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Characteristics of Coarse Woody Debris in Northern Michigan Forests

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INTRODUCTION

Forest management has increasingly focused on maintaining biodiversity and sustainability. Coarse woody debris (CWD) on the forest floor is a large contributor to biodiversity within Michigan forests. Coarse woody debris influences forest soil nutrient cycling (Fisk et al. 2002) and provides a suitable seed bed for hemlock regeneration (Ward and McCormick 1982, Godman and Lancaster 1990, O'Hanlon-Manners and Kotanen 2004). Due to its influence on forest structure at the ground, understory, and overstory levels, CWD is an essential component of mammal, bird, amphibian, arthropod, and microbial habitats (Harmon 1986, Bull et al. 1997, Burris and Haney 2005, Crow et al. 2002). Large-diameter CWD and tip-up mounds created by natural disturbances are a crucial structural component for forest biodiversity and are largely missing from managed landscapes (Goodburn and Lorimer 1998, Tyrell et al. 1998, McGee et al. 1999, Crow et al. 2002).

Although some research has been conducted in northern hardwood forests of the Great Lakes region to examine levels of CWD in old-growth stands (Tyrrell and Crow 1994) and to compare old-growth and managed stands (Goodburn and Lorimer 1998, Hale et al. 1999, McGee et al. 1999), information on CWD remains limited for the region. The Michigan Natural Features Inventory (MNFI) estimated levels of CWD in northern Michigan forests as part of a study to evaluate methods of sampling CWD (see Monfils et al. 2009). However, more study is needed to assess the range of variation of CWD parameters in managed and unmanaged forests of the region, especially with regard to levels of CWD within various decay and size classes. Because changes to CWD levels within decay and size classes over time could affect ecosystem functioning, it is important to determine if current management practices are influencing CWD patterns in Michigan forests. Hagan and Grove (1999) suggested that to determine how much

coarse woody debris is enough in managed forests, several questions need to be answered: 1) What is the natural range of CWD in our forests types? 2) How do managed stands compare with natural regimes of CWD? and 3) Are silvicultural methods diminishing the amounts of CWD over time? To evaluate forest management practices and assist decision making, we compared levels of CWD within decay and size classes among three forest types in northern Michigan: managed aspen, managed northern hardwood, and unmanaged northern hardwood. We estimated levels of CWD in the three forest types across a range of age classes and management histories.

STUDY AREA

We examined CWD in publicly owned forests of the northern Lower and Upper Peninsulas of Michigan (Figure 1). Study sites were located predominantly on mid- to coarse-textured glacial till, lacustrine sand and gravel, or outwash sand and gravel. We sampled three forest stand types: managed aspen, managed northern hardwood, and unmanaged northern hardwood. We used mesic northern forest element occurrences (EOs) documented by the MNFI for our unmanaged northern hardwood stands. Managed aspen and northern hardwood stands had undergone regular timber management, while unmanaged northern hardwoods showed little or no evidence of cutting within the last 200 yrs and were representative of old-growth conditions. Managed aspen and northern hardwood stands were located on State forest land and selected randomly from Michigan Department of Natural Resources (MDNR) Operations Inventory (OI) frozen stand GIS data layers (MDNR 2004, 2005). Aspen stands were randomly selected from four age classes: 20-25, 40-45, 60-65, and 80+ years. Aspen age was determined by the “year of origin” in OI records, which indicated when the stand was last harvested.

Randomly selected northern hardwood stands were all uneven aged and had been selectively thinned. Mesic northern forest EOs were selected from high ranking (i.e., A, B, or AB ranks) occurrences recorded within the MNFI database and were located on State forest, State park, and federally owned lands. A ranking of "AB" or higher indicates that the stand is of old-growth quality and shows minimal signs of silvicultural management.

