

Utah State University

---

From the Selected Works of James N. Long

---

1997

Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland

James N. Long, *Utah State University*



Available at: <https://works.bepress.com/jameslong/176/>

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

BRIAN R. STURTEVANT,<sup>1</sup> JOHN A. BISSONETTE,<sup>2,4</sup> JAMES N. LONG,<sup>3</sup> AND DAVE W. ROBERTS<sup>3</sup>

<sup>1</sup>Utah Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, College of Natural Resources, Utah State University, Logan, Utah 84322-5290 USA

<sup>2</sup>U.S. National Biological Service, Utah Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, College of Natural Resources, Utah State University, Logan, Utah 84322-5290 USA

<sup>3</sup>Department of Forest Resources, and Ecology Center, College of Natural Resources, Utah State University, Logan, Utah 84322-5215 USA

**Abstract.** We examined the structural attributes of coarse woody debris (CWD) in balsam fir and mixed balsam fir-black spruce forests in western and central Newfoundland. The purpose of the study was to document CWD abundance and structure within various stages of stand development, and to generate simple models to predict CWD availability as habitat for forest wildlife. Our objectives were threefold: (1) determine the temporal patterns of CWD following clear-cut disturbance, and compare these second-growth stands to old sites (>80 yr) of natural origin; (2) relate the temporal patterns of CWD to stand development; and (3) demonstrate how factors such as site conditions and disturbance may influence these temporal patterns.

Our chronosequence included 19 second-growth stands with a mean tree age ranging from 33 to 80 yr, and 7 old-growth stands ranging from 87 to 110 yr. The volume of coarse woody debris (CWD), here defined as downed wood, was relatively low to intermediate early in the chronosequence (e.g., 32.3 m<sup>3</sup>/ha in a 36-yr-old stand), lowest in a 58-yr-old stand (15.2 m<sup>3</sup>/ha), and highest in an 80-yr-old stand (78.1 m<sup>3</sup>/ha). Results indicated that CWD volume followed the general “U-shaped” temporal trend observed in other forest systems. The presence of CWD early in the sequence was strongly influenced by residual hardwoods (i.e., birch) left by the original logging operation. The highest observed volume of CWD corresponded with stand senescence and appeared to be maintained within old-growth stands. Snag (standing dead wood) density was low within the youngest stands (<200 snags/ha), and peaked within mature second growth. Defoliation disturbance increased both the volume and the structural diversity of CWD within silviculturally mature second-growth stands. Results from our study indicate that CWD in stands >50–60 yr of age is not residual but generated primarily from regenerating tree structure. Factors affecting the rate of stem growth, e.g., site quality and initial stocking levels, should influence the accumulation and overall abundance of CWD within later stages of forest development. We therefore applied yield-density relationships as a method of examining stand-level dynamics of CWD.

**Key words:** *Abies balsamea*; *balsam fir*; *Betula papyrifera*; *black spruce*; *boreal*; *chronosequence*; *coarse woody debris*; *disturbance*; *Newfoundland*; *Picea mariana*; *relative density*; *stand structure*; *white birch*.

### 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 (Raphael 1984, Tallmon and Mills 1994), cavities for den and nest sites, and foraging locations for insectivores (Raphael 1984). In cold climates, CWD may also provide important subnivean structure for nonhibernating mammals (Spencer 1984, Buskirk et al. 1989, Sherburne and Bissonette 1993, 1994, Bissonette and Sherburne 1994).

Manuscript received 24 January 1996; revised 25 August 1996; accepted 26 August 1996.

<sup>4</sup> Send reprint requests to this author.

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 more productive, diverse, and healthy forest ecosystems.

The research presented here represents part of a larger effort to characterize the habitat quality of different ages of forest for the threatened Newfoundland marten (*Martes americana atrata*). Downed logs in particular are an important structural component of marten habitat. Logs serve as conduits beneath the snow pack (i.e., the subnivean zone) to both a critical microtine prey

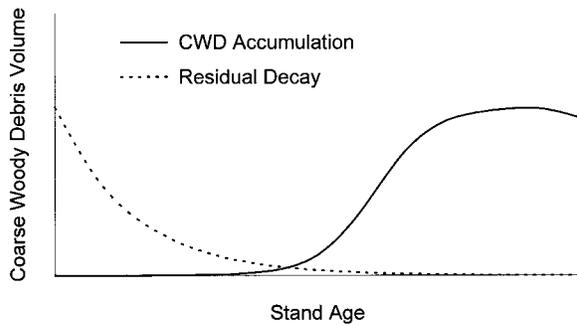


FIG. 1. Conceptual relationship between coarse woody debris (CWD) and stand age, showing the decay of residual debris following harvest disturbance, followed by the accumulation of debris from the regenerating stand. Debris levels may begin to decline after stand senescence.

resource (Bissonette and Sherburne 1994, Sherburne and Bissonette 1994), and thermally beneficial resting sites (Buskirk et al. 1989). Thus it is not only the actual abundance (volume) of logs that are important, but also the quality of the physical structure the logs provide. For example, a fresh blowdown that breaks the snow surface will provide better subnivean access than a decayed log lying flat on the ground. As boreal forests in Newfoundland and elsewhere change from old growth to more managed landscapes, the survival of subnivean obligates such as marten will require that habitat attributes such as CWD abundance and structural complexity are maintained during subsequent harvest rotations.

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. 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), Douglas-fir (*Pseudotsuga menzeisii*) (Spies et al. 1988), and Douglas-fir–western hemlock (*Tsuga heterophylla*) forests (Agee and Huff 1987). In general, debris levels tend to be high following the initial stand disturbance (Fig. 1). 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 peak during a transitional stage as the even-aged stand senesces into a more uneven age structure, after which levels decline as a result of the reverse

“J-shaped” diameter distribution of uneven-aged forests (Harmon et al. 1986, Spies et al. 1988).

