

Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan

John M. Goodburn and Craig G. Lorimer

Abstract: The effects of uneven-aged management on the availability of coarse woody debris habitat were examined in northern hardwood forests (with and without a hemlock component) in north-central Wisconsin and adjacent western Upper Michigan. Snags, cavity trees, fallen wood, and recent tip-up mounds in 15 managed uneven-aged (selection) stands were compared with levels in 10 old-growth stands and six unmanaged even-aged second-growth stands. Amounts of coarse woody debris in selection stands were generally intermediate between old-growth and even-aged stands. Density of snags >30 cm DBH in northern hardwood selection stands averaged 12/ha, approximately double that found in even-aged northern hardwoods, but only 54% of the level in old-growth northern hardwoods. Highest densities of snags >30 cm DBH occurred in old-growth hemlock-hardwood stands, averaging over 40 snags/ha. For combined forest types, the volume of fallen wood (>10 cm in diameter) was significantly lower in selection stands (60 m³/ha) and even-aged stands (25 m³/ha) than in old-growth stands (99 m³/ha). Volume differences were even more pronounced for large-diameter debris (>40 cm). Cavity tree density in selection stands averaged 11 trees/ha, 65% of the mean number in old-growth stands. Densities of snags (>30 cm DBH) and large-diameter cavity trees (>45 cm) present in selection stands exceeded current guidelines for wildlife tree retention on public forests.

Résumé : Les effets d'un aménagement inéquienne sur la disponibilité des habitats que procurent les gros débris ligneux ont été étudiés dans les forêts de feuillus nordiques, accompagnés ou non de pruche, du Centre-Nord du Wisconsin et de l'Ouest de la péninsule Nord du Michigan qui est adjacente. Les quantités de chicots, d'arbres avec des cavités, de débris ligneux au sol et de tas récents de houppiers présents dans 15 peuplements aménagés de façon inéquienne ont été comparées à celles qui étaient présentes dans 10 vieux peuplements et six peuplements équiennes de seconde venue et non aménagés. La quantité de débris ligneux grossiers dans les peuplements inéquiennes se situait généralement à mi-chemin entre les quantités retrouvées dans les vieux peuplements et dans les peuplements équiennes. La densité des chicots de plus de 30 cm au DHP atteignait en moyenne 12/ha dans les peuplements inéquiennes de feuillus nordiques, soit approximativement le double de ce qu'on retrouve dans les peuplements équiennes de feuillus nordiques, mais seulement 54% de la quantité présente dans les vieilles forêts de feuillus nordiques. Les plus fortes densités de chicots de plus de 30 cm au DHP ont été observées dans les peuplements de feuillus et de pruche, atteignant en moyenne plus de 40 chicots/ha. Pour tous les types de forêts combinés, le volume de débris ligneux au sol (>10 cm de diamètre) était significativement plus faible dans les peuplements inéquiennes (60 m³/ha) et dans les peuplements équiennes (25 m³/ha) que dans les vieux peuplements (99 m³/ha). Les différences de volume étaient encore plus prononcées pour les débris de fort diamètre (>40 cm). La densité des arbres avec des cavités atteignait en moyenne 11 arbres/ha dans les peuplements inéquiennes, soit 65% du nombre moyen dans les vieux peuplements. La densité des chicots (>30 cm au DHP) et des arbres de fort diamètre (>45 cm) avec des cavités présents dans les peuplements inéquiennes excédait les normes actuelles concernant le maintien d'arbres pour la faune sur les terres publiques.

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Introduction

Coarse woody debris, including snags and fallen wood, provides important habitat elements for a wide array of biota, in addition to its role in nutrient cycling, carbon storage, and other ecosystem functions. Organisms that use coarse woody debris for food and cover range from arthropods, herptiles, birds, and small mammals to a host of fungi and microorganisms (Jaeger 1980; Harmon et al. 1986). In the northern hard-

wood forest, over 40 species of birds and mammals use cavities in snags and dead portions of live trees for nest sites, dens, escape cover, and winter shelter (Evans and Conner 1979; DeGraaf and Shigo 1985). Fallen trees often create tip-up mounds, which can enhance establishment of some plants, provide nesting sites for certain bird species, and offer moist refuge for amphibians in pits during dry periods (Heatwole 1962; Beatty 1984; Peterson et al. 1990). In unmanaged old-growth forests, the death of large trees and subsequent gap formation result in structurally complex habitat (Franklin et al. 1981; Hunter 1990). In managed forests, efficient harvest and removal of tree boles from the stand can limit development of such features and possibly reduce populations of organisms that depend upon these structures (Haapanen 1965; Cline et al. 1980).

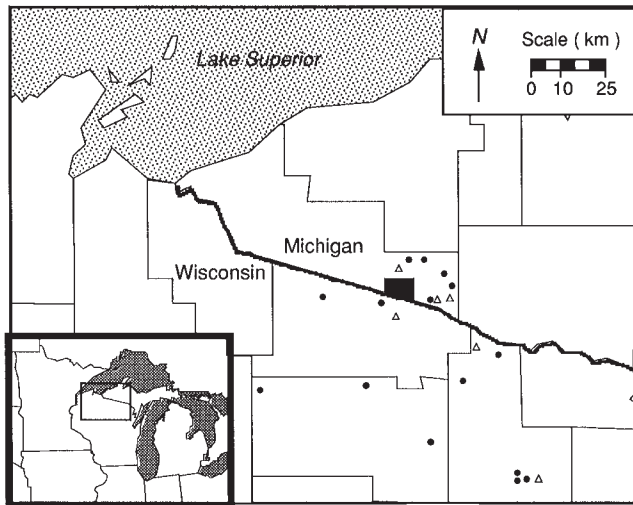
Wildlife population studies suggest that large size and advanced wood decay are two key attributes in vertebrate

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Fig. 1. Map of the study area. All old-growth stands were located within the Sylvania Wilderness Area, Ottawa National Forest (represented by the solid polygon). Locations of individual even-aged and selection stands are indicated with open triangles and solid circles, respectively.



preferences for coarse woody debris (Raphael and White 1984; Swallow et al. 1986). While small woody debris has habitat value for some organisms, large snags and fallen boles persist for a longer time before fragmenting, provide greater forage area, and meet minimum size requirements of a wider range of potential vertebrate users than do smaller elements (Conner et al. 1975; Cline et al. 1980; DeGraaf and Shigo 1985). For certain taxa such as plethodontid salamanders, the availability of cool, moist microclimate under loose bark and within the interior of fallen boles with advanced decay is even more critical to habitat suitability than bole diameter (Aubry et al. 1988; Petranksa et al. 1994).