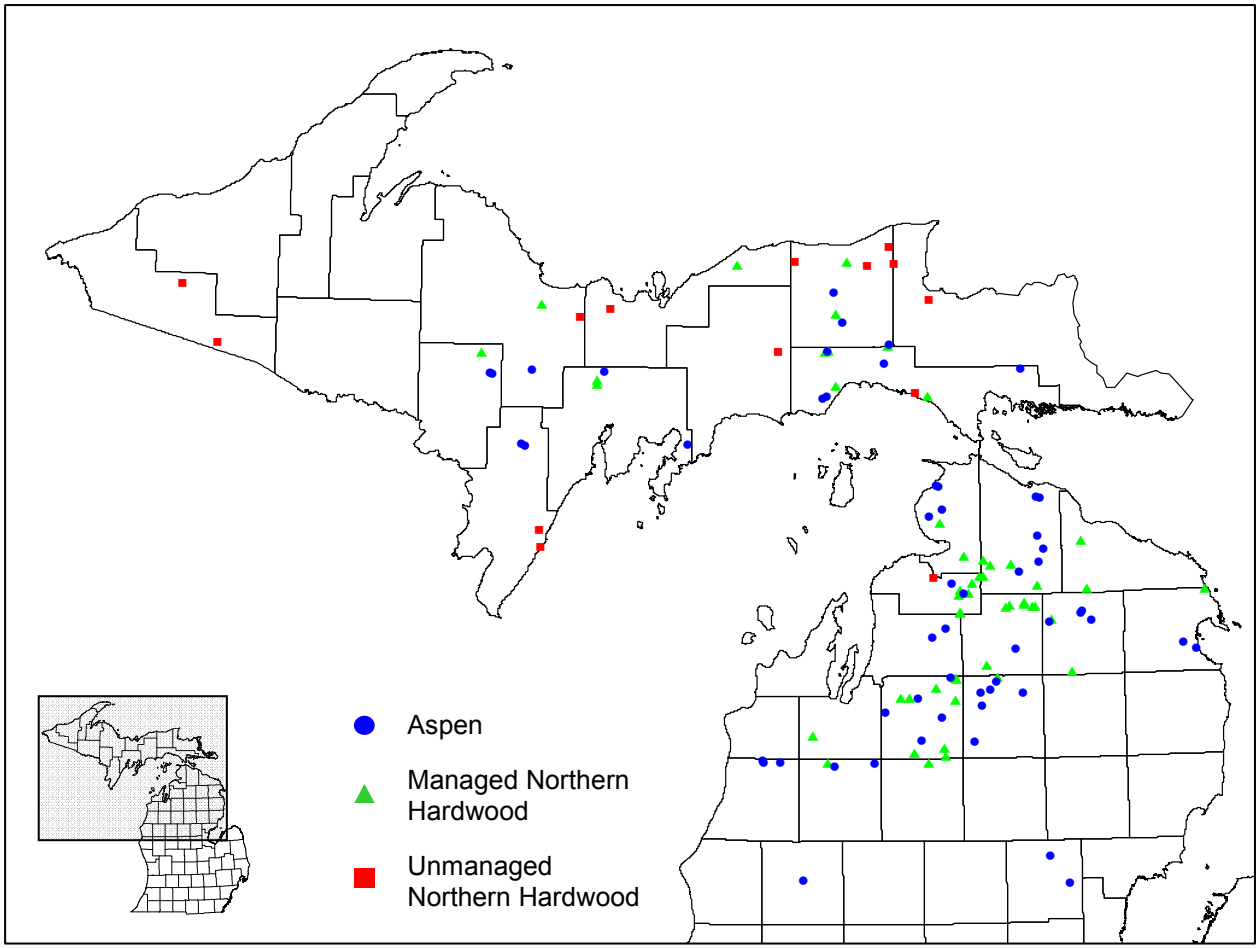

Figure 1. Locations of aspen, managed northern hardwood, and unmanaged northern hardwood stands sampled for coarse woody debris in northern Michigan during 2005-2007.

In 2005, the initial year of the study, we collected data from 20 aspen and 32 managed northern hardwood stands, but unmanaged northern hardwood stands were not sampled. All three forest types were sampled in 2006 and 2007, with an additional 37 aspen, 19 managed northern hardwood, and 14 unmanaged northern hardwood (i.e., mesic northern forest EO) stands. Thus, from 2005 to 2007 we sampled 57 aspen, 51 managed northern hardwood, and 14 unmanaged northern hardwood stands.

METHODS

Field Sampling

We defined CWD as a log or downed tree of at least 10 cm in diameter, 1 m in length, and with at least two points of ground contact or a minimum of 50 cm of ground contact anywhere along its length. Pieces originating from the same fallen tree were counted separately if they were more than 30 cm apart. Branches or boles of the same tree that met the size criteria were considered individual pieces of CWD. Logs lying at angles ≤ 45 degrees from the ground surface were considered CWD, while logs lying at angles >45 degrees were classified as snags. Stumps with diameters of at least 10 cm at the base (excluding buttress) and heights between 1 m and 1.8 m were considered CWD, whereas those greater than 1.8 m were considered snags.

We used both line intercept (De Vries 1973) and strip plot (Husch et al. 1972) sampling methods. Bate et al. (2004) found that the line-intercept and strip-plot methods can perform differently depending on stand characteristics. We implemented each method using two approaches to locate sample transects or strip-plots: 1) at systematically placed locations along a predetermined circuit route that meandered through a stand (circuit sampling), and 2) at random locations on transects that ran perpendicular to a base-line transect (random sampling). Given

two methods (line intercept and strip plot) and two sampling approaches (circuit and random), we applied four methods in the field: 1) circuit line-intercept (CLI), 2) circuit strip-plot (CSP), 3) random line-intercept (RLI), and 4) random strip-plot (RSP).

Circuit sampling points were placed systematically at equidistant intervals, beginning with a random starting point, along a pre-determined route drawn within the stand. The number of sampling points per stand depended on the size of the stand, but no more than 14 plots were allowed per stand. Random sampling points were laid out along parallel transects equidistantly spaced at a random interval along a baseline transect. Sampling points were located at random distances from the starting points of each transect. The same quantity of sampling points was used for both the random and circuit methods in a given stand.

At each line-intercept sample station, we used a measuring tape to make a straight 20 m (one chain, or 66 ft) transect. We tallied pieces of CWD that intersected a plane stretching from ground to sky along each transect. When a piece intersected the transect, we measured the following: large end diameter (LED), ignoring the buttress of the log/stump; small end diameter (SED); diameter where the intercept line crosses the log (intersect diameter); and total length. We measured total length from the large end to the small end or where the diameter reached 1 cm.

We situated strip plots at the same sample stations used for line-intercept methods. Strip plots were 4.3 m (14 ft) wide, 20 m in length, and centered along the same transect lines used for the line-intercept methods. We measured a piece of CWD if at least 50 cm of the log was located within the plot and we recorded whether or not the midpoint of the log was located within the plot to estimate density. We collected the same measurements described above for line-intercept sampling, plus the diameters of CWD at plot intercepts for pieces that crossed plot

boundaries and the length of each CWD piece within the plot. Length within plot and total length were the same if the entire piece fell within plot boundaries.

Diameter was measured by holding a measuring tape above the log at a position perpendicular to the length. If logs were not round, as in the case of extensive decay, then the diameter was estimated from the widest portion visible. Every piece of CWD was assigned a decomposition class rank from 1 (recent or least decomposed, leaves present, round in shape, bark intact, wood structure sound, and current year twigs present) to 5 (very decayed, leaves absent, branches absent, bark detached or absent, wood not solid, and oval or collapsed in form) according to Tyrell and Crow (1994). See Monfils et al. (2009; Appendix A) for further description of decay classes.

We identified snags to be sampled differently for line-intercept and strip-plot methods. We conducted a 10-factor prism sweep at the beginning of each transect to locate snags during line-intercept sampling. During strip-plot sampling, we measured any snag that had their center or pith located within the plot. We measured the diameter at breast height (DBH) and estimated the approximate height for all snags determined to be within the prism sweeps or plot boundaries. Snag height was estimated visually and we assigned each snag a rank of 1-5, with each number representing a 5-m height increment.

In 2006 and 2007 we used prism sweeps conducted at circuit line-intercept sample stations to characterize the dominant overstory composition of the three forest stand types. The species of each tree considered within each prism sweep was recorded. We used these data to estimate the frequency of occurrence for dominant overstory species and total living basal area by stand type.

Parameter Estimates

We estimated the density, total length, and volume of CWD according to the calculations of De Vries (1973) and Bate et al. (2004). We estimated density for the line-intercept methods following De Vries (1973):

$$\text{Density (logs per ha)} = (5\pi \times 10^3 / L) \sum^{n} (1 / l_i)$$

where L is the transect length (20 m), n the number of CWD pieces intersected, and l the length (m) of the ith log intersected. To estimate density for the strip-plot methods, we took the total number of logs having a midpoint within the plot and converted to logs per ha.