CWD is closely associated with stem growth, mortality, and structure within the stand, particularly after the majority of predisturbance and disturbance-generated debris has decayed (Harmon et al. 1986). However, 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 live tree 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 index (Drew and Flewelling 1977) is a quantitative, yield–density measure that evaluates the degree of competition between trees within a stand. Drew and Flewelling (1977:519) defined relative density index as “the ratio of actual stand density to the maximum stand density attainable in a stand with the same mean tree volume.” We will use this definition for relative density throughout this paper. 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 begin to cause mortality in suppressed trees. The upper limit to the ZICM is defined by the maximum relative density attainable (i.e., 1.0), 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 for black spruce (*Picea mariana*) at relative density index values of 0.13 and 0.5, respectively.

Fig. 2 illustrates a hypothetical trajectory of an even-aged, regenerated stand as it matures following a disturbance event. In the earliest stages of stand growth (a), seedlings increase in stem volume while maintaining a constant or increasing stem density, until the stand reaches the ZICM (White and Harper 1970, Westoby 1984, Newton and Weetman 1993). The stand then parallels the self-thinning line, maintaining a constant relative density within the ZICM (b). Some debris will be produced during this stage, but stem mortality is typically restricted to small, suppressed individuals (Lang 1985), and the CWD generated is small and decays quickly. Therefore, the rate of CWD accumulation remains relatively low. Further, CWD studies often have a lower size limit in defining 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 also increases. Additionally, maturing trees are more susceptible to windthrow and disease (Saville 1983). The accumu-

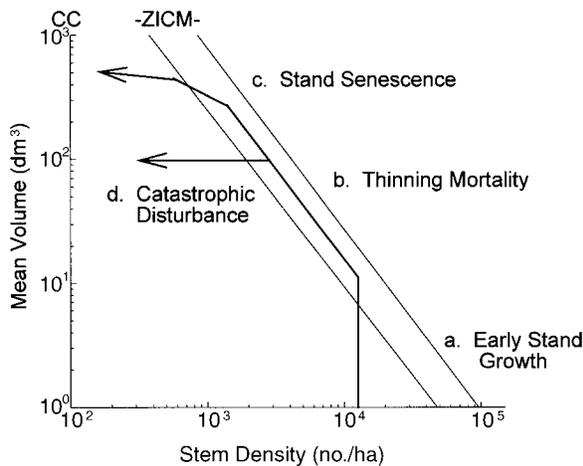


FIG. 2. Conceptual trajectory of a typical, naturally thinned stand following clear-cut disturbance. Note log scale of  $x$  and  $y$  axes. (a) Early Stand Growth: stem density remains constant while mean stem volume increases. (b) Thinning Mortality: stand maintains a constant relative density upon entering the zone of imminent competition mortality (ZICM), paralleling the self-thinning line. (c) Stand 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).

lation of CWD increases as large dominants and co-dominants fall to the forest floor. The rate of CWD input rises to a maximum (c) as the even-aged trees approach their longevity, and the stand senesces into a transitional stage between even-aged and uneven-aged structure (Harmon et al. 1986, Oliver and Larson 1996).

Site quality influences forest biomass production, affecting in turn both the rate and volumetric production of debris (Spies et al. 1988). However, site quality will not alter the pattern of the hypothetical trajectory shown in Fig. 2. Instead, stands on better quality sites progress along the trajectory faster than stands growing in poorer conditions (Yoda et al. 1963, Westoby 1984, Newton and Weetman 1993). Thus, we would expect the CWD accumulation curve in Fig. 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 live stem density (d) and a concomitant pulse of accumulated debris.

The combination of hypothetical models shown in Figs. 1 and 2 provides a reasonable mechanistic explanation for observed CWD temporal patterns in even-aged systems. However, parameters for the model will vary widely among different regions. Maximum debris levels range from as high as 400 Mg/ha in a stand dominated by giant sequoia (*Sequoiadendron giganteum*) (Harmon et al. 1987) to 49 Mg/ha in northeastern deciduous forests (Tritton 1980). Both climate and spe-

cies decay rates affect 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, species-specific tree longevity will influence 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 goal of this research was to examine the temporal dynamics of both CWD volume and structural complexity in second-growth, balsam-fir-dominated stands following clear-cutting disturbance in western and central Newfoundland and to compare these sites with "old-growth" stands of natural origin. Our objective was to determine the stage of forest stand development at which second-growth stands began to assume the characteristics of old-growth forests, both in terms of CWD abundance and function as habitat structure. Based upon CWD patterns observed in eastern hardwoods (Tritton 1980), and the Pacific Northwest (Spies et al. 1988), we hypothesized that debris should follow a U-shaped trajectory, followed by an asymptote. However, we did not know the critical parameter values of the model. 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?

Our examination of CWD dynamics in balsam-fir-dominated forests of Newfoundland incorporated three distinct phases: (a) analysis of CWD volume and structural diversity 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 fitting the conceptual model of CWD shown in Fig. 1 to observed levels of debris; and (c) providing 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 CWD and habitat research in Newfoundland. We discuss the implications of our research to habitat quality within managed landscapes, with an emphasis on the implications to marten.

#### 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]). Study areas 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 >80 yr of age (Bissonette et al. 1989). We focused our effort on stands >40 yr of age, but we also sampled younger stands to gain insight on the impact of residual CWD (i.e., CWD generated before or during the initial dis-

turbance). Each study area was characterized by a wet, cool climate, with annual temperatures averaging 4°C, although study sites in central Newfoundland are influenced by a slightly more continental climate, with relatively colder winters and warmer summers (Banfield 1983). Western Newfoundland also has a longer frost-free period than central Newfoundland, and potential evapotranspiration (PET) values are slightly higher (350–400 mm for western sites and 300–350 mm for central sites, respectively). Mean precipitation ranges from 1200 to 1300 mm annually for western sites, and from 1300 to 1500 mm for central sites, while average snowfall for both regions is  $\approx$ 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 are 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 our study sites ranged from 120 to 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*) is common throughout the area, and white spruce (*Picea glauca*) is locally abundant. Rubus–balsam fir and *Dryopteris*–*Hylocomium*–balsam fir (Meades and Moores 1994) are the most common forest ecosystem types associated with our study sites.

