Snyder and Bissonette, 1987; Bissonette et al., 1989; Thompson, 1994), and the subsequent second-growth forest is often of much lower habitat quality (Bissonette et al., 1989; Thompson, 1994; Thompson and Harestad, 1994; Thompson and Curran, 1995). As a result, marten populations have suffered throughout much of their range, most notably in the Atlantic Provinces of Canada (Thompson, 1991; Thompson and Harestad, 1994). On the island of Newfoundland, where the marten is currently listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as threatened, the situation has reached a crisis (Bissonette et al., 1989; Thompson, 1991). Unregulated pulpwood harvest during the past century has skewed the forest age-class distribution toward the youngest (regeneration) stage of forest succession (Thompson, 1991), and the majority of the island now is characterized by relatively contiguous blocks of second-growth forest. At present, a single recognized viable population of marten exists in one of the few remaining blocks of old-growth forest, despite the fact that the trapping of marten has been prohibited since 1934 (Bissonette et al., 1989).

A system of forest reserves has been offered as a method of preserving marten populations in several locations in Canada (Thompson and Colgan, 1987; Thompson, 1994); the delineation of reserves is one of the major objectives of the marten's recovery plan (Forsey et al., 1995). However, because of the dynamic nature of forested systems, habitat reserves cannot be sustained in perpetuity unless they are large enough to sustain the impacts of natural disturbance over the long term (Lilieholm et al., 1993). Boreal systems in particular are shaped by natural disturbance events (Hunter, 1993), suggesting that a system of permanent habitat reserves may not be a stable management strategy in Newfoundland. For this reason, Bissonette et al., (1989) proposed a more dynamic approach to marten habitat management, by orchestrating timber harvest patterns so that marten habitat is always available on the landscape.

Bissonette et al.'s (1989) approach relies upon two related assumptions:

a) Regenerating forests will provide suitable marten habitat at some point in the future; and b) the stage of forest development that provides this critical habitat structure falls within an economically feasible rotation age (Thompson and Harestad, 1994). This approach implies that second-growth forests will provide marten with a temporal "window" of habitat before the forests are ready to be harvested. However, recent examination of second-growth forest in Newfoundland (Thompson and Curran, 1995; Chapter III) suggests that marten there may be particularly dependent upon the structures associated with an overmature stage of forest development. Balsam fir (*Abies balsamea*), the dominant tree species of this system, is typically ruled by a pathological rotation (Seymour, 1992). Hence, the overmature state within this region is characterized a rapid increase in tree mortality, resulting in a substantial decrease in standing volume. Because this represents decreased fiber yield, the marten's dependence on this senescent stage suggests continued conflict.

In this chapter, I examine how the critical aspects of marten habitat change as forest stands develop through time, focusing on three main attributes: vertical escape cover, microtine abundance, and coarse woody debris. I also discuss the mechanisms underlying the distribution of these components across the landscape, and how these elements might be perceived by marten. I then offer a silvicultural prescription designed to mitigate the impact of past timber harvest methods by creating the structure characteristic of old growth within younger stages of forest development. This stand-level prescription is not intended as a definitive methodology, but rather as an approach that may be employed within an overall adaptive, landscape-level management strategy.

2. Marten Habitat Requirements

Several mechanisms may explain the marten's association with older coniferous forests: escape cover from predation (Pullianen, 1981; Thompson, 1994; Drew, 1995), prey availability and accessibility (Campbell, 1979; Corn and Raphael, 1992; Sherburne and Bissonette, 1993;1994; Bissonette and Sherburne, 1994, Thompson and Curran, 1995; Hargis and Bissonette, in press; Chapter III), thermoregulation (Buskirk et al., 1988; 1989), and den sites (Buskirk and Powell, 1994). However, recent research suggests that marten do not necessarily require old forests per se, but rather the structure associated with these later successional stages of forest development (Harrison et al., in press; Drew, 1995).

The vertical stem structure of trees provides marten with escape cover from larger terrestrial predators (Drew, 1995). While canopy closure is often considered a critical element of marten habitat (e.g., Allen, 1984), the presence of vertical stem structure and downed woody debris appear to provide adequate security, even when overhead cover is absent. For example, marten showed extensive use of defoliated stands in Newfoundland (Drew, 1995) and Maine (Harrison et al., in press), as well as burned forests in Wyoming (Drew, 1995) and Alaska (Paragi et al., in press). Still, marten typically avoid areas that are devoid of trees (Campbell, 1979; Soutiere, 1979; Spencer et al., 1983; Hargis and McCullough, 1984; Snyder and Bissonette, 1987; Bissonette et al., 1989).

Marten also require available prey. Newfoundland supports a depauperate small mammal fauna (Tucker, 1988; Bissonette et al., 1989). Only three mammalian prey species are found throughout the marten's forested range: meadow voles (Microtus pennsylvanicus), masked shrews (Sorex cinereus), and snowshoe hares (Lepus americanus) (Chapter III). Red squirrels (Tamiascurius hudsonicus), deer mice (Peromyscus maniculatus), and eastern chipmunks (Tamia striatus) are recent introductions that may be locally abundant (Tucker et al., 1989; Thompson and Curran, 1995). The absence of the red-backed vole (Clethrionomys gapperi) leaves the meadow vole as the sole microtine available to Newfoundland marten. The meadow vole is typically an open habitat species; however, it is accessible to foraging marten only when found within a forested environment. The lack of alternative prey species suggests that the prey resource requires special attention (Thompson and Curran, 1995; Chapter III).

Finally, marten must have access to a reliable prey resource throughout the winter months. Microtines remain active beneath the snow pack during winter, but marten need some way to access this resource. Downed logs and other coarse woody debris (CWD), typically provided by late successional forests, provide access by maintaining interstitial spaces beneath the snow layer (Campbell, 1979; Corn and Raphael, 1992; Sherburne and Bissonette, 1994; Bissonette and Sherburne, 1994). CWD may also function as structural cover necessary for the persistence of forest vole populations. Birney et al. (1976) stressed the importance of graminoid vegetation in providing structure necessary for the construction of protective runways and subnivean conduits; CWD may provide similar structure in forested environments, where vegetation is inherently less dense (Thompson and Curran, 1995).