We calculated total length of CWD for line-intercept methods using the following equation from De Vries (1973):

$$\text{Total length (m)} = n\pi \times 10^4 / 2L$$

For strip-plot methods, we estimated total length by first summing the total length (m) of all portions of CWD pieces that fell within the plot and then converting to total length per ha.

We estimated CWD volume for line-intercept methods following De Vries (1973):

$$\text{Volume (m}^3\text{/ha)} = (\pi^2 / 8L) \sum^{n} d_i^2$$

where d is the diameter (cm) of each log. During strip-plot sampling, we treated each CWD piece or portion of a piece as a cylinder or frustum to calculate volume. The volumes of all the logs that fell within a plot were summed and then converted to m^3/ha.

Because prism sweeps do not produce unbiased density or mean DBH estimates, snag density and average DBH were only estimated using data from strip-plot sampling. We determined snag density using the same method described above for CWD density. Mean DBH was estimated by averaging the DBHs of all snags that fell within each plot. We estimated snag basal area for line-intercept methods using data from 10-factor prism sweeps. The number of snags falling within in each sweep was multiplied by 10 to produce an estimate of basal area in ft^2/acre, which was then converted to m^2/ha. We used the same process to estimate total live basal area for the three forest stand types. For strip-plot samples, we estimated snag basal area using the following equation:

$$\text{Snag basal area } (m^2/\text{ha}) = \sum^{n} \pi \, (d_i / 200)^2$$

where d is the DBH of the ith snag.

Statistical Analyses

We used mixed models (MIXED procedure, SAS Institute 2004) to compare estimates of CWD, snag, and basal area parameters among forest types. Because the four sampling methods provided similar results among the three forest types (Monfils et al. 2009), we used data from all four methods when comparing CWD parameters among stand types to maximize the number of samples in our analyses. All plot- and transect-level data were averaged by site (i.e., forest

stand) prior to analysis. We used a mixed model containing method (CSP, CLI, RSP, and RLI), forest type (aspen, managed northern hardwood, and unmanaged northern hardwood), and method*stand type interaction as fixed effects, and sample site (i.e., forest stand) as a random effect, to compare CWD variables among stand types. We compared the following dependent variables: density, length, and volume of CWD; snag density, DBH, and basal area; and total basal area of living trees. We also compared the density, length, and volume of CWD within each of the five decomposition classes described above and three size classes (10-25 cm, 26-50 cm, and >50 cm). Size class was determined using the LED of each CWD piece as recommended by Bate et al. (2009). When variables had residuals that were not normally distributed, we used square-root and log (natural) data transformations (Zar 1996). We square-root transformed CWD density and length and snag density and DBH, and log transformed CWD volume and snag basal area. Comparisons of least squares means between pairs of forest types were conducted using the PDIFF option of the LSMEANS statement (SAS Institute 2004).

RESULTS

Overall Stand Type Characteristics

Prism sweeps indicated that aspen stands were dominated by trembling aspen (*Populus tremuloides*) and/or bigtooth aspen (*Populus grandidentata*) clones that had regenerated from stump sprout and root suckers following past harvests (Figure 2). Sugar maple (*Acer saccharum*) was the second most common species observed in aspen stands. Red maple (*Acer rubrum*), balsam fir (*Abies balamea*), and white birch (*Betula papyrifera*) were also regularly observed in aspen stands, but each species made up <10% of the trees sampled. Sugar maple was the dominant tree species in both managed and unmanaged northern hardwood stands