Study sites from central Newfoundland are located within the Red Indian Lake subregion of the Central Newfoundland Ecoregion. The undulating topography of this subregion is characterized by relatively nutrient-rich soils, although limestone is absent within the area. This subregion contains 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 is similar to that described for the western sites, and *Rubus*–balsam fir, *Dryopteris*–*Lycopodium*–balsam fir, and *Hylocomium*–balsam fir (Meades and Moores 1994) are the most common forest ecosystem associations.

Natural disturbance regimes for both study locations are dominated by periodic insect defoliation by spruce budworm (*Choristoneura fumiferana*) (Raske 1986) and more recently hemlock looper (*Lambdina 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

yr are rare in Newfoundland (Thompson 1991). While we considered unharvested stands older than 80 yr to be “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 1940s (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 contained some residual trees. The least accessible sites commonly were left as residual stands. We established additional study sites just southwest of Corner Brook, which were harvested around 1950. Pulpwood harvest began in the vicinity of Victoria Lake (central Newfoundland) in the late 1950s, and all wood accessible by major waterways was harvested within approximately a 10-yr period, ending by the late 1960s (Abitibi-Price historical files, Grand Falls, Newfoundland).

#### METHODS

We defined study sites by stand boundaries interpreted from air photos (Newfoundland Department of Forestry 1990). Approximately 15–20 sample plots were placed at 50-m intervals along a predetermined transect (i.e., transects were plotted on stand maps before entering the site) within each study site. We collected CWD and stand structural data from a total of 454 plots within 26 sites. For the purpose of this paper, CWD was defined as downed woody debris >7.6 cm in diameter, based on Brown's (1974) definition of logs. Snags were considered separately as standing dead wood. Because the focus of this study was to examine the structural characteristics of CWD, we chose to focus on volume rather than mass.

We measured downed logs using a modified version of Brown's (1974) 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 >7.6 cm were measured to the nearest centimeter. Our lower limit (i.e., 7.6 cm) was set as the minimum log size we would expect a marten to use as a subnivean conduit. We classified logs as sound or decayed. A log was classified as decayed if the outer layer could be fragmented by hand, and branches could be pulled free from the bole, indicating heartrot (Brown 1974). We identified logs to species wherever possible. Finally, we categorized intersected logs into four different height classes (<0.5, >0.5–1.0, >1.0–1.5, and >1.5 m), defined as the height the log was suspended above the ground at the point of plane intersection.

We measured standing live and dead trees at each CWD sample plot. We used a variable radius plot sampling methodology (Husch et al. 1972); trees were tallied using a prism, and we measured the diameters of

tallied trees to the nearest centimeter. At alternating plots along the transect, we randomly chose two trees during the basal sweep and aged each at breast height using an increment borer. Sample ages were averaged as an estimate of overall stand age, defined as the age taken at breast height, plus 8 yr. 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 our samples. Within western Newfoundland, regeneration typically takes 8 yr to reach breast height (D. Harris, *personal communication*). Our ages reflect the year (i.e., 1993 or 1994) that the stand was measured for forest structure. An additional dominant tree was aged and measured for height ( $\pm 0.25$  m) using a clinometer.

We classified each plot into forest ecosystem types (based upon plant indicators, topography, and soil type) as a measure of site potential (Meades and Moores 1994). The site index (SI) values (i.e., the dominant height [m] at a stand age of 50 yr) were interpreted from the classification system, and verified using our own dominant tree height data. We classified each plot into poor ( $SI < 12$  m), medium ( $SI \geq 12$  m < 14 m), and good ( $SI > 14$  m) quality sites. Individual plot SI values were then averaged to yield the overall stand SI.

Relative density was calculated by the following method. Using dominant heights measured at individual plots, we calculated individual tree heights using Page and van Nostrand's (1973) height-diameter regression functions:  $Ht = b_0 - (b_1 \times D \times Ht_d) - (b_2 \times D^2)$ , 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. We then employed a preliminary relative density index equation provided by Newton (Forestry Canada, *unpublished data*) specific for balsam fir-black spruce stands in Newfoundland:  $Pr = N_o / (v/10^{7.452})^{-2.04}$ , where  $Pr$  = relative density index,  $N_o$  = number of trees per hectare, and  $v$  = mean stem volume in cubic decimeters.

We analyzed stem structure graphically using a stand density management diagram specific for mixed balsam fir-black spruce stands (B. R. Sturtevant et al. *unpublished manuscript*). We also used Page's (1968) site index curves to predict the time necessary to generate stems of a specified size. We fit the CWD model shown in Fig. 1 to our log data from the chronosequence using two line equations, one for the residual decay phase and one for the residual accumulation phase. The decay phase of the model is characterized by exponential de-

TABLE 1. Stand age and structure within the chronosequence.

Site	Location†	Stand age	Basal area	Density (no. trees/ha)	$D_q$ ‡	Site index§	Relative density
12¶	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

† VL = Victoria Lake, CBL = Corner Brook Lakes, SB = South Brook.

‡ Quadratic mean diameter.

§ Site Potential, based upon the Forest Ecosystem Classification system for Newfoundland (Meades and Moores 1994).

|| Stands with relative density index values  $> 0.5$  are within the zone of imminent competition mortality (Newton and Weetman 1993).

¶ Stand structure information was not collected for this site.

cay (Lang 1985). The logistic growth equation (Ratkowski 1990) defines the accumulation curve, with the form  $V = b_0 / \{\exp[b_1 - (b_2 \times A)]\}$ , where  $V$  = sound volume of CWD in cubic meters per hectare 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  $R^2 = 0.909$ ) and were estimated at 10.64 and 0.15, respectively. We focused on the temporal dynamics of logs because of their particular importance to marten. This model has utility not as a predictive model per se, but rather as a mechanistic working hypothesis to be tested. We therefore removed stands showing obvious differences in structural characteristics.