Studies in the eastern United States comparing habitat structure of old-growth forests and younger stands have been limited by the scarcity of old-growth stands. Available studies of coarse woody debris in eastern deciduous forests have focused primarily on second-growth stands originating after heavy logging in the early twentieth century, but that have received little or no silvicultural treatment since the time of stand initiation (e.g., Tritton 1980; Carey 1983; McCarthy and Bailey 1994). Less is known regarding the effects of various management strategies such as intermediate thinning, timber stand improvement, or uneven-aged management on the distribution of cavity trees and coarse woody debris.

Uneven-aged management is the predominant silvicultural system for managing mature northern hardwoods in the upper Midwest on both public and private lands (Jacobs 1987). On public lands, harvests removing 20–30% of the trees in each size class are made at 12- to 15-year intervals. Normally the maximum tree size retained in the stands is 60 cm diameter at breast height (DBH) (Arbogast 1957; Tubbs 1977). It has been suggested that by discriminating against large-diameter, low-vigor, and defective trees, uneven-aged management could restrict the development of cavity trees and coarse woody debris (Zeedyk and Evans 1975; McComb and Noble 1980). Partially in response to these concerns, management guidelines were introduced on some Wisconsin and Michigan national forests

in the early 1980s calling for the retention of all active cavity trees and approximately 5–10 snags (>30 cm DBH)/ha (U.S. Department of Agriculture 1980). However, information regarding the actual levels of snags, cavity trees, and fallen wood present in managed uneven-aged northern hardwood forests appears to be limited to two stands in Connecticut and New Hampshire examined by McComb and Noble (1980) and by Gore and Patterson (1986).

The present study is part of a larger interdisciplinary research project investigating differences in forest structure, ecosystem processes, and biological diversity between old-growth and managed hemlock–hardwood forests. Our objective was to examine the effects of uneven-aged management on forest habitat structure in northern hardwood stands (with and without a hemlock component). Snags, cavity trees, fallen wood, and tree-fall mounds in managed uneven-aged stands (hereafter termed selection stands) were compared with base-line levels in unmanaged uneven-aged old-growth stands and in unmanaged even-aged second-growth stands. Unmanaged even-aged second-growth stands (hereafter referred to as even-aged) were included in the study because of their current prevalence on Wisconsin's public lands and because questions regarding their future management remain unresolved (Alverson et al. 1994).

Methods

Study areas

This study was conducted in mesic northern hardwood and hemlock–hardwood stands in north-central Wisconsin and adjacent western upper Michigan (Fig. 1). Most research sites are located on the Winegar terminal moraine complex, within sub-subsection IX.3.2 in Albert's (1995) regional landscape classification. The region is characterized by a thick layer of sandy glacial drift underlain by iron-rich Precambrian bedrock. Rolling irregular topography formed by disintegrating glacial ice includes many kettle lakes and steep sandy ridges (Albert 1995). Elevations range from approximately 500 to 550 m. The upland soils are predominantly sandy loams and loamy sands classified as either well-drained coarse-loamy Typic Haplorthods or moderately well-drained Alfic Fragiorthods. In the Fragiorthods a moderately developed fragipan is found at a depth of 50–100 cm (Hole 1976; Spies and Barnes 1985). The remainder of research sites (those outside the Winegar moraine) were located on similar upland loam and sandy loam spodosols that formed in ground moraines and areas of pitted outwash (i.e., within sub-subsections IX.3.1, IX.3.3, and IX.5; Albert 1995). The climate of the entire region is continental with heavy snows, extremely cold winters, and a frost-free period of less than 100 days (Albert et al. 1986). Mean monthly temperatures range from –12.2°C in January to 18.6°C in July. Annual precipitation averages 850 mm, with 60% of that amount falling between May and September (Lac Vieux Desert weather station, National Climatic Data Center, Asheville, N.C., 1993).

All old-growth stands were located in the Sylvania Wilderness Area on the Ottawa National Forest, Mich. This tract has had only localized past cutting and includes over 6000 ha of old-growth forest (U.S. Department of Agriculture 1964). Trees range in age up to a maximum of about 350 years (Dahir 1994). Ten old-growth stands larger than 20 ha in size were selected, including six stands dominated by sugar maple (*Acer saccharum* Marsh.) and four dominated by a mixture of eastern hemlock (*Tsuga canadensis* (L.) Carrière), sugar maple, and yellow birch (*Betula alleghaniensis* Britt.). Hemlock–hardwood stands were defined as those in which hemlock composed >30% of the basal area for trees ≥2 cm DBH.

Ecological classification systems developed for the Sylvania

Wilderness Area (Spies and Barnes 1985), the Ottawa National Forest, and for the forest habitat types in Michigan (Coffman et al. 1983) and Wisconsin (Kotar et al. 1988) were used to select old-growth, selection, and even-aged stands with similar soil and site characteristics. All northern hardwood and hemlock-hardwood study stands had been classified as forest habitat type *Acer-Tsuga-Dryopteris* (ATD) (Coffman et al. 1983; Kotar et al. 1988), although a few plots were transitional between the ATD habitat type and the *Acer-Viola-Osmorhiza* (AViO) or the *Acer-Tsuga-Maianthemum* (ATM) type.

The primary criteria for managed uneven-aged (selection) study sites were previous management by the selection system on a cutting cycle of 8–15 years, a minimum residual basal area of 16.1 m²/ha (70 ft²/acre), and a maximum residual tree diameter >45 cm DBH. These selection stands typically have a range of tree ages, with some individuals more than 200 years old (Cole and Lorimer 1994). Although stands were managed under wildlife tree retention guidelines, they were not managed using a prescription to restore old-growth characteristics, a more recent treatment being introduced on some public forests (e.g., Rominske and Busch 1991).