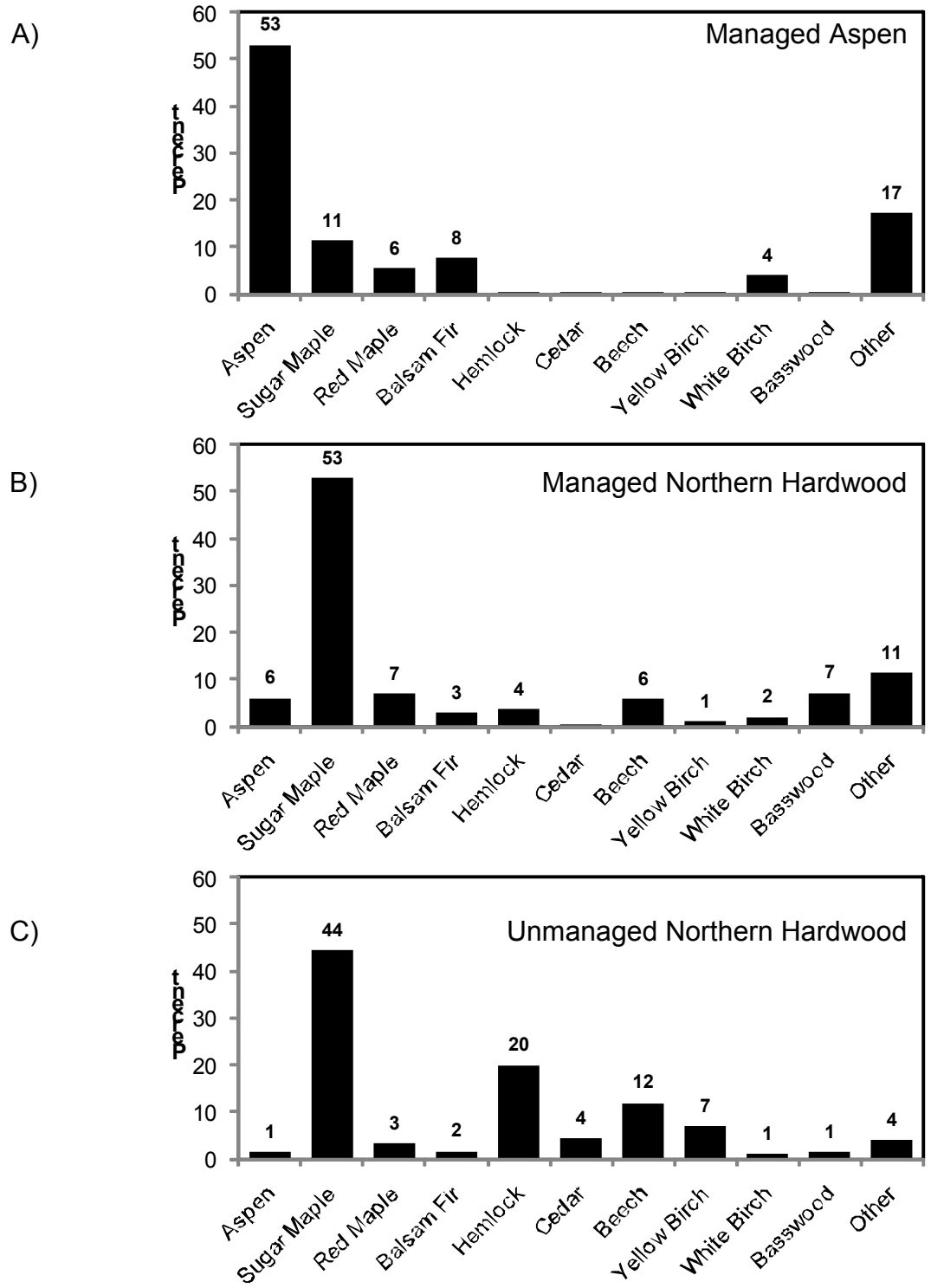

Figure 2. Composition of dominant overstory tree species in A) managed aspen, B) managed northern hardwood, and C) unmanaged northern hardwood stands sampled in Michigan during 2006-2007. Percentages are based on mean frequency of occurrence during basal area sweeps conducted at CLI transects. Species in the "other" category each represented ≤3% of all trees sampled.

(Figure 2). Although red maple, American basswood (*Tilia americana*), American beech (*Fagus grandifolia*), aspen, and eastern hemlock (*Tsuga canadensis*) were also observed in managed northern hardwoods, they each represented <10% of the trees sampled. Other species recorded sporadically in managed northern hardwood stands included balsam fir, white birch, and yellow birch (*Betula alleghaniensis*). When compared to managed northern hardwood stands, unmanaged northern hardwoods were characterized by lower frequencies of sugar maple, red maple, American basswood, and aspen, and greater frequencies of eastern hemlock, American beech, yellow birch, and northern white cedar (*Thuja occidentalis*) (Figure 2).

Most of the CWD and snag variables we compared differed between managed and unmanaged forest types (Table 1). In pair-wise comparisons, estimates for managed aspen and northern hardwood stand types tended to be similar, but were typically lower than unmanaged northern hardwood forest. Coarse woody debris density was similar among the stand types ($F=2.33$, $df=119$, $p=0.1014$), but average CWD length ($F=7.92$, $df=119$, $p=0.0006$) and volume ($F=23.83$, $df=119$, $p<0.0001$) differed by forest type. Mean length for unmanaged northern hardwoods was more than two times greater than estimates from managed aspen and northern hardwood stands. Average CWD volumes from unmanaged northern hardwood stands were more than seven times greater than estimates from managed aspen and northern hardwood forests.

Although snag density was similar among the three forest types ($F=0.13$, $df=119$, $p=0.8754$), snag DBH ($F=31.40$, $df=99$, $p<0.0001$) and basal area ($F=18.90$, $df=119$, $p<0.0001$) differed. Average snag DBH for unmanaged northern hardwoods was about 70-100% greater than estimates from managed aspen and northern hardwood stands. Mean snag basal area of unmanaged northern hardwoods was more than three times greater than estimates for managed

forest types. Average total live tree basal area also differed among the three stand types (F=22.37, df=66, p<0.0001), with the greatest estimate from unmanaged northern hardwood and lowest in managed aspen (Table 1).

Table 1. Least squares mean and lower and upper 95% confidence limit (LCL and UCL) estimates for coarse woody debris, snag, and basal area parameters in northern Michigan forests during 2005-2007. Bolded p-values indicate significant differences among forest types (p<0.05). Means followed by the same letter were not significantly different (p>0.05).

	Managed Forest Types						Unmanaged N. Hardwood (n=14)			
	Aspen (n=57)			N. Hardwood (n=51)						
Parameter	Mean	LCL	UCL	Mean	LCL	UCL	Mean	LCL	UCL	P value
Coarse Woody Debris										
Density (logs/ha)	101.7	78.2	128.3	100.3	75.1	129.1	167.9	109.3	239.0	0.1014
Length (m/ha)	517.4 A	399.9	649.9	530.2 A	402.4	675.7	1205.2 B	851.2	1620.6	**0.0006**
Volume (m^3/ha)	8.2 A	6.1	10.9	9.3 A	6.8	12.6	65.4 B	38.4	110.7	**<0.0001**
Snag										
Density (snags/ha)[1]	26.8	18.6	36.4	29.3	19.0	41.7	31.6	15.5	53.2	0.8754
DBH (cm)[1]	17.8 A	16.1	19.6	19.9 A	17.6	22.4	35.8 B	30.4	42.2	**<0.0001**
Basal Area (m^2/ha)	0.9 A	0.7	1.2	1.0 A	0.7	1.3	3.3 B	2.4	4.5	**<0.0001**
Live Tree										
Basal Area (m^2/ha)[2]	15.3 A	13.4	17.1	21.3 B	18.7	23.8	26.6 C	23.6	29.6	**<0.0001**

[1] Estimates produced using CSP and RSP methods only.
[2] Estimates produced using CLI method from 2006 and 2007 only.

Decomposition Class Comparisons

In unmanaged northern hardwood stands, mean estimates of CWD density, length, and volume were greatest in decomposition class 4, whereas in managed stands estimates peaked in decay class number 3 (Figure 3). Coarse woody debris density, length, and volume estimates from the individual decay classes generally differed by forest type, with means from managed aspen and northern hardwood stands typically being similar and lower than unmanaged northern hardwood forest (Table 2). Density was similar among forest types for decomposition classes 1 and 3, but estimates for the other decay classes were at least 2-3 times greater in unmanaged northern hardwood forest stands. Average total CWD length differed by stand type within all but decomposition class 3, and mean length estimates in unmanaged northern hardwood were about 3-5 times greater than those of managed forest types, depending on decay class. Coarse woody debris volume was significantly greater in unmanaged northern hardwood forest compared to managed stands for all five decomposition classes. Volume estimates within individual decay classes ranged from being approximately 3 to 11 times greater in unmanaged compared to managed stands.