## RESULTS AND DISCUSSION

### Chronosequence data

Table 1 describes the mensurational characteristics of each site. Total volume (sound plus decayed) of logs ranged from 15.2  $m^3/ha$  in 64-yr-old second-growth stand to 78.1  $m^3/ha$  in an 80-yr-old second-growth stand (Fig. 3a), while sound volume of logs ranged from 4.0

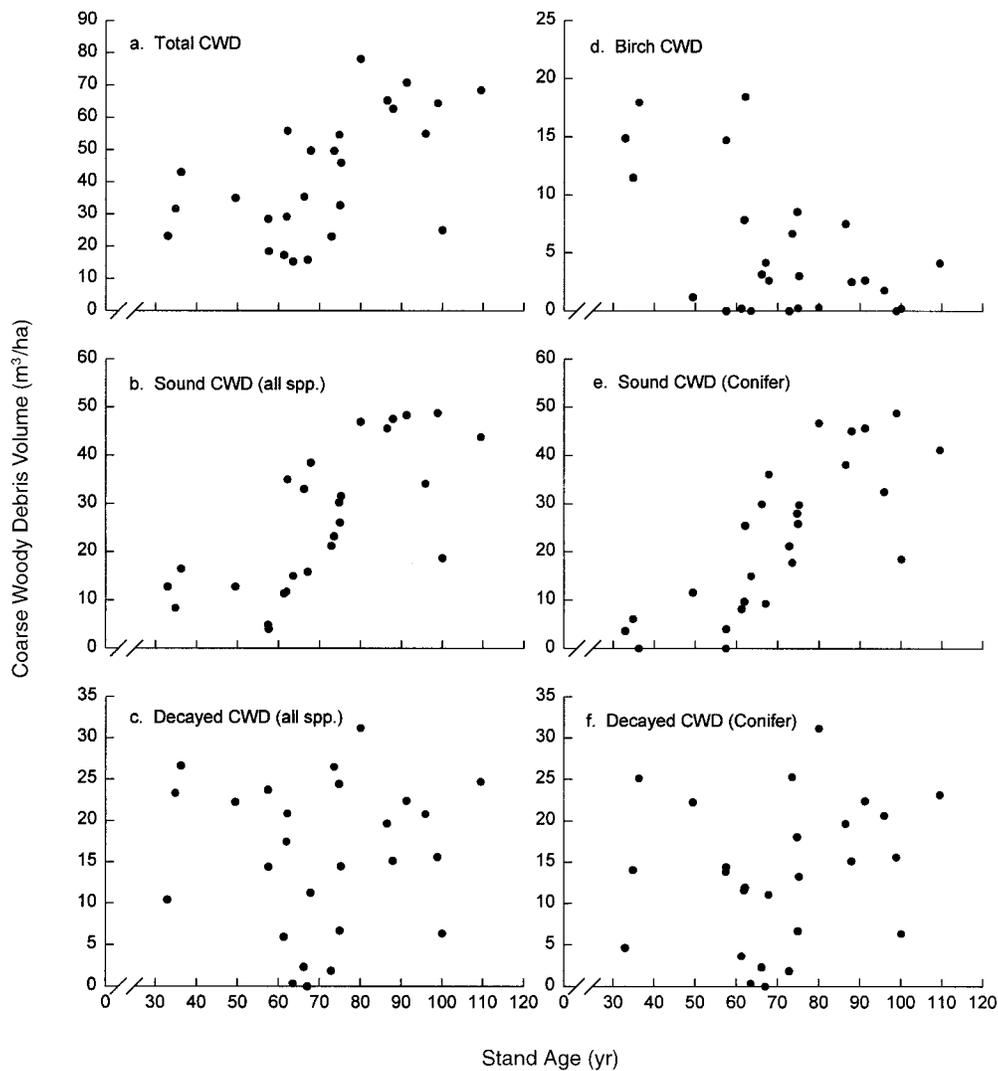


FIG. 3. Coarse woody debris (CWD) as a function of stand age, based upon chronosequence data.

m<sup>3</sup>/ha in a 58-yr-old second-growth stand to 48.8 m<sup>3</sup>/ha in a 91-yr-old old-growth stand (Fig. 3b). In general, log volume decreased with stand age to a low at 55 yr. The accumulation period followed for a relatively short, 30–40 yr period and plateaued at 80 yr. Decayed log volume was highly variable and showed no detectable trend besides a slight low point at 60–70 yr (Fig. 3c). In the early to midsuccessional stages of the chronosequence, decayed wood is likely to be a function of the abundance of residual trees and CWD remaining after disturbance, and may be quite variable. Additionally, rotten wood often is fragmented along its length, and could have contributed to significant volumetric sampling error.

In Newfoundland, birch is left standing during harvesting, and most dies soon after harvest due to the rapid change in site water balance, and vulnerability to windthrow. Therefore, volume of logs early in the chronosequence was strongly influenced by the pres-

ence of residual birch (Fig. 3d). We observed both standing and fallen residual birch as long as 60 yr after disturbance (B. R. Sturtevant, *personal observation*), suggesting birch may serve as an important reservoir of CWD during earlier stages of stand development, depending on the initial birch component. The contribution of new (sound) logs from maturing stands is more apparent after removing sound birch logs from the data (Fig. 3e). Similarly, the removal of birch from the decayed log data highlights the reduced volume of decayed logs at stand ages of ≈65 yr (Fig. 3f).

We observed a similar U-shaped temporal pattern in the structural complexity of logs (Fig. 4a, b). We used the estimated volume of logs recorded in the higher height classes as an indication of the structural complexity of CWD for each stand. However, while our sampling methodology successfully recorded logs within each height class, there were few samples in the highest classes (i.e., >1 m above the ground surface).

