# Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A.

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**Abstract**: We examined the dynamics of down coarse woody debris (CWD) under an expanding-gap harvesting system in the Acadian forest of Maine. Gap harvesting treatments included 20% basal area removal, 10% basal area removal, and a control. We compared volume, biomass, diameter-class, and decay-class distributions of CWD in permanent plots before and 3 years after harvest. We also determined wood density and moisture content by species and decay class. Mean pre-harvest CWD volume was 108.9 $m^3$/ha, and biomass was 23.22 Mg/ha. Both harvesting treatments increased the volume and biomass of non-decayed, small-diameter CWD (i.e., logging slash), with the 20% treatment showing a greater increase than the 10% treatment and both treatments showing greater increases than the control. Post-harvest reduction of advanced-decay CWD due to mechanical crushing was not evident. A mean of 18.48 $m^3$ water/ha (1.85 L/$m^2$) demonstrates substantial water storage in CWD, even during an exceptionally dry sampling period. The U-shaped temporal trend in CWD volume or biomass seen in even-aged stands may not apply to these uneven-aged stands; here, the trend is likely more complex because of the superimposition of small-scale natural disturbances and repeated silvicultural entries.

**Résumé** : Nous avons étudié la dynamique des débris ligneux grossiers au sol en lien avec un système de récolte par expansion de trouées dans la forêt acadienne du Maine. Les traitements de récoltes par trouées incluaient l'enlèvement de 10 ou 20 % de la surface terrière et un témoin. Nous avons comparé le volume, la biomasse, la distribution des classes de diamètre et de décomposition des débris ligneux grossiers dans des parcelles permanentes avant et 3 ans après la récolte. Nous avons aussi déterminé la densité du bois et sa teneur en eau par espèce et par classe de décomposition. Avant la récolte, le volume moyen atteignait 108,9 $m^3$/ha et la biomasse moyenne 23,22 Mg/ha. Les deux traitements de récolte ont augmenté le volume et la biomasse des débris ligneux grossiers non décomposés (c.-à-d. les déchets de coupe). Le traitement à 20 % a causé une plus forte augmentation que celui à 10 % et les deux traitements ont causé une augmentation plus forte que le témoin. Il n'y a pas eu de réduction évidente des débris ligneux grossiers au stade de décomposition avancée après la récolte due au broyage mécanique. Même pendant une période d'échantillonnage exceptionnellement sèche, les débris ligneux grossiers ont conservé une teneur en eau appréciable avec une moyenne de 18,48 $m^3$/ha (1,85 L/$m^2$). La forme en U caractéristique de l'évolution dans le temps du volume et de la biomasse des débris ligneux grossiers dans les peuplements équiennes peut ne pas s'appliquer dans ces peuplements inéquiennes. Dans ce cas-ci, la tendance est probablement plus complexe à cause de la superposition de perturbations naturelles à petites échelles et d'interventions sylvicoles répétées.

[Traduit par la Rédaction]

## Introduction

Recent research on coarse woody debris (CWD) has established its importance in many aspects of forest ecosystem structure and function. Harvesting systems can potentially reduce CWD volume through the removal of large living trees that would otherwise die and fall to the forest floor (Hansen et al. 1991; Fridman and Walheim 2000). Harvesting can also alter the size- and decay-class distributions of CWD through the short-term addition of small-diameter, non-decayed pieces (logging slash), and the mechanical fragmentation of larger pieces in advanced states of decay (Freedman et al. 1996). For these reasons, when previously unmanaged forests are brought under management, we can expect to see long-term changes in the pool of CWD. Recovery of CWD after harvesting or natural disturbance can be quite slow, requiring as much as ca. 1000 years in forests of the Pacific Northwestern United States (Spies et al. 1988). Thus, understanding the role and natural dynamics of CWD in both managed and unmanaged forests is vital to improving forest management strategies.

Previous research on CWD has addressed a variety of topics including descriptive inventories, dynamics, decomposition rates, water relations, geomorphic functions, nutrient

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cycling, animal and insect use, and suitability as substrate for fungi and plants. Reviews of these topics can be found in Triska and Cromack (1979), Maser and Trappe (1984), Harmon et al. (1986), Freedman et al. (1996), Stevens (1997), Hagan and Grove (1999), and McComb and Lindenmayer (1999).

To date, the majority of the descriptive work on CWD in terrestrial systems can be divided into two categories: (*i*) volume or biomass estimates from old-growth forests, which provide baseline conditions against which the results of forest management can be compared, and (*ii*) comparisons of CWD volume or biomass among stands of different ages (sometimes including old growth) using a type of chronosequence referred to as a space-for-time substitution (sensu Pickett 1989). Here, stands are arranged according to time since the last stand-replacing disturbance, allowing inferences to be made about general trends in CWD through time. This method, however, is severely limited in forest types, such as those of the Acadian region in the northeastern North America, where stand-replacing disturbances are relatively rare (Lorimer 1977; Chokkalingam 1998; Seymour et al. 2002). Understanding the dynamics of CWD in these forests requires long-term and repeated measurements on the same sites. In addition, controlled experimentation that quantifies changes in CWD in both managed and unmanaged forest conditions is needed.