We also located study areas in six even-aged second-growth northern hardwood stands with a predominant age of 65–75 years. These stands had not been previously thinned and were essentially unmanaged since stand initiation. They contain only scattered larger trees from the former stand and no significant biological legacy of snags and fallen wood. Even-aged hemlock-hardwood stands were not included in the comparison because they are uncommon in the region. The final 31 stands selected included 22 northern hardwood stands (six old-growth, 10 selection, and six even-aged) and nine hemlock-hardwood stands (four old-growth, five selection).

Field procedures

A single large 30 × 100 m rectangular plot was established in each stand. This design accommodated our measurement of forest structural features as well as the sampling needs of various research team members using the same sites for related studies (e.g., soils, fungi, invertebrates, birds, small mammals). Plot center was randomly located within the stand after allowing a 200-m buffer from stand boundaries. The long axis of the plot was oriented east-west and divided into three contiguous 10 × 100 m transects.

The species, DBH, and total height were recorded for all dead trees ≥10 cm DBH and >1.5 m tall within the 30 × 100 m plot. Heights were measured with a clinometer or telescoping height pole. Snags were examined for presence of loose bark plates larger than 25 × 25 cm (i.e., bark cavities), which might serve as bat roosts or brown creeper (*Certhia americana*) nests (Evans and Conner 1979; Brady 1983). Additional information was collected on decay class (see classification for fallen wood below), fragmentation status (1, crown intact; 2, only large branches remaining; 3, bole only; 4, broken bole), and the percentage of bark remaining on snag. Snag size diversity (Raphael and White 1984) was calculated with Shannon's diversity index (H') using four diameter classes (10–30, 30–45, 45–60, >60 cm) and four height classes (<6, 6–12, 12–18, >18 m).

Within a 20 × 100 m area (the center transect plus one randomly selected outer transect), all trees >10 cm DBH were searched for dens and nesting cavities using 8× binoculars (Healy et al. 1989). Following the criteria of Carey (1983), a nesting cavity was considered a hole in any live or dead tree more than 1 m above the ground that provides overhead shelter from precipitation and has no cracks or openings except the entrance. For all cavity trees, data were collected on tree species, live-dead status, and DBH, along with cavity height, location (bole, branch, dead top), opening size (2–5, 5–10, 10–20, >20 cm), and cavity origin (bird excavated or natural wound). Cavities were checked during the winter for better visibility, but no attempt was made to monitor nesting species or verify use during the survey year. Holes were examined for tooth marks, nesting material, rubbing marks, and debris near the entrance to judge the certainty of use.

Cavity use certainty was tallied as (i) definite, (ii) fairly certain, or (iii) uncertain. To avoid counting cavities of questionable value to wildlife, only cavities classified as "definite" or "fairly certain" were included in calculations of cavity tree density. Hollow trees and cavities with a second or overhead opening were not considered as nesting cavities, but were recorded as dens or escape structures.

Fallen wood (fallen boles, branches, natural and cut stumps, or harvest tops) was measured within the center 10 × 100 m transect, which was divided into ten 10 × 10 m quadrats. The smallest size class (10.0–19.9 cm in diameter) was subsampled only in the northwest 5 × 5 m quarter of each 10 × 10 m quadrat. For each piece, species, decay class, and origin were recorded. Decay status was recorded using a system of five classes based upon bark slippage and degree of decay into the sapwood and heartwood, modified from Sollins (1982) and Lambert et al. (1980), and similar to that used by Muller and Liu (1991) for deciduous forests in Kentucky. Extent of decay was inspected with a 0.5-cm-diameter pointed metal rod. Decay classes were defined as class I (tight bark and no visual decay), class II (some bark slippage with incipient decay in the sapwood), class III (decay obvious in the outer layers, pointed metal rod penetrates more than half the radius), class IV (some of the outer xylem layers missing, decay extending well towards the core, metal rod penetrates clear through the bole), or class V (organic debris collapsed to ground level and mixing with soil, little structural integrity).

Volume of each piece of fallen wood was calculated from piece length and the cross-sectional area of each end with Smalian's formula for cubic volume (Wenger 1984). Using metal tree calipers, stem diameter was measured at each end, or where the piece either extended beyond the transect boundary or dropped below the minimum measurable diameter. Diameter measurements at additional points along the axis were taken if total length exceeded 5 m. The volumes of any hollow portions of logs or stumps were similarly calculated and subtracted from the total. "Large" fallen wood included all pieces within the sample area that had a midpoint diameter >40 cm, calculated as the quadratic mean of the end diameters. The volume of coarse woody debris in snags was calculated using species-specific regression equations from Hahn (1984), which allow computation of cubic volume from our measures of snag DBH and height.

Sample wood disks ($n = 167$) were collected for estimates of coarse woody debris mass. Disks were cut into rectangular cubes with a band saw or knife and the dimensions of the subsample measured with vernier calipers. Subsamples were oven-dried to a constant mass at 70°C and then weighed. Wood density for the various species and decay combinations was determined from mass and volume of subsamples, in grams of dry mass per cubic centimetre of "green" volume. Density for decay class I debris was obtained from published tables (U.S. Department of Agriculture Forest Products Laboratory 1976). Stand-level estimates for the biomass of coarse woody debris (>10 cm in diameter) were calculated from these density estimates and from the debris volume in each species and decay class combination sampled in each plot.

Because of the great longevity of tree-fall microtopography and the difficulty in distinguishing mounds from mechanical disturbances in managed landscapes, only recent tip-ups were considered in which woody debris of at least decay class V was still evident from the fallen tree. For all such tip-up mounds and pits within the 10 × 100 m center strip, perpendicular length and width of both pit and mound were measured to the nearest decimetre with a fiberglass tape and treated as ellipse diameters in area calculations.

Statistical analyses

The single large plot in each stand was considered to be the experimental unit. The five stand types included two different forest types (northern hardwood and hemlock-hardwood) and three management histories (even-aged, selection, and old-growth). Of primary interest, a priori, were four comparisons among these five forest type – management history combinations. Two of these involved comparing

Table 1. Summary of two-way and one-way ANOVA tests for the effects of management history and forest type on coarse woody debris characteristics.