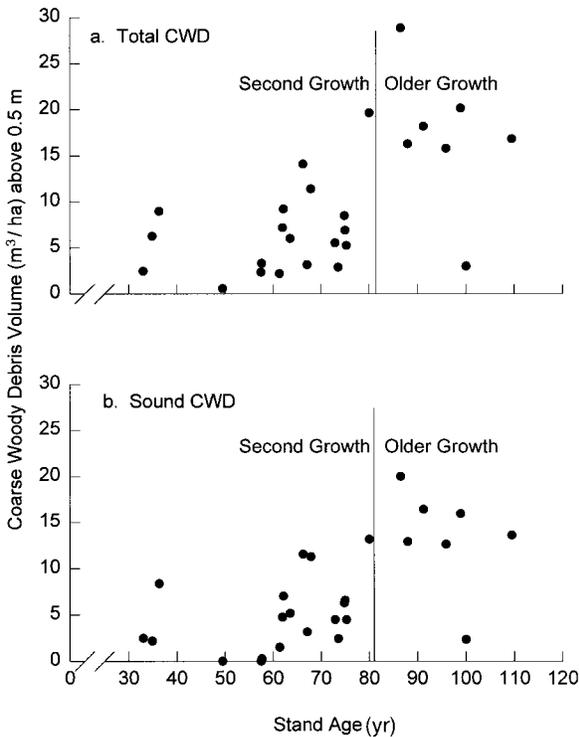


FIG. 4. Structural diversity of coarse woody debris (CWD) as a function of stand age. Vertical diversity is defined as the volume of logs encountered that were a minimum of 0.5 m above the ground surface.

We therefore combined the three highest height classes and used the volume of CWD suspended  $>0.5$  m above the ground surface as an index of structural complexity. Very little structural complexity was observed in the 40–60 yr old second stands. While some complexity 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 that is reduced in height over time by decomposition. In contrast, the highest structural diversity was clearly present in the old-growth stands.

Standing dead wood generally was rare within young stands, but snag density increased dramatically after 60 yr (Fig. 5a). Similarly, the basal area of standing dead wood increased substantially after 60 yr. However, snag basal area in older second growth was much more similar to that in old-growth stands (Fig. 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).

#### *CWD relationship to stand structure*

Mean relative density index values in measured stands ranged from a high of 0.63 in a 49-yr-old second-growth stand to a low of 0.22 in a 99-yr-old old-growth stand (Table 1). Relative densities reflected the degree of competition within each stand. A majority of second-

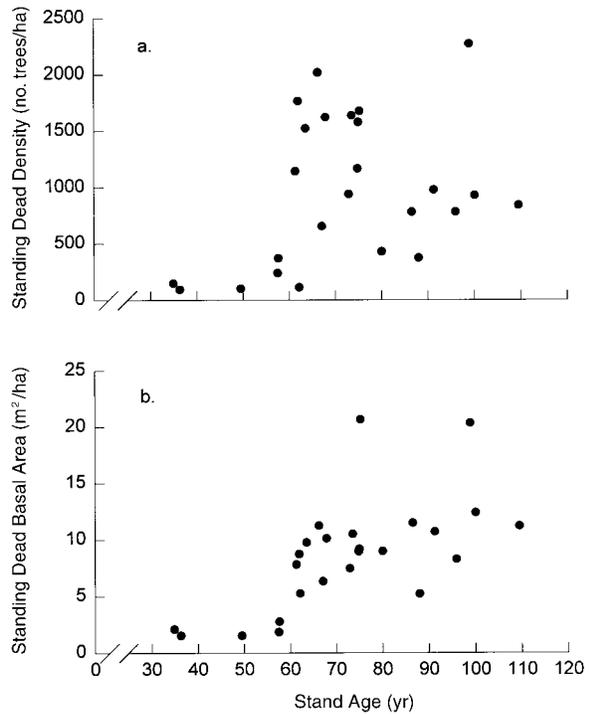


FIG. 5. Standing-dead wood: (a) density and (b) basal area, as a function of stand age.

growth stands had relative density index values  $>0.5$ , indicating competition pressure and active self-thinning, while most old-growth stands fell outside the estimated ZICM (see Table 1). A notable exception was site 18, a 61-yr-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 degree of competition was probably underestimated. The decrease in relative density observed in older stands indicates the eventual senescence of mature even-aged stands into what Oliver and Larson (1996) referred to as a “transition old-growth” state. This transition corresponds to the high log volume observed within stands  $>80$  yr of age, and indicates a critical change in both standing tree and sub-canopy structure.

Conceptually, by examining standing tree structure within a stand, one can begin to assess when the stand can potentially generate CWD. Our graphic analysis using a stand density management diagram approach (B. R. Sturtevant et al., *unpublished manuscript*) 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 (Fig. 6), which is roughly our lower limit for log diameter (see *Methods*). However, we expect self-thinned stems to be considerably smaller than the average stem size (Lang 1985). Assuming that a  $D_q$  of 12 cm would be necessary to generate self-thinned stems averaging 8 cm in diameter at breast height, the stand should reach

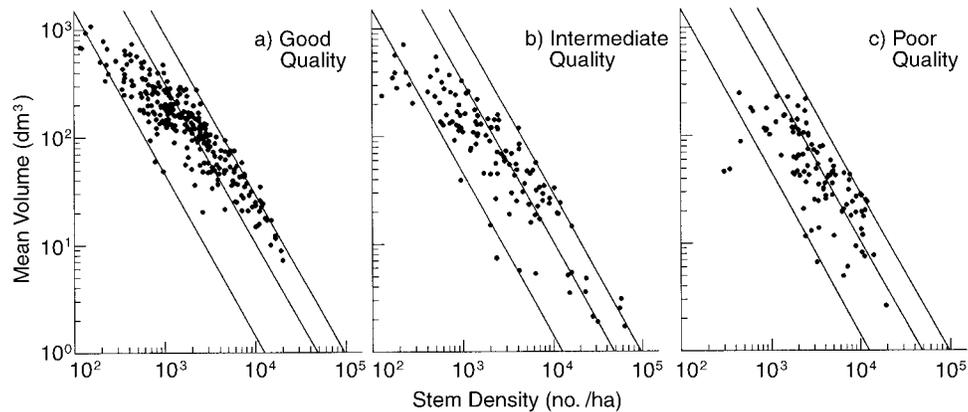


FIG. 6. Size–density relationships of individual plot data, stratified by site quality: (a) good quality, (b) intermediate quality, and (c) poor quality. Note log scale of  $x$  and  $y$  axes. The pattern observed suggests that the conceptual stand trajectory shown in Fig. 2 is followed regardless of 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.