3. Stand Dynamics

The core of the Newfoundland marten population falls within the Western Newfoundland Zone (Forest Section B28b) of the Canadian Boreal Forest Region (Rowe, 1972). The absence of prolonged dry periods within this region minimizes fire disturbance. Consequently, balsam fir dominates the forested landscape, and although black spruce (Picea mariana) is present, pure black spruce stands are generally restricted to rocky outcrops and poorly drained locations (Damman, 1983). White birch (Betula papyrifera) is present throughout the area, and white spruce (Picea glauca) is sporadic. Balsam fir is a relatively short-lived species: Stands older than 120 years are rare in Newfoundland (Thompson, 1991). Old-growth is defined as unharvested stands greater than 80 years of age (Bissonette et al., 1989). Trees are harvested for pulpwood, and the advance regeneration of balsam fir generally insures that most stands will regenerate to a coniferous cover type.

Yield-density relationships, such as relative density (Drew and Flewelling, 1977) or Rieneke's (1933) stand density index, can be useful tools for assessing forest structure, by evaluating the state of competition between trees within a stand, while also providing information on stem density and size. Relative density is essentially a packing ratio that relates the mean volume of trees to the density of stems, as a function of the self-thinning rule (Drew and Flewelling, 1977). In Chapter IV, I incorporated relative density into a stand density management diagram (SDMD) for mixed balsam fir--black spruce stands in western Newfoundland (see Fig. IV-1). Some of the critical elements of the diagram include: a) the crown closure (CC) line, a threshold above which trees begin to compete; and b) the zone of imminent competition mortality (ZICM), where limited resources cause mortality in suppressed trees (Drew and Flewelling, 1977). A relative density value of 1.0 (maximum) is defined approximately by the -3/2 rule of self-thinning (Yoda et al., 1963).

Based upon relationships observed in other tree species (see Westoby, 1984 for review), and in balsam fir in Newfoundland (see Chapter II), I illustrate a hypothetical trajectory of an unmanaged stand as it matures following clear-cut disturbance (Fig. V-1). In the earliest stages of stand development, seedlings will increase in stem volume while stem density remains constant, until the stand reaches the ZICM (Drew and Flewelling, 1977). The stand then begins to self-thin, increasing in mean volume and decreasing in stem density, but maintaining a fairly constant relative density. In Newfoundland, precommercial thinning is a relatively recent practice, initiated about 15 years ago (K. Hutchinson, personal communication). Thus, most older second-growth

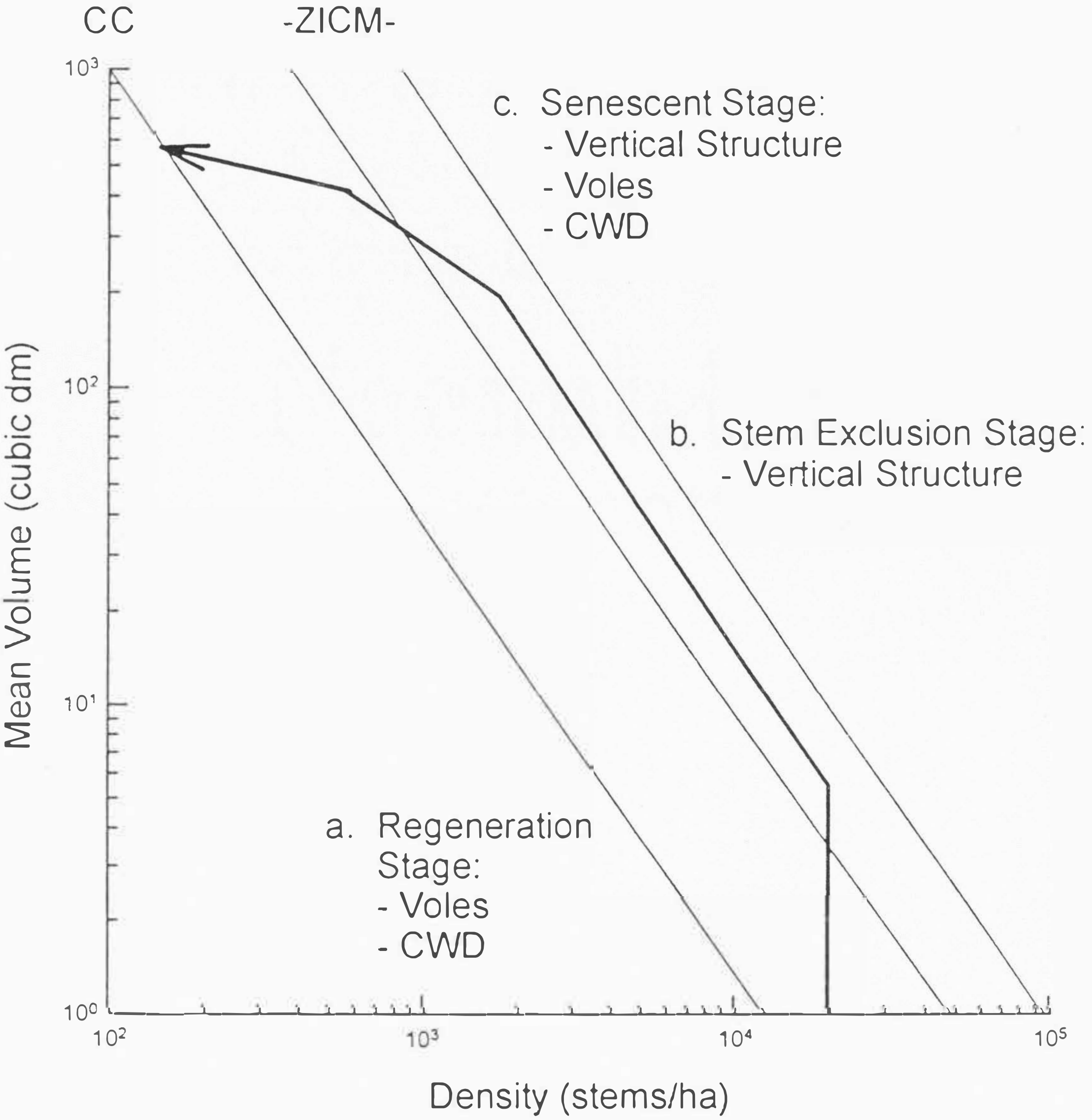


Fig. V-1. Size-density relationships showing the predicted trajectory of an unmanaged stand in the absence of disturbance. In the regeneration stage (a) I expect voles and some CWD to be present, but no vertical structure is available for a foraging marten. During the stem exclusion stage (b) vertical stem structure is present, but there is little understory structure and very few voles. Only the senescent stage (c) contains all three critical elements of marten habitat.

stands are naturally thinned and tend to fall within the ZICM (see Chapter II). At some point, usually between 80 and 100 years, mortality occurs at a faster rate than the remaining trees can use the released resources, relative density decreases, and the stand trajectory falls out of the ZICM. The decrease in relative density indicates the senescence of mature, even-aged stands into an overmature state (Chapter II, White and Harper, 1970).