Source of variation	Two-way ANOVA for old-growth and managed uneven-aged stands				One-way ANOVA for northern hardwood stands			
	df	Mean squares	<i>F</i> value	<i>P</i> > <i>F</i>	df	Mean squares	<i>F</i> value	<i>P</i> > <i>F</i>
Cavity tree density								
Management history	1	3.568	3.44	0.079	2	2.062	1.23	0.318
Forest type	1	2.387	2.30	0.146				
Management history × forest type	1	0.118	0.11	0.740				
Error	19	1.038			17	1.679		
Density of snags >10 cm DBH								
Management history	1	19.826	10.77	0.004*	2	23.633	8.47	0.002*
Forest type	1	2.902	1.58	0.223				
Management history × forest type	1	14.920	8.10	0.010*				
Error	21	1.841			19	2.791		
Density of snags >30 cm DBH								
Management history	1	35.697	37.72	0.001*	2	11.247	7.60	0.004*
Forest type	1	2.261	2.39	0.137				
Management history × forest type	1	7.275	7.69	0.011*				
Error	21	0.947			19	1.479		
Density of snags >45 cm DBH								
Management history	1	49.118	29.98	0.001*	2	17.746	11.34	0.001*
Forest type	1	1.295	0.79	0.384				
Management history × forest type	1	1.571	0.96	0.339				
Error	21	1.638			19	1.564		
Density of snags with loose bark plates								
Management history	1	2.045	0.87	0.362	2	0.472	0.19	0.827
Forest type	1	1.943	0.82	0.374				
Management history × forest type	1	5.553	2.36	0.140				
Error	21	2.358			19	2.501		
Snag coarse woody debris volume								
Management history	1	64.587	32.78	0.001*	2	4.483	2.16	0.142
Forest type	1	3.333	1.69	0.208				
Management history × forest type	1	19.469	9.88	0.005*				
Error	21	1.970			19	2.071		
Fallen coarse woody debris volume								
Management history	1	29.240	23.03	0.001*	2	40.731	34.4	0.001*
Forest type	1	0.807	0.64	0.434				
Management history × forest type	1	0.021	0.02	0.900				
Error	21	1.270			19	1.184		
Large fallen coarse woody debris volume (>40 cm in diameter)								
Management history	1	18.627	5.47	0.029*	2	38.474	16.63	0.001*
Forest type	1	0.164	0.05	0.829				
Management history × forest type	1	1.010	0.30	0.592				
Error	21	3.404			19	2.313		
Total coarse woody debris volume (snag plus fallen)								
Management history	1	72.326	36.03	0.001*	2	38.153	19.09	0.001*
Forest type	1	0.127	0.06	0.804				
Management history × forest type	1	4.330	2.16	0.157				
Error	21	2.007			19	1.999		

Table 1 (concluded).

Source of variation	Two-way ANOVA for old-growth and managed uneven-aged stands				One-way ANOVA for northern hardwood stands			
	df	Mean squares	F value	P > F	df	Mean squares	F value	P > F
Area covered by recent tip-up (pit plus mound)								
Management history	1	0.052	0.01	0.935	2	21.719	2.98	0.075
Forest type	1	15.428	2.01	0.171				
Management history $\times$ forest type	1	4.931	0.64	0.432				
Error	21	7.679			19	7.283		

*Statistically significant difference ($P < 0.05$).

old-growth stands and selection stands within each forest type. The other two comparisons involved even-aged versus old-growth northern hardwood stands and even-aged versus old-growth northern hardwood stands. Because there were no even-aged hemlock–hardwood stands, the four selection and old-growth combinations were compared in a two-way analysis of variance (ANOVA) testing for the effects of both forest type and management history (fixed effects model). This was followed by a comparison of the three northern hardwood management histories in a one-way ANOVA (Table 1). The four planned pairwise comparisons between means of different stand types were made only if the overall ANOVA indicated significant differences ($P < 0.05$). The individual pairwise comparisons were tested using Fisher's least significant difference method with a common estimate of experimental error (MSE). Statistical analyses were performed using the general linear models procedure in SAS (SAS Institute Inc. 1990). Some variables were transformed prior to ANOVA testing to correct for unequal variance among types and nonnormality. Density and volume values were square root transformed, while values for the percent area in pit and mound microtopography were arcsine square root transformed.

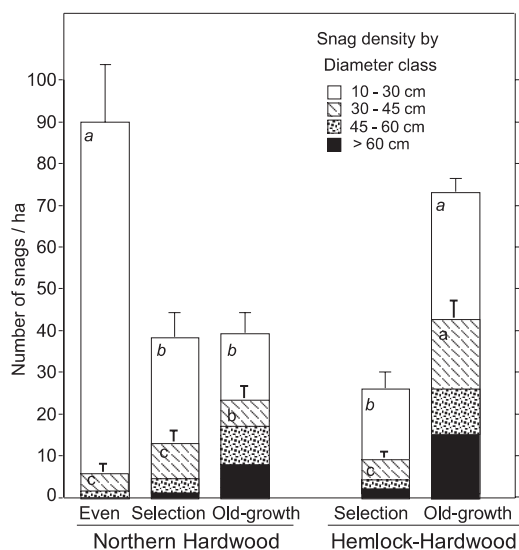
Prior to testing differences in means among the five forest type – management history combinations, two-way ANOVA was used to determine if the means are influenced by two site characteristics found to vary between study stands on the same forest habitat type: (i) fragipan (presence or absence) and (ii) location on the Winegar moraine (yes or no). Fragipan presence–absence was evenly split for all treatments except selection hemlock–hardwoods, in which no plots had a fragipan. Neither of these factors nor factor $\times$ stand type interactions were found to have a significant effect. For all coarse woody debris volume and density variables, the effect of blocking on these two factors resulted in P values that exceeded 0.44 in all cases except one (i.e., for fragipan effect on large fallen wood, $P = 0.13$). Consequently, all stands were grouped by the five forest type – management history combinations (i.e., no further blocking on fragipan or location) and analysis conducted as described above.

Results

Snag density and diameter distribution

For northern hardwoods, total snag density (>10 cm DBH) in selection stands was similar to the density measured in old-growth (Fig. 2). Snag density was significantly higher in even-aged stands, but composed primarily of small stems. Nearly three quarters of the snags in even-aged stands were from size classes smaller than the mean live tree diameter. In selection stands, snags were rather evenly distributed above and below the mean live tree diameter (Table 2). Snags in old-growth northern hardwoods had a wide diameter range, but 42% of the dead trees were >45 cm DBH, well above the mean live tree diameter. Combined medium (30–45 cm DBH) and large

Fig. 2. Density of snags by size class. Top error bars show 1 SE for all snags (>10 cm) and bottom error bars are for snags >30 cm DBH. Treatment means with the same letter are not significantly different at $P = 0.05$.