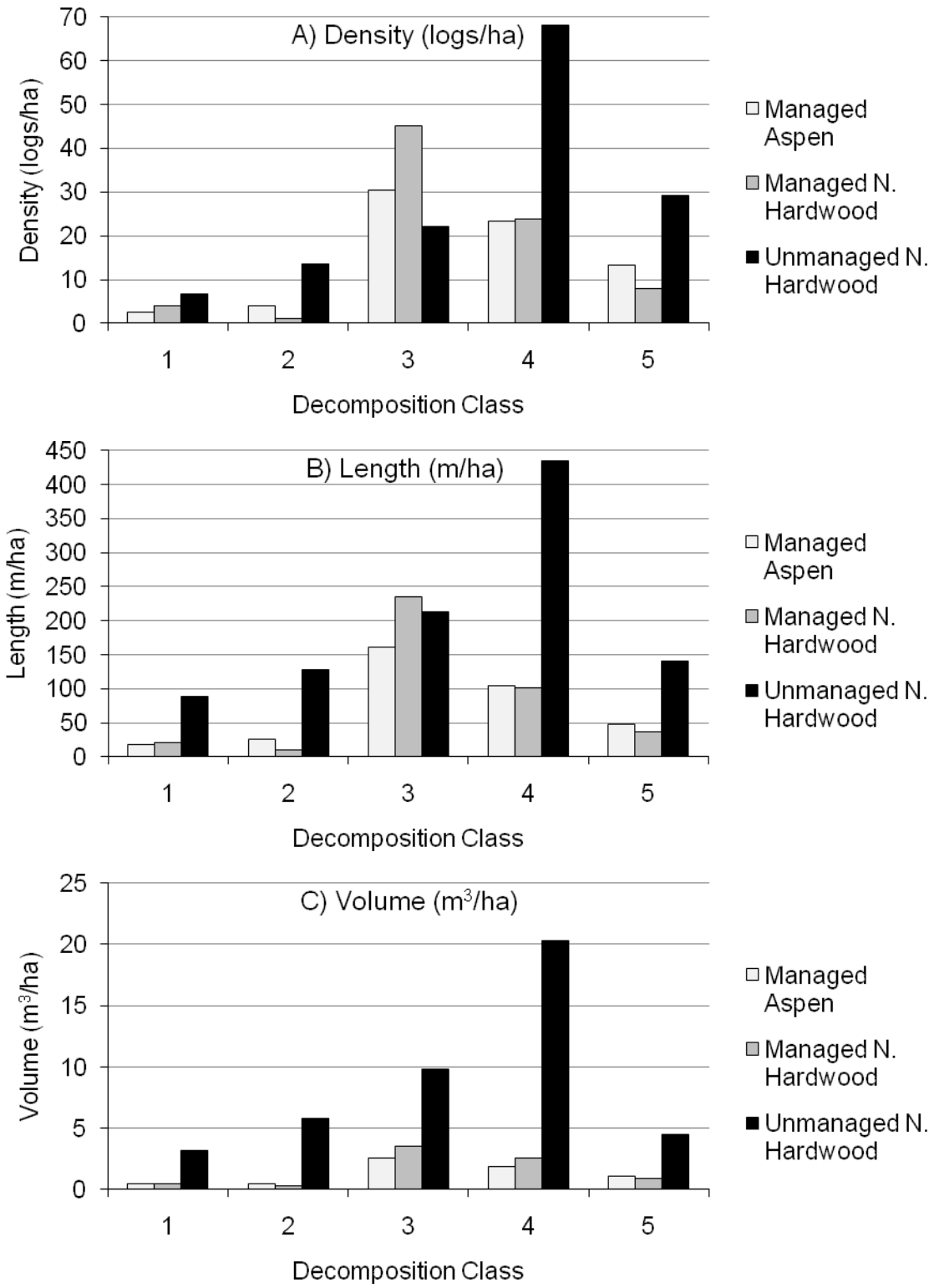

Figure 3. Estimated mean A) density, B) length, and C) volume of coarse woody debris by forest type among five decomposition classes in northern Michigan during 2005-2007.

Table 2. Least squares mean and lower and upper 95% confidence limit (LCL and UCL) estimates for coarse woody debris parameters by decomposition class for northern Michigan forests during 2005-2007. Bolded p-values indicate significant differences among forest types ($p<0.05$). Means followed by the same letter were not significantly different ($p>0.05$).

	Managed Forest Types						Unmanaged			
Decay Class	Aspen (n=57)			N. Hardwood (n=51)			N. Hardwood (n=14)			
Parameter	Mean	LCL	UCL	Mean	LCL	UCL	Mean	LCL	UCL	P value
Density (logs/ha)										
Class 1	2.6	1.0	4.7	3.9	1.8	6.7	6.7	2.1	13.7	0.2950
Class 2	4.0	2.5	6.0	1.2	0.3	2.7	13.6	8.1	20.5	**<0.0001**
	A			B			C			
Class 3	30.3	20.0	42.8	45.1	31.2	61.4	22.2	6.9	46.2	0.1488
Class 4	23.4	15.6	32.6	23.9	15.3	34.4	68.0	42.0	100.2	**0.0024**
	A			A			B			
Class 5	13.4	8.6	19.3	8.0	4.0	13.3	29.3	15.6	47.1	**0.0104**
	A			A			B			
Length (m/ha)										
Class 1	18.0	7.5	32.9	20.6	8.3	38.2	88.7	41.4	153.6	**0.0087**
	A			A			B			
Class 2	26.1	14.4	41.3	10.1	2.8	21.6	128.7	75.8	195.4	**<0.0001**
	A			A			B			
Class 3	161.5	109.3	223.8	235.1	165.8	316.3	212.7	100.9	365.6	0.2885
Class 4	104.9	70.2	146.5	101.1	64.1	146.5	434.6	292.4	605.0	**<0.0001**
	A			A			B			
Class 5	48.5	29.5	72.3	36.3	18.6	59.8	141.2	77.4	224.0	**0.0053**
	A			A			B			
Volume (m^3/ha)										
Class 1	0.5	0.2	0.8	0.5	0.2	0.9	3.2	1.9	5.0	**<0.0001**
	A			A			B			
Class 2	0.5	0.3	0.8	0.3	0.1	0.6	5.8	4.0	8.3	**<0.0001**
	A			A			B			
Class 3	2.6	1.8	3.6	3.5	2.4	4.9	9.8	5.4	17.1	**0.0011**
	A			A			B			
Class 4	1.9	1.3	2.7	2.6	1.8	3.7	20.3	12.1	33.4	**<0.0001**
	A			A			B			
Class 5	1.1	0.7	1.6	0.9	0.6	1.4	4.5	2.7	7.2	**<0.0001**
	A			A			B			