Site quality should not alter the conceptual trajectory shown in Fig. V-1; instead, it will influence the rate at which the stand traces the trajectory (Drew and Flewelling, 1977). While time is not explicitly included within the SDMD shown in Fig. IV-1 and Fig. V-1, time may be related to the diagram using site index-height relationships. Thus a stand on a relatively good-quality site should progress along the trajectory at a faster rate than a stand on a relatively poor-quality site. This relationship has profound implications for marten habitat management, because marten are likely to respond to the structure available within a forest rather than actual stand age (e.g., Harrison et al., in press).

The change in stand structure is reflected in the temporal pattern of CWD (Fig. V-2) (see also Chapter II). As observed in other forested systems (Lambert et al., 1980; Tritton, 1980; Romme, 1982; Lang, 1985; Spies et al., 1988), CWD is relatively abundant immediately following disturbance, but then declines over time as residual debris decays without replacement from the regenerating stand. Decay of balsam fir is fairly rapid in comparison with more xeric systems, and little residual wood typically remains by 50-60 years after

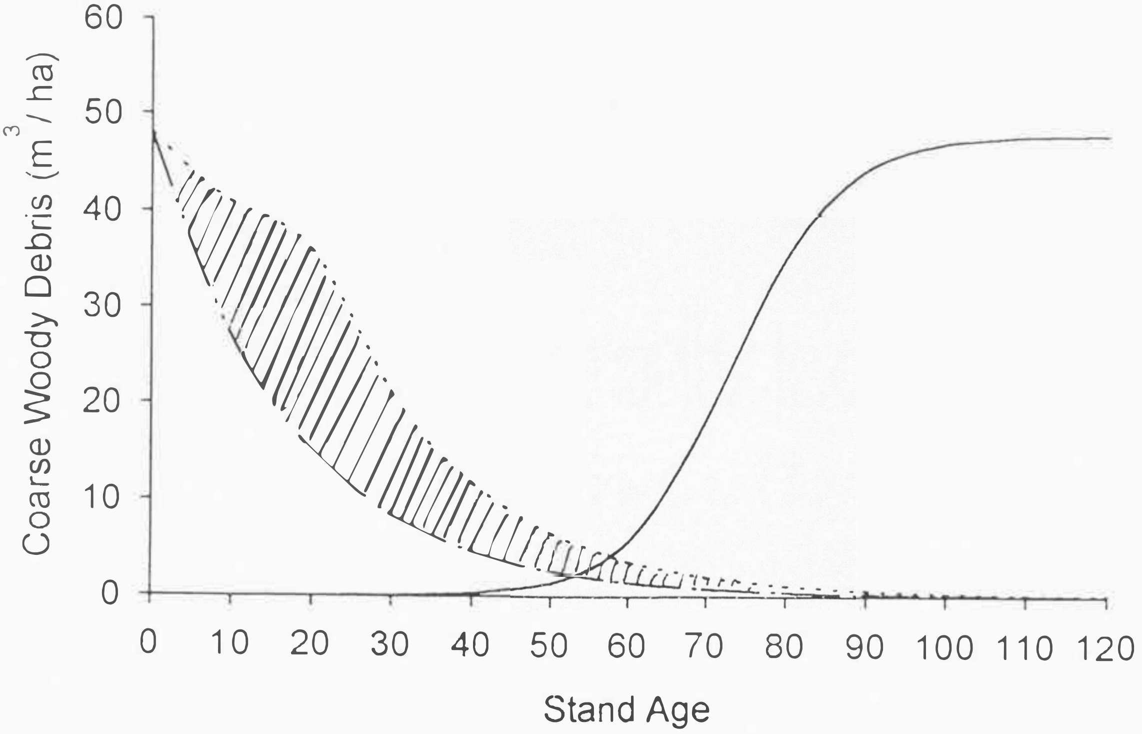


Fig. V-2. Temporal dynamics of coarse woody debris following clear-cut disturbance. The hatched area refers to the volume of debris due to residual birch, which are commonly left standing during harvest. This model, adapted from Chapter II, shows the volume of sound CWD only; decayed volume of CWD is also most limited around 60 years post disturbance (see Chapter II).

harvest disturbance. Once stands reach maturity, debris levels increase due to increased windthrow, defoliation mortality, and eventual stand senescence.

Stand structure also influences the prey base. Meadow voles are typically most abundant within open, grassy habitats (Getz, 1970; Grant, 1971; Folinsbee et al., 1973). Forest stands within the ZICM are typically very dense, and the high canopy closure associated with competitive stems tends to inhibit understory growth. Additionally, there is little subcanopy structure in the form of CWD and shrubs to serve as protective cover for voles within these stands (Thompson and Curran, 1995; Chapter II). Thus, while meadow vole abundance may increase after tree harvest (Kirkland, 1977; Monthey and Soutiere, 1985; Yahner, 1992), data from Chapter III indicate that Newfoundland meadow voles become scarce at the time of canopy closure, and may not increase significantly in abundance until the stand enters the senescent stage. This observation is supported by the trapping results of Thompson and Curran (1995).