(>45 cm DBH) snags were significantly more numerous in old-growth than in selection or even-aged northern hardwood stands (Table 1). Selection stands averaged 12 medium and large snags/ha, just over half the level found in old-growth and approximately twice the number in even-aged stands (Fig. 2).

For hemlock–hardwoods, snag densities in old-growth were significantly higher than in selection stands for all size comparisons shown in Fig. 2. The density of large snags was more than five times greater in old-growth than in selection stands. Total snag density in old-growth hemlock–hardwood was higher than in old-growth northern hardwood, although the proportions of medium and large snags were similar in both. Yellow birch composed 65% of the large snags, nearly half of which were in recent decay classes (I and II). A majority of the large yellow birch trees present in the old-growth hemlock–hardwood stands were snags, possibly casualties of the 1988 drought (cf. Prey et al. 1988).

In old-growth stands of both forest types, dead trees >60 cm DBH constituted 20% of snag density. Snags of this size were absent from all even-aged plots and had low densities in the selection stands (Table 2). In 10 of the 15 selection stands sampled across both forest types, no snags >60 cm DBH

Table 2. Structural characteristics of live trees and snags by forest type and management history.

Characteristic*	Northern hardwood			Hemlock–hardwood	
	Even-aged	Selection	Old-growth	Selection	Old-growth
Total no. of snags sampled	162	115	71	39	88
No. of stands	6	10	6	5	4
Mean DBH (cm)					
Snags [†]	17.6 (12.3, 22.4)	26.8 (16.5, 32.0)	38.9 (18.7, 55.0)	26.0 (12.3, 36.8)	38.8 (21.9, 55.0)
Live trees	20.7	24.2	31.4	24.3	30.8
Density (stems/ha)					
Snags	90	38	39	26	73
Live trees	828	446	313	469	388
% dead trees of total	9.8	7.9	11.2	5.2	15.9
Large snags					
>45 cm DBH	1.7	4.3	16.7	4.0	25.8
>60 cm DBH	0	1.0	7.8	2.0	15.0
Basal area (m ² /ha)					
Snags	2.8	2.8	6.0	2.0	10.9
Live trees	32.3	25.5	34.4	28.0	37.5
% snag basal area of total	7.8	9.9	14.9	6.7	22.5
% of total snag density in each stage					
Snag fragmentation stage					
1. Crown intact	12	6	6	3	8
2. Large branches and bole	37	15	10	21	28
3. Bole only	23	28	27	23	14
4. Broken bole	28	51	58	54	50
% of total snag density in each decay class					
Snag decay class					
I. Sound	17	6	4	5	8
II. Slight decay	55	37	34	36	36
III. Moderate decay	25	52	58	56	53
IV. Advanced decay	2	4	4	3	2
Snags with loose bark plates					
Loose-barked snags/ha [‡]	3.3 (±2.1)	5.3 (±2.4)	3.3 (±1.7)	2.7 (±1.2)	10.0 (±5.6)
% snags with bark plates	3.7	13.9	8.5	10.3	13.6

*Includes trees >10 cm DBH only for both live tree and dead tree characteristics.

[†]First and third quartiles of the snag diameter range presented in parentheses.

[‡]Mean value followed by SE in parentheses.

occurred in the 0.3-ha study plot whereas at least one was present in all of the old-growth plots.

Snag height distribution and size diversity

Snag heights are reduced over time by progressive fragmentation (Tyrrell and Crow 1994b), altering the suitability of snags for nesting sites and perches. More than half of all snags in both selection and old-growth northern hardwoods had broken boles (fragmentation stage 4), skewing the height distribution toward the shorter height classes. Medium and large snags in these stands were likewise concentrated in shorter height classes (Fig. 3). While absolute densities of medium and large snags were significantly different in selection and old-growth northern hardwoods, these stands had similar proportions of shorter snags (1.5–4.5 m height class), 33 and 35%, respectively, and similar proportions throughout the height profile (Fig. 3). The frequency distributions of snags >30 cm among four 6-m height classes were not significantly different for selection and old-growth stands ($\chi^2 = 0.862$, $P = 0.834$, $df = 3$). In even-aged northern hardwoods, medium and large snags were more evenly distributed through the height profile, but no

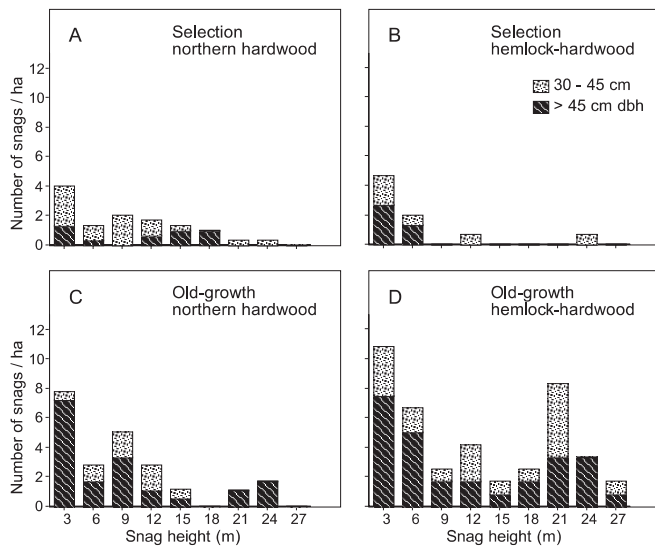
snags reached above the 18-m class. Snag size diversity (H'), based on four diameter classes and four height classes, was highest in old-growth ($H' = 1.049$), intermediate in managed uneven-aged ($H' = 0.830$), and lowest in even-aged ($H' = 0.704$).

In hemlock–hardwood selection stands, most snags were relatively short (<7.6 m tall; Fig. 3B). Height distribution in old-growth hemlock–hardwood was distinctly bimodal. Besides a concentration in the two shortest height classes, there was a second grouping in the 19.5- to 22.5-m height class. One third of all large snags, mostly yellow birch in early fragmentation stages, were >18 m tall. Snag size diversity was 30% lower in selection stands ($H' = 0.749$) than in old-growth ($H' = 1.071$). Index values were similar to those for snags in corresponding treatments in northern hardwoods.