Size Class Comparisons

Patterns in CWD parameter estimates were consistently similar between managed aspen and managed northern hardwood forest types, with average density, length, and volume estimates being greatest in the smallest size class (Figure 4). Although density, length, and volume estimates within the smallest size class were similar among forest types, these parameters were consistently greater in unmanaged compared to managed types in the two larger size classes (Table 3). In unmanaged northern hardwood forest, average total CWD length was similar between the 10-25 cm and 26-50 cm categories and mean volume was greatest in the 26-50 cm class (Figure 4). Mean CWD density in unmanaged northern hardwood was more than five times greater in the 26-50 cm class and over nine times greater in the >50 cm class compared to managed aspen and northern hardwood stands. Average length of unmanaged northern hardwood stands was over eight times greater in the 26-50 cm category and more than 40 times greater in the >50 cm class compared to managed forests. Volume estimates in unmanaged northern hardwood stands were more than 10 times greater for the 26-50 cm class and over 20 times greater in the >50 cm class compared to managed aspen and northern hardwood forest estimates.

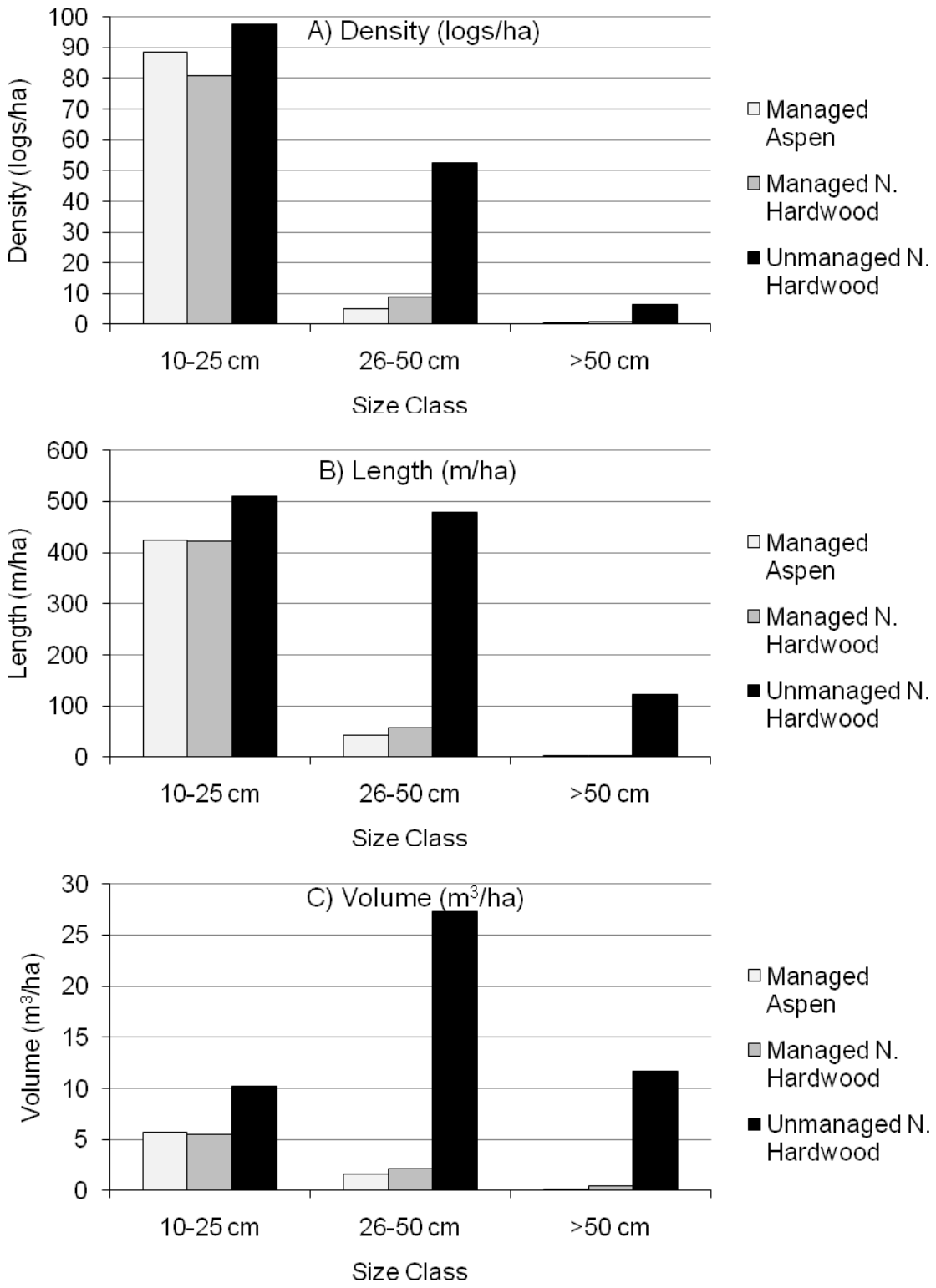

Figure 4. Estimated mean A) density, B) length, and C) volume of coarse woody debris by forest type among three size classes in northern Michigan during 2005-2007.

Table 3. Least squares mean and lower and upper 95% confidence limit (LCL and UCL) estimates for coarse woody debris parameters by size class for northern Michigan forests during 2005-2007. Bolded p-values indicate significant differences among forest types ($p<0.05$). Means followed by the same letter were not significantly different ($p>0.05$).