By using the SDMD to trace the conceptual trajectory of a typical unmanaged stand as it progresses from regeneration to overmaturity, one can predict when various habitat resources become available (Fig. V-1). Immediately after a clear-cutting there is typically abundant herbaceous growth (Meades and Moores, 1994), as well as some residual coarse woody debris. While voles should be present, there is no vertical structure available for marten. In the absence of subsequent disturbance, this stand should enter and remain within the ZICM as it develops. Though vertical structure becomes available as trees increase in size, the subcanopy structure is sparse, with little CWD and very few voles. Vertical stem structure is still available as the stand senesces, but the canopy becomes more open, allowing for herbaceous growth and the potential for increased vole abundance. Furthermore, the subcanopy debris structure also is available to provide access to the small mammal prey resource in winter. Thus, the elements necessary for marten winter foraging habitat are only present simultaneously within senescent stands, suggesting that marten within this system should be highly dependent on the overmature stage of forest development.

4. Disturbance Regimes

Disturbance affects marten populations not only at the stand level, but also at the landscape scale (Bissonette et al., 1989; Harrison et al., in press). In this section, I discuss how natural disturbance affects both stand structure and landscape pattern. I then compare the natural disturbance regime with current harvest practices, based on my conceptual model of stand development. From a marten's perspective, differences between the two types of disturbance are noticed at both the stand and the landscape scale. These differences suggest that the conversion of natural landscapes into managed forests will have long-term effects on marten habitat suitability.

The disturbance ecology of western Newfoundland forests differs from the majority of the boreal forest region in that fires are infrequent (Damman, 1983). Instead, episodic defoliation by spruce budworm (Choristoneura fumiferana), and more recently hemlock looper (Lambidina fiscellaria), is the primary form of natural stand-replacing disturbance (Raske, 1986; Thompson, 1991). Mortality response to defoliation in balsam fir typically begins about 4-5 years after budworm infestation; spruce mortality begins 2-3 years later (Ostaff and MacLean, 1989). Weakened trees may continue to die due to blowdown and disease after the epidemic has ended, resulting in the cumulative degeneration of the overstory over a period of 10-12 years. Understory within defoliated stands is typified by a surge of released advance regeneration, interspersed with herbaceous growth, and abundant CWD (Chapter II; W. Adair, unpublished data).

A wide range of stand structures may result from a budworm defoliation event, depending on the species and age composition of the original stand (Seymour, 1992). For example, a mature, even-aged balsam fir stand should experience the highest mortality rates, resulting in even-aged regeneration (Seymour, 1992). Conversely, successive budworm outbreaks should have a lesser impact on spruce-dominated stands (Ostaff and Maclean, 1989), resulting in a more uneven-age distribution (Seymour, 1992). Immature stands may suffer incomplete mortality similar to a heavy crown thinning, leading to dense regeneration of second-growth overtopped by widely spaced residuals (Baskerville, 1975; Seymour, 1992).

The availability and connectivity of stands providing suitable host trees appear to influence the pattern of defoliation across a landscape (e.g., Ostaff and MacLean, 1989). Morin (1994, p. 731) characterized defoliation pattern within a virgin forest of Quebec as newly defoliated openings interspersed among patches created by previous outbreaks, creating a "patchy mosaic of variable age." In contrast, historic harvest within forests of eastern Canada has converted this mosaic into a more contiguous, even-aged forest landscape. Consequently, this condition potentially has increased the spatial extent of defoliation disturbance events on landscapes dominated by mature age classes (Mattson et al., 1991; Miller and Rusnock, 1993).

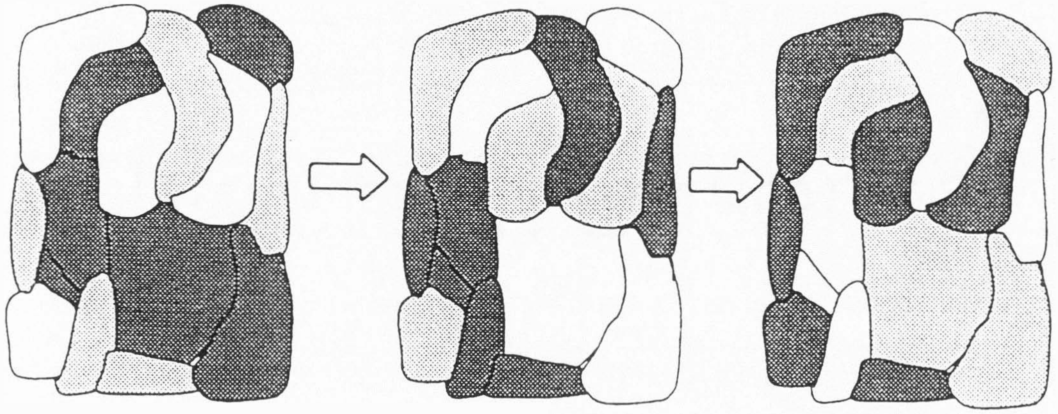
In Newfoundland, defoliated patches usually range from about 1-100 hectares in size, although larger patches occur (Newfoundland Department of Forestry, unpublished data). Because a marten's home range in Newfoundland is typically an order of magnitude larger than the average defoliated patch size (Fredrickson 1990), marten can respond to defoliation disturbance by adjusting their behavior, and even their home ranges, to suit their habitat needs. Furthermore, data from Chapter III suggest that defoliated patches may serve as reservoirs for voles within the forest matrix. Defoliated stands often retain a high degree of vertical structure and CWD following disturbance; thus marten can use these patches as foraging locations (Drew, 1995).

Historically, defoliation may have been a key factor in maintaining marten habitat in Newfoundland. Defoliation typically creates openings characterized by standing dead trees and a high degree of ground-level structure within an otherwise intact forest matrix (Fig. V-3a). These patches could be viewed as temporal windows of foraging habitat, which may be used by marten for perhaps as long as 15 years before tree regeneration becomes too dense to support voles. As these patches regenerate, subsequent defoliation events should provide new foraging patches, creating a stand-level analogy to