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 yr) would be able to generate logs at  $\approx 26$  yr, although self-thinned debris  $> 8$  cm in diameter would not be available until 48 yr after disturbance. Similarly, a poor quality site (i.e., 12 m at a breast height age of 50 yr) would not be able to generate logs until 36 yr postdisturbance, and self-thinned logs  $> 8$  cm in diameter (breast height) would not be available until 78 yr postdisturbance. The impact of site quality on a stand's ability to produce logs becomes evident when CWD dynamics are viewed in this context.

However the question remains: does the age of stand senescence differ according to site quality? Two hypotheses are pertinent. First, if senescence were related to a size threshold, we would expect a stand on 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 may limit stem size in Newfoundland's maritime climate. Second, senescence may be acquired with age. For example, old balsam fir is prone to heartrot, which increases its vulnerability to windthrow mortality, and may limit its longevity (Seymour 1994). Vulnerability of stands to defoliation mortality may be associated with age as well as the structural characteristics of the host trees (Ostaf 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.

Fig. 6 shows yield–density relationships of individual plot data, categorized into the three site quality classes. The pattern of stand senescence appears similar. Few plots with mean volumes  $> 300$   $\text{dm}^3$  exist within the ZICM, regardless of site quality, indicating

similar patterns of yield–density and stand senescence. Our data were not designed to address the hypotheses suggested above, however we suggest that the mechanisms governing stand senescence will lend valuable insight into the role of site quality in the dynamics of CWD.

#### CWD model

Temporal dynamics of CWD can be summarized in two phases: the residual decay of predisturbance and disturbance-generated debris, and the residual accumulation of debris from the regenerating stand (Harmon et al. 1986, Spies et al. 1988). We fit the two-stage conceptual model in Fig. 1 to our observed sound log volume within the chronosequence. This model has utility not as a predictive model per se, but rather as a mechanistic working hypothesis to be tested.

The residual decay phase of the model is characterized by exponential decay (Lang 1985). Based upon our field observations, we assumed a 95% loss of sound log volume by 55 yr, although this may vary according to the species of logs present. Sound logs do not disappear, but rather enter the decayed log class. Decayed wood, therefore, lags behind the sound volume model, although our data indicate that much of the decayed residual wood structure is gone by 65–70 yr. The majority of residual debris is then overtaken by mosses and incorporated into the forest floor (B. R. Sturtevant, *personal observation*). Residual birch adds sound log volume to stands in the young ( $< 50$  yr old) stages of development.

The shape of the residual accumulation curve is sigmoidal, following Spies et al. (1988), and applies to naturally thinned, intermediate to good quality, balsam-fir-dominated stands. Based upon our observed minimum amount of sound CWD volume, sites younger than 50 yr were excluded from the accumulation analysis. We assumed that the majority of sound birch debris within second-growth stands was residual debris,

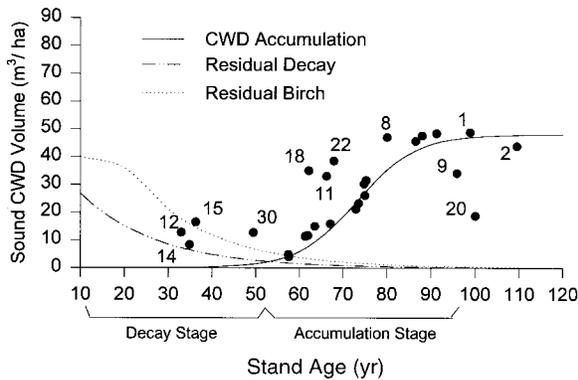


FIG. 7. Theoretical model of coarse woody debris (CWD) decay and accumulation. Stands 1, 2, 8, 11, and 22 represent sites where >20% of the plots were affected by insect defoliation. Notice that the only second-growth stands (sites 11 and 22) that approached the structural diversity of old-growth stands were those affected by defoliation (compare with Fig. 4). The influence of site quality and stand history on CWD volume is shown by stands 18 and 30, which represent relatively good sites characterized by relatively large, widely spaced trees, and stands 2, 9, and 20, which were on relatively poor sites. Eight stands (11, 12, 14, 15, 18, 20, 22, and 30) were not used in creating the model.

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 completed model is shown in Fig. 7. Points falling above the accumulation line during earlier stages of development indicate additional residual CWD. Defoliation disturbance increased both log volume and structural diversity (Fig. 7; sites 1, 2, 8, 11, and 22). Defoliators affected stands in a patchy spatial pattern, with a typical patch size of  $\approx 0.5$ – $2.0$  ha. In 50–80 yr old second-growth stands, defoliated patches created locally abundant logs and standing-dead wood within a matrix of more typical second growth (i.e., within the ZICM). Second-growth sites 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. 7). Sites 30 and 18 (ages 49 and 63, respectively), both good-quality sites, were characterized by widely spaced, large-diameter trees (see Table 1) with high live-crown ratios. Both sites were beginning to generate new logs. Additionally, site 30 was young enough to contain some residual sound debris, 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 shallow soils, contained two distinct age classes. Old patches (>80 yr) were dispersed among areas of 50-yr regeneration, suggesting the stand was affected by an earlier defoliation event. Occasional residual dominants were present throughout. The difference in struc-

ture probably lowered overall levels of debris. Site 2 also was 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 characterized by small, widely spaced trees (see Table 1) and a relatively open canopy. This site showed extremely low log volume 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. We expect that its low log abundance was related to its low productivity.