Snag fragmentation stage and decay class distributions

Fragmentation and decay class categories were not independent (e.g., almost all fragmentation stage 1 snags were decay class I). The large proportion of broken bole snags (fragmentation stage 4) in both selection and old-growth

Fig. 3. Height distribution of medium and large snags for uneven-aged and old-growth stands. Numbers on the y-axis refer to the midpoint of 3-m height classes.



stands resulted primarily from advancing decay in older snags, as opposed to wind or mechanical breakage of recently formed snags. In every stand type, >75% of these broken bole snags were in advanced decay class III or IV.

In northern hardwood selection stands, approximately 43% of all snags were recent (i.e., decay classes I or II), while 56% of snags were in advanced decay class III or IV. Similar decay class distributions were found in old-growth northern hardwoods, as well as in both selection and old-growth hemlock-hardwoods (Table 2). Even-aged stands, in contrast, had a considerably greater percentage of snags (73%) in early decay classes I and II.

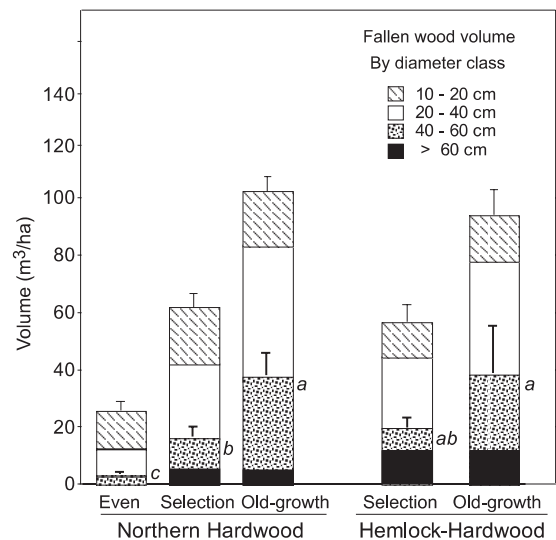
Mean density of snags with loose bark plates ranged from 3 to 10/ha for the five forest type – management history combinations, with highest values in old-growth hemlock-hardwood (Table 2). The proportion of snags with loose bark plates was <15% in all stand types. No significant effects were detected for either management history or forest type (Table 1). Density of loose-barked snags appeared related to tree size and species composition in that they were more common on medium and large snags (22%) than on small snags (4%). Thirty-eight percent of yellow birch snags >30 cm had loose bark plates, and these accounted for over half the total loose-barked snags of this size.

Cavity tree density

Of the 2791 live trees and snags (>10 cm DBH) examined in all stands, 67 contained cavities. Although only 15% of these cavities were in snags, the proportion of stems with cavities was nearly twice as high for snags (3.9%) as for live trees (2.2%). That is, cavities were more common in live trees only because live trees themselves are so much more abundant than snags. More than 70% of the bird-excavated cavities in northern hardwood stands were located in snags or dead portions of live trees. Cavities resulting from natural wounds were more common than those excavated by birds (Table 3).

Estimated cavity tree density in selection stands of both forest types was 50–70% of the density in old-growth (Table 3).

Fig. 4. Size distribution of fallen coarse woody debris volume showing a positive trend for both total volume of fallen debris and volume of large-diameter (>40 cm) fallen debris. Error bars show 1 SE for mean volume of large-diameter debris. Treatment means with the same letter are not significantly different at $P = 0.05$.



These differences were not statistically significant, however, because of great variability among plots (Table 1). Large trees (>45 cm DBH) containing cavities were present at a mean density of 11/ha in old-growth stands (both forest types combined) compared with 5/ha in selection stands (Table 3).

Cavity presence was clearly related to tree size. Mean diameters for live cavity trees were 73–104% larger than the overall mean live diameter for the stand type. The proportion of live trees with cavities was consistently greater for larger trees across all five forest type – management history combinations (Table 3). Old-growth stands had the highest proportion of all live trees (>10 cm) with cavities, but in large-diameter live trees the proportion with cavities was similar among selection and old-growth stands.

Snag volume

Mean snag volume in northern hardwood selection stands was very similar to levels in even-aged stands, but just over half the snag volume in old-growth stands (Table 4). More than 75% of standing snag volume in even-aged northern hardwoods was concentrated in trees <30 cm DBH. In contrast, over half of the snag volume in selection stands and over three quarters of the snag volume in old growth were from snags >45 cm DBH, which will eventually contribute to the pool of large-diameter fallen wood.

In old-growth hemlock-hardwoods, mean snag volume was greater than twice the level in northern hardwood old-growth, and standing snags accounted for 38% of total coarse woody debris volume (Table 4). Most of the snag volume in old-growth was yellow birch in early decay classes.

Volume and size distribution of fallen wood

Mean total volume of fallen wood (i.e., fallen boles, branches, stumps, or tops) in northern hardwood selection stands was about double the volume measured in even-aged, but only 60% of volume in old-growth (Fig. 4). These differences were

Table 3. Density and characteristics of trees with nesting cavities in stands of different forest type and management history.

Characteristic	Northern hardwood			Hemlock–hardwood	
	Even-aged	Selection	Old-growth	Selection	Old-growth
No. of trees searched	633	800	512	467	379
No. of cavities found	7	20	22	7	11
Cavity tree density (no./ha)					
Total (>10 cm DBH)*	10.8 (± 3.3)	12.5 (± 2.5)	18.1 (± 4.9)	7.0 (± 1.2)	13.8 (± 4.3)
>45 cm DBH	0.0	5.2	11.4	5.0	8.8
>60 cm DBH	0.0	0.6	3.1	1.0	2.5
Mean DBH (cm)					
Live cavity trees	27.6	44.8	54.3	49.5	56.2
Snag cavity trees	23.1	50.7	31.2	25.0	36.2
% of total trees searched containing cavities					
Cavities in live trees					
Live >10 cm DBH	0.9	2.1	4.5	1.3	3.0
Live >30 cm DBH	3.6	5.5	9.0	4.8	6.7
Live >45 cm DBH	0.0	13.0	12.3	14.7	11.5
Cavities in dead snags					
Snags >10 cm DBH	3.8	6.5	3.4	3.9	2.1
Snags >30 cm DBH	0.0	16.7	3.1	0.0	4.4
Distribution of located cavities (% of total cavities)					
Live–dead status					
Live trees	71	79	91	86	91
Dead snags	29	21	9	14	9
Cavity opening size class					
0–5 cm	71	70	50	43	46
5–10 cm	29	30	36	43	46
10–25 cm	0	0	14	14	9
Origin of cavity opening					
Natural wound	57	70	77	86	64
Bird excavated	43	30	23	14	36
Cavity location in tree					
Lower bole	43	65	36	29	45
Upper bole	14	5	36	29	45
Live branch	0	5	9	29	0
Dead branch	43	15	18	14	9
Dead top	0	10	0	0	0
Additional habitat features					
Density (no./ha)					
Escape cavities [†]	24.3	15.6	23.6	8.0	18.7
Den trees (>45 cm DBH)	0.0	1.3	5.0	0.0	3.8