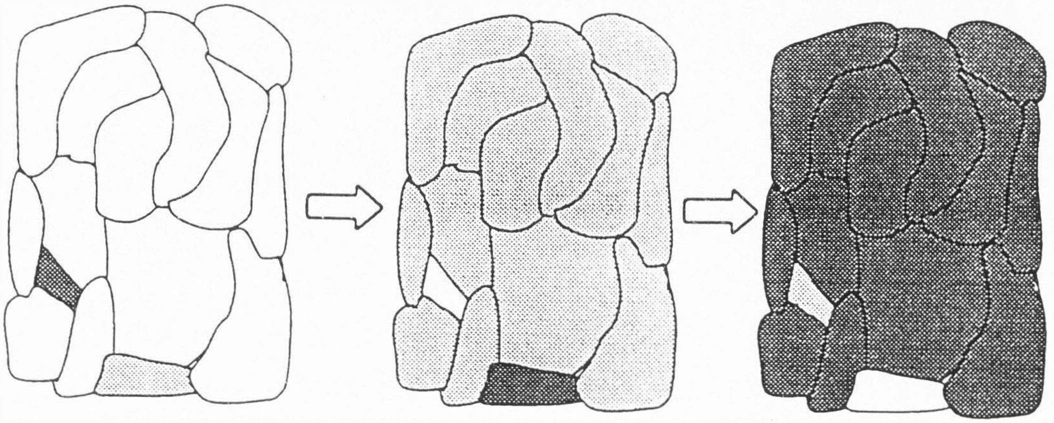
Bormann and Likens' (1979) shifting mosaic. As long as the landscape matrix is the forest, I would expect marten to continue to exist within this environment (Hargis and Bissonette, in press).

However, depending on the scale of disturbance, defoliation may either enhance or degrade marten habitat over time. For example, successive disturbance events over short time-intervals may create a landscape dominated by dead trees. A recent hemlock looper epidemic in the area associated with the core of the Newfoundland marten population has affected an estimated 25% of the available old growth (W. Adair, personal communication). When combined with stands killed by a similar budworm outbreak in 1986, defoliated stands comprise a major portion of the forested landscape. I expect that a marten home range dominated by defoliated trees is less desirable than a mixture of defoliated and forested stands. For example, Paragi et al. (in press) suggested that even though burned stands were used by marten in Alaska, large contiguous burns served as sinks (Pulliam, 1989) for those marten populations.

Currently, the pattern of timber harvests differs from defoliation disturbance because cleared patches represent the matrix (Fig. V-3b). At present, clear-cut size in Newfoundland is determined primarily by economic and logistic constraints, such as road operability, topography, and the availability of mature timber. In a given location, annual cutting operations will typically harvest all merchantable timber from a forested valley (on the order of



a. Defoliation Disturbance



b. Clearcut Disturbance

☐ New Opening

▨ Regenerated Stand

■ Mature Stand

Fig. V-3. A simplified illustration of spatial and temporal dynamics comparing natural (defoliation) disturbance and harvest disturbance on the island of Newfoundland. Individual polygons are stands 25-50 hectares in size, and the cluster of polygons is a hypothetical marten's home range. The time step is simplistic: about 40 years. Natural disturbance (a) tends to retain a diversity of stand structures across the landscape, whereas the current clear-cut disturbance (b) tends to create more homogeneous landscapes.

1000 ha), leaving economically unmerchantable stands (<42 m^3/ha [Meades and Moores, 1994]) as residuals. Adjacent valleys are harvested sequentially in successive years as new roads are constructed, creating extremely large aggregate clear-cut areas over time (see Fig. I-1). From a marten's perspective, clear-cutting is inherently different from defoliation because the vertical structure is removed. However, it is the scale of cutting regimes in Newfoundland that probably have had the greatest impact on marten populations.

As indicated by Bissonette et al. (1989), marten cannot coexist on the same landscape with logging at the present scale of harvest disturbance. Furthermore, the second growth following such large-scale disturbance will be relatively homogeneous across the landscape (Fig. V-3b). Based on the conceptual model of stand dynamics, the entire landscape will lack the critical elements of marten habitat for 60-80 years (see also Thompson and Curran, 1995). Because these second-growth forests are typically harvested on a 65- to 70-year rotation schedule (Meades and Moores, 1994), optimal habitat conditions may never be attained.

5. Manipulating Habitat Structure

Long-term maintenance of marten habitat will require tools that allow land managers to plan over the appropriate spatial and temporal scales. Bissonette et al. (1989) introduced the idea of using geographic information system (GIS) technology to coordinate landscape-level (spatial) management of marten habitat. At the stand level, stand density management diagrams can be used to evaluate the potential of silvicultural prescriptions as a method of increasing marten habitat quality within younger stages of forest development.

Here I offer a simple, stand-level silvicultural system designed to enhance forest structure for marten, graphically illustrated in Figure V-4. First, prevent trees from entering the stem exclusion zone using thinning techniques. The reduced tree competition should promote understory vegetation and provide a potential small mammal resource, though I caution that this hypothesis requires further examination of vole populations within managed stands. Second, supply logs at the ground level to further increase habitat potential for voles, and allow marten to access this prey resource in winter. Ultimately, this type of stand-level management should be incorporated into an overall landscape-level management strategy (Bissonette et al., 1989). The habitat "window" should therefore occur during a reasonable harvest rotation. In this example, I target the final harvest at a dominant height of 17 m (Fig. V-4).

The first objective is to increase the rate of stem growth, so that sufficiently large logs will be available for CWD, using a precommercial thinning. As shown in Figure V-4, I target a quadratic mean diameter (D_q) of 15 cm as the tree size necessary to generate logs of a reasonable size. Once trees reach the target D_q, a second density manipulation analogous to a commercial thinning will insure that the stand remains outside the ZICM until harvest. A