## CONCLUSIONS

The temporal pattern of CWD accumulation observed within our study was the result of residual woody material (initially conifer slash and then birch) decaying without significant sound conifer CWD input during early stages of forest development, followed by a rapid accumulation of coniferous wood. Sound CWD volume exhibited a relatively predictable trajectory, with a residual decay stage ending near 58 yr, and an accumulation stage lasting between  $\approx 50$  and 90 yr, reaching an asymptote at  $\approx 48$  m<sup>3</sup>/ha. Significantly, birch was a large component of residual CWD for as long as 60 yr postdisturbance. During early, sound coniferous CWD accumulation, the degree of decomposition of fallen logs was relatively low compared with the high input. The accumulation asymptote was reached as decomposition rates began to equal the input rates of the senescing stand at  $\approx 80$  yr. Total CWD volume exhibited a similar relationship, reaching a maximum observed volume of 78.1 m<sup>3</sup>/ha. Both CWD volume and structural diversity were greatest in silviculturally overmature stages of development, which was approached at  $\approx 80$ – $90$  yr. High CWD volumes coincided with stand senescence.

Disturbance events strongly influence CWD accumulation. The major forms of natural disturbance within our study sites were windthrow and insect defoliation. The size and relative density of standing trees are related to the susceptibility of individual trees to windthrow with larger, more isolated trees increasingly susceptible. Additionally, older stands are more susceptible to insect defoliation. Defoliation greatly increased both the volume and the structural diversity of CWD both within our second-growth and senescent stands. Site quality also influences volume potential and self-thinning rates and, thus, stand structure. Similarly, CWD is influenced by site quality, because the size of logs on the forest floor is a function of standing tree size. Certain second-growth outlier stands within our data set (sites 18 and 30) were relatively young (49 and 63 yr, respectively) but had relatively high CWD volumes, demonstrating the potential importance of this interaction. Importantly, older senescent second-growth stands had CWD levels similar to old-growth sites, suggesting that silvicultural management for marten is possible.

For this reason, we 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, although they may be adapted to uneven-aged situations (Long 1985). Because CWD within Newfoundland is dependent on stand structure, the potential exists to manipulate stand structure to manage for desired CWD volumes. The majority of our second-growth sites were within the ZICM. CWD generated during stem exclusion is small in size, and apparently remains for a period of time as standing-dead wood. 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 increases light availability on the forest floor, increasing the potential for vegetation growth and diversity. Disturbance events can increase both the volume and structural complexity of second-growth stands, increasing their value as wildlife habitat. Site quality appears to shift the debris accumulation curve to the left or right, depending on whether the site is of lower or higher quality than typical. We observed that two stands with naturally low relative densities and comparatively large-diameter trees for their age were generating CWD at a faster rate than suggested by our model.

We suggest that yield–density relationships are an appropriate tool for examining the interaction between stand structure and the generation of CWD, because the size and structure of standing trees can 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 thinned stands to increase our understanding of size- and structure-related disturbances, and the subsequent impact upon the CWD resource within managed systems.

#### *Management implications*

In Newfoundland, and in most of the boreal forest, a typical harvest rotation is between 50 and 60 yr, and coincides with the lowest CWD volume on the forest floor. If harvests are repeated over many rotations, we expect that CWD volumes will be reduced significantly, because little CWD would be generated by the system, and that available would be limited to residual volumes left over as conifer slash and standing, but declining, birch after the harvest. At the same time, structural complexity will decline. If the stand is maintained within the ZICM, the CWD generated will remain small for a longer period of time. Although perhaps sufficient for other purposes, e.g., nutrient cycling, this type of debris is unlikely to provide adequate structure for

wildlife. The implications for marten is a loss of forest floor structure as well as access to the subnivean zone. Marten do not inhabit habitats devoid of forest floor structure, because they are unable to forage for subnivean small mammals. Forest logging rotations of 50–60 yr in Newfoundland mean a loss of marten habitat. Conversely, if the stand is maintained outside the ZICM, it has the potential to generate larger logs faster than if unmanaged, increasing structural diversity of the forest floor and benefitting wildlife. This possibility should be examined further.

#### ACKNOWLEDGMENTS

This project was funded by the Western Newfoundland Model Forest, Inc. We thank the many individuals at the Model Forest for their effort in facilitating this project. Special thanks to T. Newbury and K. Chaulk for their hard work in the field. We also thank the Newfoundland Division of Wildlife, The Newfoundland Forest Service, and Forestry Canada for their support, with special thanks to L. Mayo and B. Greene for their guidance in the field. P. Newton provided the relative density equations for balsam fir in Newfoundland based on his own unpublished data, and S. Durham aided in the statistical analysis. W. Adair contributed valuable ideas and insights from the project's inception. We also thank two anonymous referees for their helpful comments.

#### LITERATURE CITED

- Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock–Douglas-fir forest. *Canadian Journal of Forest Research* **17**:697–704.
- Banfield, C. E. 1983. Climate. Pages 37–106 in G. R. South, editor. *Biogeography and ecology of the island of Newfoundland*. Dr. W. Junk Publishers, The Hague, The Netherlands.
- Baskerville, G. L. 1975. Spruce budworm—super silviculturalist. *Forestry Chronicle* **51**:4–6.
- Bissonette, J. A., R. J. Fredrickson, and B. J. Tucker. 1989. American marten: a case for landscape-level management. *Transactions of the North American Wildlife and Natural Resources Conference* **54**:89–101.
- Bissonette, J. A., and S. S. Sherburne. 1994. Subnivean access: the prey connection. *Transactions of the 23rd IUGB Congress (Halifax, Nova Scotia, Canada 1993)*: 421–434.
- Brown, J. K. 1974. *Handbook for inventorying downed woody material*. United States Department of Interior Forest Service General Technical Report **INT-16**.
- Buskirk, S. W., S. C. Forest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting site ecology of marten in the central Rocky Mountains. *Journal of Wildlife Management* **53**: 191–196.
- Damman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pages 163–206 in G. R. South, editor. *Biogeography and ecology of the island of Newfoundland*. Dr. W. Junk Publishers, The Hague, The Netherlands.
- Drew, T. J., and J. W. Flewelling. 1977. Yield-density relationships and their application to monterey pine plantations. *Forest Science* **23**:517–534.
- Griffin, R. H., and J. E. Johnson. 1980. Polymorphic site index curves for spruce and balsam fir growing in even aged stands in northern Maine. *University of Maine Life Science and Agricultural Experiment Station Bulletin* **765**.
- Harmon, M. E., K. Cromack, Jr., and B. G. Smith. 1987. Coarse woody debris in mixed conifer forests, Sequoia National Park, California. *Canadian Journal of Forest Research* **17**:1265–1272.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. J. Solkins,