	Managed Forest Types						Unmanaged			
Size Class	Aspen (n=57)			N. Hardwood (n=51)			N. Hardwood (n=14)			
Parameter	Mean	LCL	UCL	Mean	LCL	UCL	Mean	LCL	UCL	P value
Density (logs/ha)										
10-25 cm	88.5	66.9	113.1	80.7	58.5	106.3	97.7	54.9	152.6	0.7896
26-50 cm	5.1	2.6	8.4	8.9	5.2	13.5	52.5	36.1	72.0	**<0.0001**
	A			A			B			
>50 cm	0.2	-0.1	0.7	0.7	0.2	1.4	6.5	4.1	9.5	**<0.0001**
	A			A			B			
Length (m/ha)										
10-25 cm	424.5	322.9	539.9	422.1	313.3	546.9	509.7	298.1	777.7	0.7821
26-50 cm	42.9	23.6	67.9	57.0	32.4	88.5	479.4	342.2	639.6	**<0.0001**
	A			A			B			
>50 cm	0.8	-0.3	3.0	2.8	0.5	6.5	122.3	90.5	158.9	**<0.0001**
	A			A			B			
Volume (m^3/ha)										
10-25 cm	5.7	4.3	7.5	5.5	4.0	7.4	10.2	6.0	16.9	0.1159
26-50 cm	1.6	1.0	2.4	2.1	1.3	3.1	27.3	15.5	47.3	**<0.0001**
	A			A			B			
>50 cm	0.1	-0.1	0.4	0.5	0.2	0.8	11.7	7.6	17.8	**<0.0001**
	A			A			B			

DISCUSSION

Overall Stand Type Characteristics

We observed greater mean CWD length, CWD volume, snag basal area, and snag DBH in unmanaged northern hardwood stands compared to managed northern hardwood and aspen forests in Michigan, which is consistent with the findings of similar studies (Goodburn and Lorimer 1998, Hale et al. 1999, Webster and Jenkins 2005). Researchers have also documented similar patterns in European forests (Siitonen et al. 2000, Debeljak 2006). Debeljak (2006) found that management of Slovenian forests dominated by silver fir (*Abies alba*) and beech (*Fagus sylvatica*) led to the reduction and homogenization of CWD when compared to virgin stands. Greater levels of CWD in old-growth compared to managed forests could be a function of greater stand ages, increased tree diameters, and forest composition. Total volume of CWD and volume of hemlock CWD increased linearly with stand age in old-growth hemlock-hardwood forests of northern Wisconsin and Michigan (Tyrrell and Crow 1994). Hemlock is known to have a slower rate of decay, so it would likely remain on the forest floor longer than most hardwood species (Harmon et al. 1986). Managed northern hardwood and aspen stands that we investigated were missing large, 50 to 70 cm DBH (i.e., 200-300 year old) trees that frequently occurred in unmanaged northern hardwood stands. We also found that 20% of the trees recorded during basal area sweeps in unmanaged hardwoods were large-diameter hemlock, compared to 4% in managed northern hardwood stands. Eastern hemlock is a long-lived (500 years) conifer with greater CWD residence time than hardwoods species, so differences in hemlock abundance between managed and unmanaged stands will influence both present and future forest structure. Additionally, because large-diameter, highly decayed CWD retains moisture even during periods of drought, they serve as successful nurse logs for hemlock

seedlings (Curtis 1959) and thereby strongly influence future forest structure. Differences in forest structure between managed and unmanaged stands are likely affecting wildlife use, because CWD and snag variables, such as size, location, and density are important factors in determining wildlife use (DeGraaf and Shigo 1985, Bull et al. 1997). Wildlife management guidelines stress the importance of large-diameter snags for cavity nesting birds and larger-bodied mammals (DeGraaf and Shigo 1985, Tubbs et al. 1987). In the Pacific Northwest, Carey and Johnson (1995) found that understory vegetation and CWD accounted for a major part of the variation in abundance for six of eight small mammal species in managed forests but only two of eight species in old-growth stands; they suggested that management for biodiversity should focus on providing multispecies canopies, CWD, and well-developed understories. Howe and Mossman (1996) found that several bird species were associated with eastern hemlock forests in northern Wisconsin and western Upper Michigan, and that uneven-aged managed stands containing hemlock supported greater bird densities than even-aged managed northern hardwood stands.

We found mean CWD density for unmanaged northern hardwoods to be similar to previous studies (Tyrrell et al. 1998), whereas our volume estimate varied from those reported by other researchers in the Great Lakes region and northeastern United States (Tyrrell and Crow 1994, Goodburn and Lorimer 1998, Tyrrell et al. 1998, Hale et al. 1999). We estimated mean CWD density for unmanaged northern hardwoods at 168 logs/ha, which was within the range of densities reported in Tyrrell et al. (1998) for old-growth northern hardwoods (99-481 logs/ha) and below the range for old-growth conifer-northern hardwoods (200-288 logs/ha). We estimated total CWD volume at 65 m^3/ha for unmanaged northern hardwoods, which was lower than estimates reported by Tyrrell et al. (1998; range 121-213 m^3/ha), Goodburn and Lorimer

(1998; mean 102 m^3/ha), and McGee et al. (1999; mean 136.7 m^3/ha) for old-growth northern hardwoods. Hale et al. (1999) estimated mean volume at 55 m^3/ha for old-growth maple-basswood forest, but only measured CWD with diameters ≥15 cm. Our mean volume (65 m^3/ha) was intermediate between the estimates of Tyrrell and Crow (1994) (mean 54 m^3/ha) and Goodburn and Lorimer (1998) (mean 93.9 m^3/ha) for old-growth hemlock-hardwoods. However, Tyrrell and Crow (1994) only characterized logs with ≥20 cm diameters, whereas we used a 10 cm diameter threshold similar to other studies (Goodburn and Lorimer 1998, Hale et al. 1999). Our mean volume was also greater than estimates provided by Vanderwel et al. (2008) for unmanaged northern hardwood forests in Ontario. Differences between our volume estimate and those of previous studies could be related to varying methods used to sample and estimate CWD volume or differing stand characteristics, such as species composition, stand age, site history, and climate. Our estimates of snag density and basal area for unmanaged northern hardwoods were within the range of values summarized in Tyrrell et al. (1998) for old-growth northern hardwoods and conifer-northern hardwood forests. We observed similar mean snag density, DBH, and basal area to those reported by Goodburn and Lorimer (1998) for old-growth northern hardwoods.