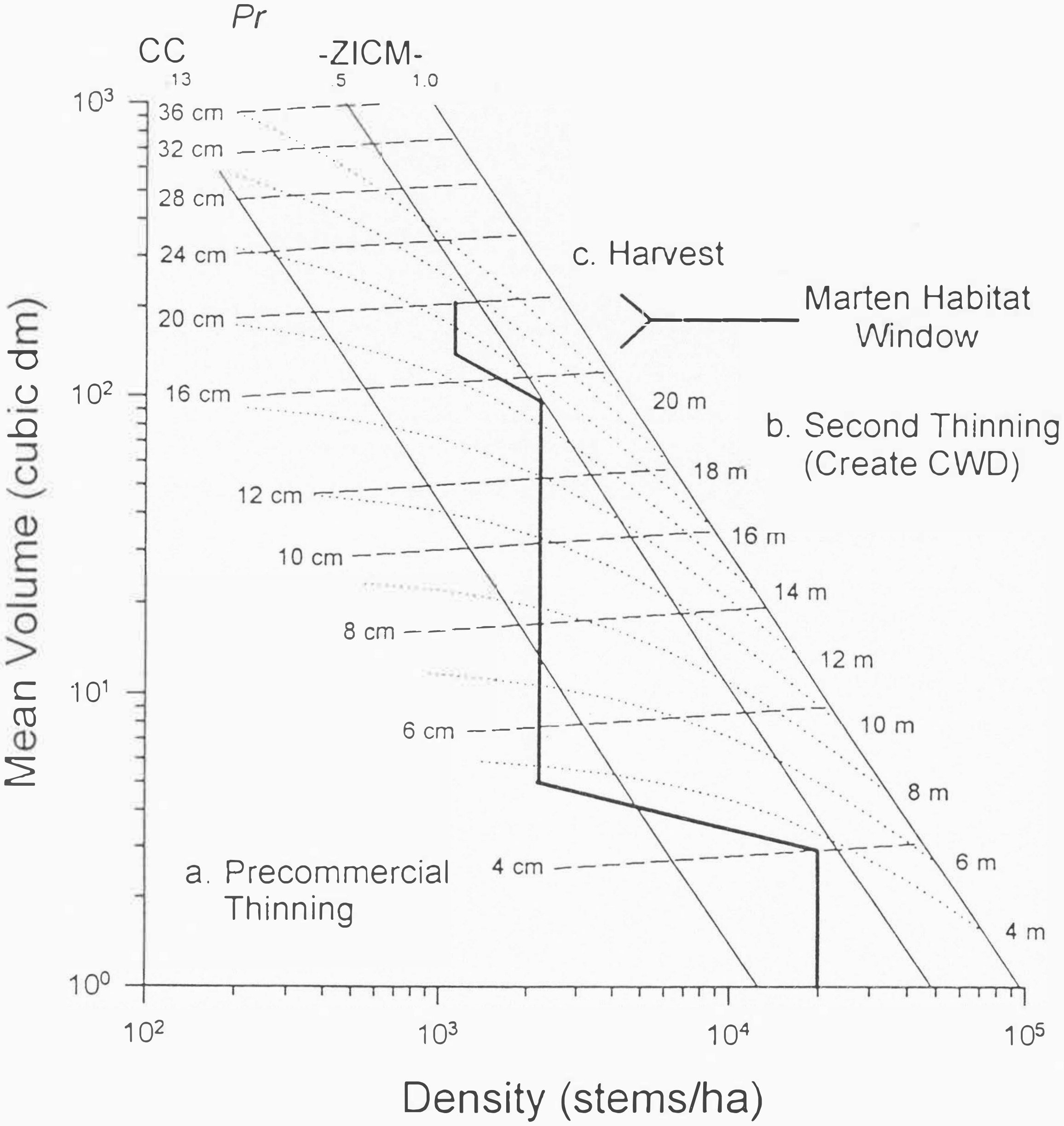


Fig. V-4. Silvicultural prescription designed to provide a marten habitat window within a pulpwood rotation.

reduction from 2200 stems/ha to 1100 stems/ha will accomplish this goal (Fig. V-4). Subcanopy structure will be created/enhanced if cut trees are left on the ground as CWD. Assuming a typical low-thinning operation, i.e., cut trees are biased toward smaller stems and dominant height is retained (Newton and Weetman, 1993), approximately 62 m^3/ha of CWD would be provided by this manipulation. This volume estimate is derived by tracing the dominant height isoline to the new stem density (Fig. V-4), multiplying stem density by the adjusted mean tree volume to obtain standing volume, and then subtracting this number from the original (prethinned) standing volume. The initial loss of pulpwood volume due to this manipulation will be recovered by increased growth of the remaining stock.

Volume of sound (undecayed) CWD within old-growth balsam fir stands in Newfoundland typically reaches 50 m^3/ha (see Chapter II) indicating that the volume of logs provided by my suggested manipulation provides comparable, if not greater, subcanopy structure for marten on the island. However, I based my estimate in Chapter II on logs that were greater than 7.6 cm in size, whereas my estimates here are calculated from total stem volume. Furthermore, I would expect a certain amount of wood decay over the duration of the habitat window. The application of 62 m^3/ha of downed wood may therefore be appropriate for a conservative habitat management strategy.

One of the consequences of a traditional, low-thinning operation on this habitat manipulation is that the CWD provided will be biased toward smaller stem sizes. As shown in Figure V-4, stand D_q was 15 cm prior to the thinning, but increased to about 17.5 cm after the thinning. The average diameter (breast height) of felled stems would therefore be approximately 11.6 cm. A larger average log size could be obtained through a more random thinning methodology. Alternatively, the density manipulation could be postponed until a larger D_q was attained.

As mentioned previously, site quality will influence the time necessary for each stand to follow the intended trajectory. Based on site index curves provided by Page (1968), a high quality site (SI_{50}=17m) will reach the target (15 cm) diameter for CWD at 45 years, and will be harvestable at 56 years, yielding an 11-year habitat window. Similarly, a medium/good-quality site (SI_{50}=15m) may yield CWD at 57 years and may be harvested at 74 years, and a relatively poor-quality site (SI_{50}=13m) may provide CWD at 78 years and will be ready for harvest at 108 years, creating a 17-year and 30-year habitat window, respectively. These figures assume that trees on good-, medium-, and poor-quality sites reach breast height at 6, 7, and 8 years, respectively (Page and van Nostrand, 1973).

Because the time necessary to reach particular stages of stand development is readily calculated using the SDMD, habitat management may be tailored to fit site-specific conditions. For example, forest structure within the best quality sites may be manipulated on two successive occasions to create a longer habitat window, taking advantage of the ability of these sites to generate sizable logs (Fig. V-5). Final harvest could occur at 70-75 years, yielding a 25-30-year habitat window. Given the relatively rapid decay rate of balsam fir (Lambert et al., 1980; Chapter II), two applications of CWD may be necessary to maintain adequate habitat structure, assuming there is little natural input from the maturing stand. Stands of lesser quality could be entered during the second manipulation. Analysis of the SDMD suggests that stands located on poor soil conditions (i.e., SI < 12 m) would not be as effective in producing the appropriate structure within a reasonable pulpwood rotation age. A land manager could decide whether to extend the rotation, or simply depend on the more productive stands to provide the necessary habitat structure.