*Mean value for treatment followed by SE in parentheses.

[†]Includes cavities not meeting the criteria for nesting cavities as outlined in the Methods section.

statistically significant (Table 1). Large-diameter fragments (>40 cm) made up approximately 25% of total fallen wood volume in selection stands, averaging 16 m³/ha. The volume of large-diameter material was significantly higher in old-growth northern hardwoods and contributed over 35% of the total fallen wood volume in these stands (Fig. 4). In the even-aged stands, large-diameter debris made up only 5% of the total fallen wood volume. Similar trends in total and large-diameter fallen wood volumes were found in hemlock–hardwood stands.

Decay class distribution of fallen wood

In addition to greater total volumes of fallen wood, old-growth stands generally had greater volumes across all decay classes relative to selection stands. In northern hardwood selection

stands, volume of large-diameter (>40 cm), advanced decay (classes III–V) fallen wood was 11 m³/ha, half the volume present in old-growth stands, but substantially higher than the 2 m³/ha in even-aged stands. In hemlock–hardwoods, volume of large, advanced decay fallen wood in selection stands was 13 m³/ha compared to 29 m³/ha in old-growth.

Despite large volume differences among northern hardwood stand types, distributions of fallen wood among decay classes were similar (Table 4). Using three separate ANOVA tests, no significant differences were detected among stand types in the proportion of volume in each of three decay class groupings (I and II: $P = 0.57$, $MSE = 179.9$, $df = 4, 26$; III: $P = 0.83$, $MSE = 59.8$, $df = 4, 26$; IV and V: $P = 0.63$, $MSE = 147.1$, $df = 4, 26$).

Table 4. Distribution of fallen wood volume by size class, decay class, and origin for different stand types, and contribution of fallen wood and snags to the total coarse woody debris.

	Northern hardwood			Hemlock–hardwood	
	Even-aged	Selection	Old-growth	Selection	Old-growth
Decay class of fallen wood (% of volume)					
I	1	2	7	0.4	1
II	19	17	20	24	10
III	52	56	55	49	54
IV	25	21	16	24	19
V	3	4	2	3	16
Origin of fallen wood (% of volume)					
Fallen logs	82	41	81	22	73
Stumps (natural)	3	2	2	1	10
Stumps (cut)	3	11	0	28	0
Fallen branches	9	8	17	4	17
Harvest tops	3	38	0	45	0
Fallen wood volume (m ³ /ha)*					
Mean	24.6c	61.3b	102.2a	56.0b	93.9a
SE	±4.1	±6.3	±6.4	±7.1	±10.6
Snag volume (m ³ /ha)*					
Mean	14.6bc	13.1bc	25.4b	5.2c	57.5a
SE	±3.0	±3.7	±7.1	±1.1	±11.5
Total coarse woody debris volume (m ³ /ha)*					
Mean	39.2c	74.4b	126.9a	61.1b	151.4a
SE	±5.8	±8.6	±12.3	±7.2	±18.1
Mass of coarse woody debris (Mg/ha)					
Fallen wood mass	6.0	14.9	28.7	13.9	20.3
Snag mass	5.5	3.8	7.7	1.5	19.8
Total mass coarse woody debris	11.5	18.7	36.4	15.4	40.1
No. of stands sampled	6	10	6	5	4

*Treatment means followed by the same letter are not significantly different at $P = 0.05$ (protected least significant difference).

Origin of fallen wood

Harvest tops and discarded (unmerchantable) portions of boles contributed much of the fallen wood volume in northern hardwood selection stands, with additional amounts from fallen trees and cut stumps (Table 4). In old-growth and even-aged northern hardwood stands, fallen boles accounted for more than 80% of the fallen volume.

Cut stumps constituted a larger proportion of the total fallen debris volume in hemlock–hardwood selection stands compared with northern hardwood selection stands. This difference was even more dramatic for large-diameter fallen wood, which in northern hardwood selection stands came primarily from logs. In hemlock–hardwood selection stands, 72% of large-diameter fallen wood volume was from cut stumps, nearly half of which was hemlock.

Recent tip-up mounds and pits

There were no statistically significant differences detected among treatments for percentage of stand area in recent pit and mound microtopography. Values were <1% of plot area in all five forest type – management history combinations. Among northern hardwood stand types, the percent area in pits and mounds was highest in selection stands, averaging 0.8% area from a density of 28 tree falls/ha. Some of the tip-ups in selection stands were caused by the felling of neighboring trees. Even-aged stands had the least area in pits and mounds (0.1%)

from an average of 7 tree falls/ha. Recent tip-up mounds and pits in old-growth covered 0.6% of the area in northern hardwood and 0.4% in hemlock–hardwood stands.