- S. V. Gregory, J. P. Lattin, N. H. Andersen, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133–302.
- Horwood, H. 1986. *Corner Brook: a social history of a paper town*. Newfoundland History Series Number 3. Breakwater Books, St. John's, Newfoundland, Canada.
- Husch, B., C. I. Miller, and T. W. Beers. 1972. *Forest mensuration*. Second edition. Ronald Press, New York, New York, USA.
- Lambert, R. L., G. E. Lang, and W. A. Reiners. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* **61**:1460–1473.
- Lang, G. E. 1985. Forest turnover and the dynamics of bole wood litter in subalpine balsam fir forest. *Canadian Journal of Forest Research* **15**:199–293.
- Long, J. N. 1985. A practical approach to density management. *Forestry Chronicle* **61**:23–27.
- Meades, W. J., and L. Moores. 1994. *Forest site classification manual: a field guide to the Damman forest types of Newfoundland*. Second edition. FRDA Report 003. Forestry Canada and Newfoundland Department of Forestry and Agriculture, St. John's, Newfoundland, Canada.
- Muller, R. N., and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. *Canadian Journal of Forest Research* **21**:1567–1572.
- Newfoundland Department of Forestry. 1990. *Forest type map*. Corner Brook, Newfoundland, Canada.
- Newton, P. F. 1992. Base-age invariant polymorphic site index curves for black spruce and balsam fir within central Newfoundland. *Northern Journal of Applied Forestry* **9**:18–22.
- Newton, P. F., and G. F. Weetman. 1993. Stand density management diagrams and their development and utility in black spruce management. *Forestry Chronicle* **69**:421–430.
- Oliver, C. D., and B. C. Larson. 1996. *Forest stand dynamics* (updated). John Wiley & Sons, New York, New York, USA.
- Ostaff, D. P., and D. A. MacLean. 1989. Spruce budworm populations, defoliation, and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Breton Island, Nova Scotia. *Canadian Journal of Forest Research* **19**:1077–1086.
- Page, G. S. 1968. Site index curves for spruce and fir in the forest regions of Newfoundland. Information Report N-X-22. Canadian Department of Environment, Canadian Forest Service, Newfoundland Forest Research Center, St. John's, Newfoundland, Canada.
- Page, G., and R. S. van Nostrand. 1973. *Empirical yield tables for the major forest cover types of Newfoundland*. Information Report N-X-100. Canadian Department of Environment, Canadian Forest Service, Newfoundland Forest Research Center, St. John's, Newfoundland, Canada.
- Raphael, M. G. 1984. Wildlife populations in relation to stand age and area in Douglas-fir forests of northwestern California. Pages 259–274 in W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, editors. *Fish and wildlife relationships in old-growth forests: proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982*. American Institute of Fish Research and Biology, Juneau, Alaska, USA.
- Raske, A. G. 1986. Vulnerability rating of the forests of Newfoundland to spruce budworm. Information Report N-X-239. Canadian Department of Environment, Canadian Forest Service, Newfoundland Forest Research Center, St. John's, Newfoundland, Canada.
- Ratkowsky, D. A. 1990. Handbook of nonlinear regression models. In R. G. Cornell, W. J. Kennedy, A. M. Kshirsagar, and E. G. Schilling, editors. *Statistics: textbooks and monographs*. Volume 107. Marcel Dekker, New York, New York, USA.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* **52**:199–221.
- Rowe, J. S. 1972. *Forest regions of Canada*. Publication 1300. Canadian Department of Environment, Canadian Forest Service, Ottawa, Ontario, Canada.
- Saville, P. S. 1983. Silviculture in windy climates. *Forestry Abstracts* **44**:472–488.
- Seymour, R. S. 1994. The northeastern region. Third edition. Pages 31–79 in J. W. Barrett, editor. *Regional silviculture of the United States*. John Wiley & Sons, New York, New York, USA.
- Sherburne, S. S., and J. A. Bissonette. 1993. Squirrel mid-dens influence marten (*Martes americana*) use of subnivean access points. *American Midland Naturalist* **129**:204–207.
- Sherburne, S. S., and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. *Journal of Wildlife Management* **58**:400–405.
- Spencer, A. W. 1984. Food habits, grazing activities, and reproductive development of long-tailed voles, *Microtus longicaudus* (Merriam) in relation to snow cover in the mountains of Colorado. Pages 67–90 in J. F. Merritt, editor. *Winter ecology of small mammals*. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* **69**:1698–1702.
- Tallmon, D., and L. S. Mills. 1994. Use of logs within home ranges of California red-backed voles on a remnant of forest. *Journal of Mammalogy* **75**:97–101.
- Thompson, I. D. 1991. Could the marten become the spotted owl of eastern Canada? *Forestry Chronicle* **67**:136–140.
- Tritton, L. M. 1980. *Dead wood in the northern hardwood forest system*. Dissertation. Yale University, New Haven, Connecticut, USA.
- Warren, G. R., and J. P. Meades. 1986. Wood defect and density studies. II. Total and net volume equations for Newfoundland's forest management units. Information Report N-X-100. Canadian Department of Environment, Canadian Forest Service, Newfoundland Forest Research Center, St. John's, Newfoundland, Canada.
- Westoby, M. 1984. The self-thinning rule. *Advances in Ecological Research* **14**:167–225.
- White, J., and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. *Journal of Ecology* **58**:467–485.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology (Osaka City University, Japan)* **14**:107–129.