If the logs are intended as potential subnivean access sites, then the structural characteristics of the logs should be as important as the total volume of CWD on the ground. For example, Corn and Raphael (1992) determined that stacked or crossed logs were used more often as access sites than one would expect based on availability on the landscape. Chapter II also indicated that the structural diversity of CWD was greatest within typical, old-growth stands (i.e., marten habitat) in Newfoundland. Thus, small clusters of trees cut to simulate a blowdown would be preferred over the standard, uniform distribution of cut trees following a traditional thinning. Additionally, crown closure would be delayed within these openings, allowing for a more diverse canopy structure, greater understory growth, and enhanced vole habitat.

Seymour (1994) and Seymour and Hunter (1992) suggest that the

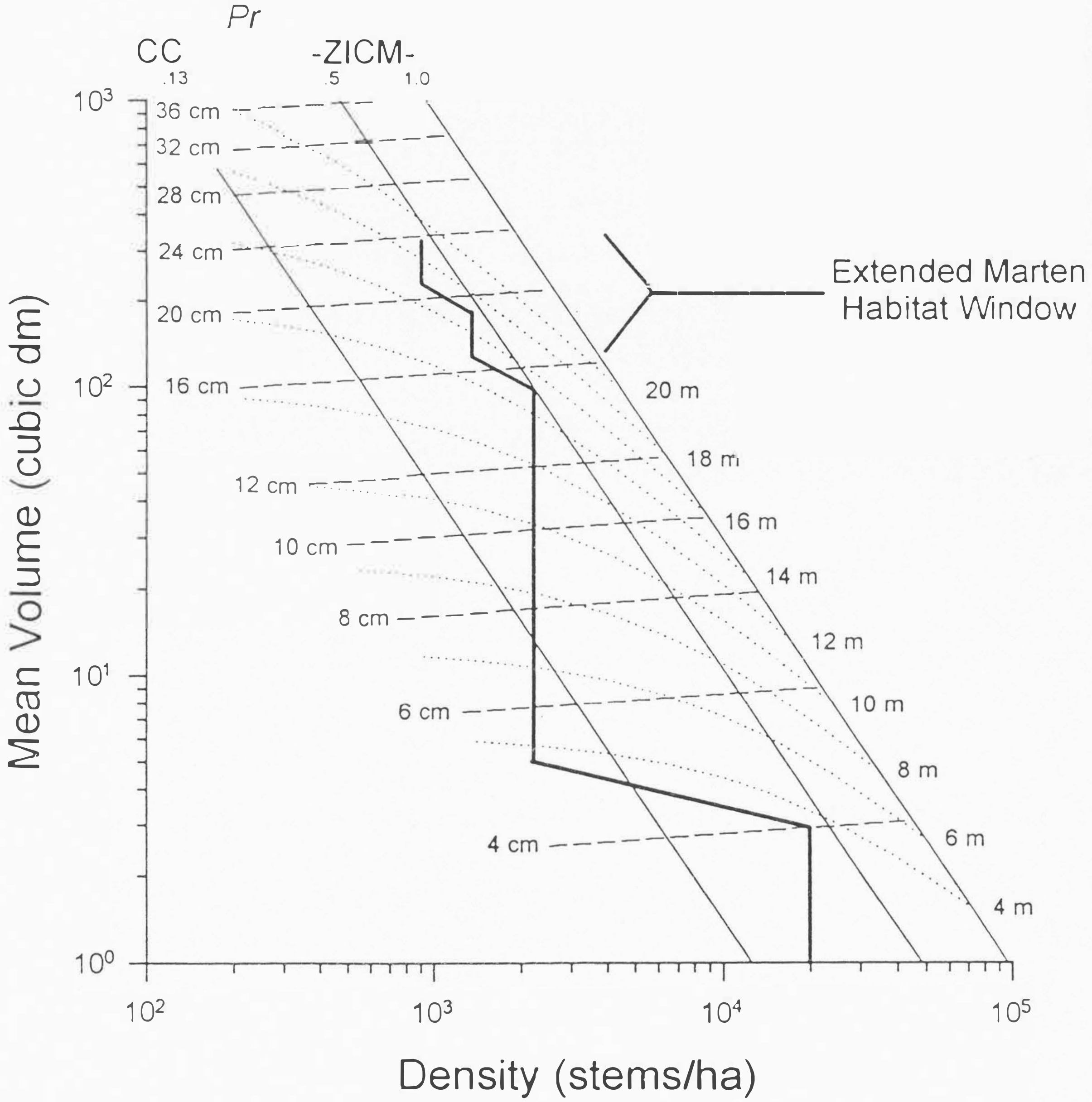


Fig. V-5. An alternative silvicultural prescription specifically designed for high quality sites, illustrating the diagram's ability to evaluate trade-offs between time, yield, and habitat quality.

retention of both dead and live trees during the harvest operation, along with the maintenance of the existing CWD, will provide more diverse structure within managed forests. These practices might be combined with my own approach to lengthen the habitat window for marten, by providing a CWD source within regenerating stands.

It should be recognized that this type of habitat manipulation is focused at the stand level, and that the objective of the manipulations is to provide suitable foraging locations. It is unlikely that marten would require this type of intensive habitat management in all forest stands; rather the goal is to increase the diversity of habitat across the landscape. Other requirements, such as denning structures and thermoregulation, are also important considerations and may be incorporated into a similar analysis when more data are available (W. Adair, personal communication). Similarly, the importance of snowshoe hare as a prey item is recognized, and is presently being considered for future research. However, by focusing on the structural attributes of marten habitat, while still recognizing the constraints imposed by a depauperate prey resource, we should be able to promote future marten habitat using proactive silviculture, and sound adaptive management.

6. Conclusion

Seymour (1992, p. 70) suggested that

> large scale, episodic removal of trees, by logging in combination with spruce budworm, bark beetles and windstorms, have [sic] transformed Maine's spruce-fir

> forest from one dominated by mixed-age, old-growth stands, to a forest dominated by younger, more uniform stands that may be more extensive in area, and lack the within-stand height and age diversity of old-growth.

Though Newfoundland lacks the tree species diversity of Maine's subboreal forest, Newfoundland's forests may be experiencing a similar phenomenon (Thompson, 1991; Thompson and Curran, 1995). Because the Newfoundland marten appears to be particularly dependent on structure associated with old-growth forests, this transformation is probably one of the main factors contributing to the marten's decline on the island.