We recorded lower CWD density and volume estimates for managed hardwood forests than those of other studies (Goodburn and Lorimer 1998, Hale et al. 1999, McGee et al. 1999). A variety of factors could account for these differences, including differing stand selection processes (e.g., random versus selected), sample sizes, stand ages, management histories, regional climates, and sampling methodologies. We observed similar mean snag density in managed northern hardwoods to those of comparable managed forest types in the Great Lakes region (Goodburn and Lorimer 1998, Hale et al. 1999), whereas estimated snag density from

managed northern hardwoods in New York were greater than ours (McGee et al. 1999). Our mean snag DBH estimate for managed northern hardwood stands was intermediate between estimates reported by Goodburn and Lorimer (1998) for even-aged and selectively cut northern hardwood stands. We observed a mean snag basal area for managed northern hardwoods that was similar to McGee et al. (1999) but lower than Goodburn and Lorimer (1998).

Decomposition Class Comparisons

Our study indicated low levels of CWD in advanced stages of decay in managed northern Michigan forests. We found significantly lower volume of CWD in managed compared to unmanaged forests in all five decomposition classes. Goodburn and Lorimer (1998) similarly observed greater CWD volumes across all decay classes in old-growth forests compared to selective and even-aged harvested stands in northern Michigan and Wisconsin. Likewise, significantly greater volume of highly decayed CWD was observed by Webster and Jenkins (2005) in primary forest compared to forests with documented histories of settlement or diffuse disturbance that included small-scale or mechanized logging. Consistent with the above studies, Jenkins et al. (2004) found low volumes of highly decayed CWD in managed hardwood forests of Indiana. Vanderwel et al. (2008) found that individual pieces of CWD in unmanaged stands tended to move through decay classes 1–3 faster than those in managed stands, which could help explain some of the differences we observed between managed and unmanaged stands. However, because the unmanaged northern hardwood stands we studied had significantly greater densities of large-diameter CWD and large-diameter hemlock, both of which are slow to decay, their findings may have limited applicability to this study.

Previous authors have noted the diversity of animals that use highly decayed CWD. Maser and Trappe (1984) stated CWD in the class 4 stage presents the most diversified habitat and hence supports the greatest array of inhabitants. Invertebrates such as mites, centipedes, millipedes, slugs, and snails use spaces within decaying heartwood and vertebrates, including salamanders, shrews, and voles, use cover provided by sloughed bark and rotten wood alongside decaying logs and burrow within the undersides of dead logs (Maser and Trappe 1984). The presence of CWD in late stages of decay (i.e., decomposition classes 4 and 5) has been found to be an important habitat component for both southern red-backed vole (*Myodes gapperi*) in Ontario (Vanderwel et al. 2010) and western red-backed vole (*Myodes californicus*) in southwestern Oregon (Tallmon and Mills 1994). Red-backed voles are a common food source for American marten (*Martes americana*; Buskirk and Ruggiero 1994).

Decayed logs are known to be important as nurse logs for small-seeded conifer species, such as pines, hemlock, and cedar. Hemlock is a species that often germinates on decayed CWD (Ward and McCormick 1982, Godman and Lancaster 1990), which may be due to increased moisture availability and reduced fluctuations in moisture levels in decayed logs compared to the forest floor (Tubbs 1996). O'Hanlon-Manners and Kotanen (2004) indicated that nurse logs also provided eastern hemlock seeds a refuge from pathogenic soil fungi.

Coarse woody debris has also been shown to influence nutrient cycling in northern hardwood forests. Fisk et al. (2002) observed greater mass of CWD across all five decay classes in old-growth compared to second-growth forests in the western Upper Peninsula. They determined that CWD and microbial nitrogen uptake and turnover were greater nitrogen sinks in old-growth than in second-growth northern hardwood forests.

Size Class Comparisons

The managed forests we examined in northern Michigan generally lacked CWD of sizes larger than 25 cm in diameter. Goodburn and Lorimer (1998) also observed greater volumes of large-diameter (>40 cm) debris in old-growth compared to managed forests in northern Michigan and Wisconsin. McGee et al. (1999) documented similar patterns of CWD within size class categories when comparing old-growth and managed northern hardwood forests in New York. They found old-growth stands contained four to seven times greater volume of downed CWD ≥25 cm diameter than managed stand types, but this was less than the 10 to 20 times greater volume in our study. Consistent with our results, Jenkins et al. (2004) observed low volumes of large-diameter (>40 cm) CWD in managed hardwood forests of Indiana.

Along with overall volume and density, the size of CWD present in a forest will likely influence wildlife use. Smaller downed logs provide escape cover and shelter to a variety of species, including small mammals, amphibians, and reptiles, whereas large-diameter logs, especially hollow ones, benefit other vertebrates, including American marten, mink (*Neovison vison*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*) (Bull et al. 1997). Bull and Holthausen (1993) found that Pileated Woodpeckers (*Dryocopus pileatus*) foraged more on logs with large-end diameters >37 cm compared to smaller logs in Oregon. Hayes and Cross (1987) found the number of western red-backed voles captured in Oregon was positively associated with mean log diameter and overhang area, thus the species appeared to use large-diameter logs more often than small-diameter logs. Buskirk and Ruggiero (1994) stated that coarse woody debris, especially in the form of large-diameter boles, is an important feature of marten habitat in the western U.S. Many researchers have found that coarse woody debris is an important component of marten habitat, by being associated with the presence of prey species

and providing sites used by martens for foraging, resting, scent marking, and access to subnivean spaces for themoregulation and foraging (see literature summary in Godbout and Ouellet 2010).

Conclusions

In comparison to unmanaged forests, the managed northern hardwood and aspen stands we sampled had significantly less CWD as measured by mean CWD length, CWD volume, snag basal area, and snag DBH. This difference between managed and unmanaged stands was especially pronounced in the larger and more highly decayed classes of CWD and larger snags. By serving as nurse logs, large diameter, highly decayed CWD is an important resource for successful conifer regeneration and thus has the potential to significantly influence future forest structure. In addition, large-diameter CWD and snags serve as important wildlife habitats for a wide range of animal species representing a diversity of trophic levels and animals groups. Future studies of the importance of CWD to wildlife and successful conifer regeneration will help improve our ability to sustainably manage Michigan's forests.

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