Discussion

Since the early 1980s, efforts have been made to incorporate retention of snags and cavity trees into silvicultural treatments on many public forests. Selection (i.e., managed uneven-aged) stands in the present study exceeded the minimum target density (5–10/ha) for snags >30 cm recommended in local U.S. Forest Service guidelines (Evans and Conner 1979; De-Graaf and Shigo 1985). The mean levels of large snags, fallen wood, and cavity trees in these selection stands were generally intermediate between those measured in unmanaged even-aged and in old-growth stands. Snag densities (>10 cm DBH) in our selection stands were more than double those found by McComb and Noble (1980) in a managed uneven-aged hemlock–hardwood stand in Connecticut. Likewise, large-diameter fallen wood (>40 cm) was much more abundant in our selection stands than in the managed uneven-aged northern hardwood stand in New Hampshire sampled by Gore and Patterson (1986), which had no fallen stems >38 cm. The volume of debris >40 cm in diameter constituted over 28% of total fallen wood volume in our selection stands, owing to input from discarded portions of the lower bole, fallen snags, and stumps. Total and large-diameter fallen wood volumes in selection

stands were significantly greater than those accumulated in the unmanaged second-growth stands of this study, and also exceeded levels reported for unmanaged mature (65–89 years old) and old (>100 years old) mixed mesophytic stands in Maryland (McCarthy and Bailey 1994).

Our estimates of fallen wood volume and mass for even-aged and old-growth northern hardwoods were within the range reported elsewhere for northern hardwood stands of comparable age (Tritton 1980; Gore and Patterson 1986; McCarthy and Bailey 1994). Likewise, the total coarse woody debris volume (i.e., snags and fallen wood) measured in our old-growth hemlock–hardwood stands approximated levels reported by Tyrrell and Crow (1994a) for their older hemlock stands containing trees >300 years old. Differences in coarse woody debris attributable to increasing stand age in our unmanaged stands matched trends reported for other eastern forests, including an increase in mean snag diameter and large snag density (Rosenberg et al. 1988; Tyrrell and Crow 1994a), an increase in the diameter and total amount of fallen debris (Tritton 1980; Gore and Patterson 1986; McCarthy and Bailey 1994), and a decrease in total snag density (McComb and Muller 1983; Carey 1983; Rosenberg et al. 1988). And as has been reported in other eastern deciduous forests, we found that nesting cavities were positively correlated with increasing tree diameter and that a large percentage of all cavities found were in live trees (Carey 1983; Healy et al. 1989; Welsh and Capen 1992).

Differences in coarse woody debris levels between selection and old-growth stands were most pronounced for large stems. Large-diameter snags and fallen boles have received particular attention in wildlife management guidelines (Thomas et al. 1979; DeGraaf and Shigo 1985; Tubbs et al. 1987) because they are preferentially selected by large-bodied species such as raccoon (*Procyon lotor*), fisher (*Martes pennanti*), marten (*Martes americana*), and pileated woodpecker (*Dryocopus pileatus*). For instance, all marten dens (natal and maternal) observed by Wynne and Sherburne (1984) in northwestern Maine were in large logs or trees >40 cm DBH, and the average size of nest trees selected by pileated woodpeckers is approximately 55 cm DBH (Evans and Conner 1979). Recommended densities of large-diameter (>45 cm DBH) cavity or den trees required to meet the needs of all cavity nesting species range from 0.35 to 2.5 trees/ha (summarized in Table 2 of Tubbs et al. 1987). Densities of large-diameter snags and cavity trees both exceeded 4/ha in our managed uneven-aged stands, although these values were only 21 and 50%, respectively, of the large snag and cavity tree densities that we measured in old-growth.

While low amounts of coarse woody debris can be limiting to wildlife populations (Haapanen 1965; Newton 1994; Carey and Johnson 1995), it is presently unclear whether population densities continue to increase along with coarse woody debris abundance beyond some moderate level of coarse woody debris availability (Raphael and White 1984). Certainly, other factors besides available habitat structure can influence population densities (e.g., territory size requirements, winter habitat, predator population levels). Raphael and White (1984) found that the density of all cavity nesting birds in the Sierra Nevada increased with the density of large snags (>38 cm DBH) until reaching a snag density of about 7.5/ha. Above this snag density level, bird densities were evidently limited by other factors. Maximum density of large snags reached similar

levels of 6.7 snags/ha (>38 cm DBH) in our selection stands. However, bird survey data collected by other research project members in our study sites suggest that at these snag levels in the Lake States, population densities of cavity nesting birds may still be limited by available coarse woody debris habitat (Howe and Mossman 1996). Pileated woodpeckers and chimney swifts (*Chaetura pelagica*), two species that prefer snags >50 cm DBH (Evans and Conner 1979), were both significantly more abundant in old-growth than in selection stands (R.W. Howe and M. Mossman, Avian Productivity Study Progress Report, 1997). For eight other bird species generally associated with coarse woody debris (including woodpeckers, brown creeper, and others), trends in the average number of breeding pairs observed appear to be positively correlated with coarse woody debris availability. For instance, the average number of winter wren pairs (*Troglodytes troglodytes*) in old-growth northern hardwood stands was over two times greater than in selection stands and eight times greater than in even-aged stands (Howe and Mossman 1996). For six of the eight species, the number of breeding pairs was at least 30% higher in old-growth northern hardwood than in selection stands. For five of these species, breeding pair numbers were at least 25% higher in selection than in even-aged stands (>85% higher for four of eight species).

The reason for fewer large snags in selection stands compared with old-growth is not simply that trees are not allowed to reach large size. Dahir and Lorimer (1996) found that the average size of canopy trees at the time of death in old-growth northern hardwoods was 51 cm DBH, which is somewhat smaller than the maximum tree size of 60 cm DBH retained in most managed uneven-aged stands. However, active management generally attempts to reduce senescence-related mortality of large canopy trees through the selective retention of vigorous trees. Short intervals between harvests enable efficient salvage of any low-vigor trees from a variety of size classes before or shortly after death. In addition, mortality of 30–50 cm DBH trees is lower in unmanaged mature stands than for the same size classes in old-growth stands (Dahir 1994), partly because of less competition from larger trees. Thus, among large trees, the rate of snag formation appears to be lower in mature stands even without the intervention of management practices.

Because of the short time interval between cutting cycles in uneven-aged stands, managers have the opportunity to reassess and modify the dead wood structure each time the stand is marked for selection harvest. It appears that efforts to identify and retain wildlife trees during timber marking in managed uneven-aged stands may lead to snag and cavity tree abundances above the target levels currently recommended by regional U.S. Forest Service biologists. If it becomes a management objective to increase the density of large-diameter coarse woody debris in uneven-aged stands, this could be similarly accomplished by allowing designated reserve trees to live out their natural life-spans. This approach would provide additional cavity trees, future snags, and subsequent large fallen logs without requiring longer rotation ages for all trees in the stand.

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