Currently, timber harvest is incompatible with marten sustainability in Newfoundland, because at present anthropogenic disturbance leads to coarse-grained landscapes that exclude marten. Unfortunately, the landscape is now dominated by contiguous tracts of young, regenerating forests because of previous timber management practices. Our understanding of forest dynamics and marten habitat requirements suggests that it will be decades before these forests become suitable habitat for marten. Furthermore, additional harvest will occur before the structure required by marten becomes available.

By applying silvicultural techniques to marten habitat, we can address the temporal aspect of this problem by replicating the structure of older forests within younger stages of forest development. Here I use a stand density management diagram to adapt current timber management to incorporate the specific structural needs of marten in Newfoundland. The advantages inherent in this type of approach are: a) it focuses on forest structure, rather than surrogates such as stand age and b) it may be adapted to a variety of site conditions (Lilieholm et al., 1993; Smith and Long, 1987).

However, to insure the maintenance of healthy marten populations in Newfoundland, this type of stand-level management needs to be incorporated into a landscape-level management approach, such as that provided by Bissonette et al. (1989). The spatial and temporal configuration of habitat on the landscape will ultimately determine the long-term stability of marten populations within forests managed for pulpwood production. Future research should address how much foraging habitat is necessary within a forested matrix to sustain an actively reproducing marten population on the landscape. Additionally, several spatial patterns of harvesting will need to be examined on an experimental basis to determine the scale of harvesting most compatible with marten over the long term. I expect that a combination of simulation modelling and adaptive management will ultimately address these complex questions.

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CHAPTER VI

CONCLUSIONS

The American marten (Martes americana) is associated with relatively undisturbed, old coniferous forests. Though marten are found in second-growth forests, they are typically far less abundant within these landscapes (Thompson 1994, Thompson and Curran 1995). Past research indicates that marten are particularly dependant on certain structural elements that are common within old forests (Sherburne and Bissonette 1993, 1994, Drew 1995, Harrison et al. in press). I examined stand development, coarse woody debris (CWD) structure, and small mammal abundance within second-growth stands as a measure of their potential for marten habitat, in comparison with typical old-growth marten habitat in western Newfoundland.

CWD volume observed within the chronosequence demonstrated the typical U-shaped temporal relationship observed in other forested systems. Lowest CWD volumes were observed within semimature to mature second growth. Highest levels of both CWD volume and structural complexity corresponded with stand senescence and old growth. Little residual CWD was observed in 50- to 60-year-old stands, suggesting that any CWD subsequent to this stage must be generated from trees within the maturing stand. Defoliation disturbance apparently increased both CWD volume and structural complexity within some older second-growth stands, as indicated by certain outliers within my chronosequence. Additionally, site quality may influence CWD volume by influencing rate of stem growth and stand development.

My analysis of stem structure indicated that intertree competition was high within second growth, with dense canopy closure and active self-thinning, until stand senescence at approximately 80 years. Old-growth stands had lower relative densities, thus offering more canopy openings and a more complex understory structure.

A discrete structural difference exists between old-growth and second-growth stands less than 80 years of age. My small-mammal trapping data suggest that this difference is critical to marten in Newfoundland. Vole abundance was significantly higher in overmature stands than in all other forest age classes. Furthermore, vole abundance was negatively correlated with relative density, and positively correlated CWD volume. In short, meadow voles within a forested environment appear to be most abundant within locations characterized by a senescent stand structure. Because few alternative prey species exist for marten in Newfoundland, I expect marten on the island to be particularly dependent on overmature stands. Further, marten will be sensitive to the volatile population dynamics characteristic of northern vole populations. In combination, these phenomena separate the Newfoundland marten situation from its counterpart on the mainland.

This study focused on stand-level relationships. However, a typical marten home range will encompass multiple stands, suggesting that marten may respond to scales larger than observed in stand-level phenomena. I therefore reviewed the literature, Newfoundland forest harvest records, and data from the Newfoundland Forest Service inventory to compare current second-growth landscapes with a more pristine forest condition. My review indicated that anthropogenic disturbance transformed a historically heterogeneous forest landscape into a more contiguous even-aged environment.

I hypothesized that marten in unharvested areas may benefit from small-scale disturbance because the structural elements available within senescent (i.e., disturbed) stands will be available somewhere on the landscape. My observations of marten foraging behavior (Sturtevant, unpubl. data) support this hypothesis, because tracked marten appeared to concentrate foraging efforts within defoliated locations. Further, Drew (1995) observed that marten used defoliated patches more often than expected based on their availability on the landscape. In contrast, I would expect second-growth landscapes to lack the structural elements necessary for foraging, because of their relatively homogeneous age class distribution.

I demonstrated the potential benefits of applying progressive silviculture to second-growth stands as a habitat management technique. In essence, this approach would create a senescent stand structure (i.e., large tree size, open canopy, and abundant CWD) within younger stages of forest development. The advantages inherent in this type of approach are: a) it focuses on forest structure, rather than surrogates such as stand age and b) it may be adapted to a variety of site conditions (Lilieholm et al. 1993, Smith and Long 1987). More importantly, manipulated stands may be harvested after providing a 10- to 25-year marten habitat window, allowing the integration of pulpwood and marten habitat objectives. However, I caution that the proposed habitat manipulation focuses on stand-level dynamics. The technique will not be truly effective unless incorporated into a landscape-level management system. In principle, old forests should remain as the matrix of the landscape. Hargis and Bissonette (unpubl. data) have shown that marten densities decline dramatically when 25-35% of the landscape has been fragmented, long before the matrix of old growth changes to the disturbed habitat type.

In conclusion, my examination of second growth in Newfoundland indicates that these forests lack the structural complexity of old growth, and this difference is noticed at both the stand and landscape scale. Marten in Newfoundland may be particularly sensitive to the observed change in forest structure due to the rather specific habitat associations of their principal prey. I suggest that silvicultural intervention may be necessary to enhance marten habitat within second-growth forests, unless these areas are allowed to reach stand senescence, consequently compromising future pulpwood harvest. Future research in second growth should include a field test of the proposed silvicultural habitat model, particularly to assess whether microtines respond to the manipulation as expected by the model.

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