The Forest Ecosystem Research Program (FERP) at the University of Maine is documenting the long-term dynamics of a variety of ecosystem components in the Acadian forest using expanding-gap silvicultural systems. These systems are designed to emulate estimated natural disturbance frequencies in the Acadian forest. Part of this research includes a detailed monitoring of CWD on permanent plots that were established in 1995 in a mixed-species forest that is typical of the Acadian region. The objectives of the study reported here were to (*i*) determine the wood density and moisture content of CWD by tree species and decay class as descriptive baseline data for future comparisons, and (*ii*) investigate the effects of partial canopy removal on the volume, biomass, and size- and decay-class distributions of down CWD 3 years after harvest.

## Materials and methods

### Study site

FERP is being conducted on the 1540-ha Penobscot Experimental Forest (PEF) of east-central Maine (44°50′N, 68°35′W). The soils are variable but principally Aquic or Typic Haplorthods or Podzols with slopes generally less than 8% (USDA Forest Service 1959). The forest receives annual precipitation of 1060 mm, fairly evenly distributed throughout the year (Brissette 1996). Dominant tree species include eastern hemlock (*Tsuga canadensis* (L.) Carrière), red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), eastern white pine (*Pinus strobus* L.), northern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), bigtooth aspen (*Populus grandidentata* Michx.), and paper birch (*Betula papyrifera* Marsh), making it typical of the region.

Although the PEF has never been clear-cut harvested, it has experienced a complex history of repeated partial cuttings and insect outbreaks. In this sense too, the PEF is typical of forests in the Acadian region. Dendrochronological work conducted on the FERP study site revealed multicohort structures of many species (R. Seymour, unpublished data). Results from that work, coupled with historical information, suggests that harvesting of large white pines began in the study area in the 1780s followed by intense harvests of other species in the 1870s. A spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak, which killed many balsam fir and red spruce, occurred from 1911 to 1920. Intense harvesting of the 1930s and into the 1940s may have begun as salvage cuts of dead and dying fir and spruce, then shifted to cutting of hardwoods for firewood. Harvesting for shipping-box material (from any species) continued through the 1940s to supply the war effort. With the exception of a second recorded spruce budworm outbreak in the 1980s, no moderate- or large-scale harvesting or other disturbances have occurred in the PEF since the mid-1940s.

### Treatments and experimental design

FERP is an interdisciplinary, long-term research effort designed to examine the feasibility and ecological effects of alternative silvicultural systems that are based on estimated frequencies of natural disturbances (primarily tree-fall gaps). In the eastern United States, such disturbances remove between 0.5 and 2.0% of the canopy per year on average (Runkle 1985). The harvesting treatments use an expanding-gap silvicultural system with permanent reserve trees with the objective of maintaining structural diversity and controlling tree species composition. The system also seeks to maintain the economic advantages of even-aged methods while providing many of the structural features found in uneven-aged stands.

Two expanding-gap treatments are simultaneously being tested: (*i*) a 20% basal area removal on a 10-year cutting cycle (creating approximate 0.2 ha openings, emulating a 2.0% average annual disturbance frequency) with 10% of the basal area remaining in permanent reserve trees, and (*ii*) a 10% basal area removal on a 10-year cutting cycle (creating approximate 0.1 ha openings, emulating a 1.0% frequency) with 30% of the basal area remaining in permanent reserve trees. Each harvest gap is initially circular or elliptical in shape. These gaps will be systematically expanded every harvest entry, each time removing the prescribed basal area, until the entire area has been harvested. As the gap diameter expands incrementally through successive harvests, tree height in the original gap center gradually returns to its preharvest level. The 20% basal area removal treatment (which will take 50 years to complete) is designed to maintain mid-successional composition and structure, while the 10% basal-area removal (taking 100 years to complete) is intended to accelerate the development of late-successional status. Each of these treatments is being compared with experimental controls of the same size that receive no harvesting. The first sequence of gap harvesting occurred in the early spring of 1996, 1997, and 1998.

The three treatments (two expanding-gap treatments and untreated control) were each randomly assigned to three main plots (nine main plots total). Each main plot is approximately 10 ha in size (total of 90 ha under study) and serves as an experimental unit. The final design is a randomized complete block design with three treatments and three replications. Within each main plot, 20 circular sample plots (500 $m^2$ each) were permanently established at randomly selected points.

### CWD measurement and description

During the summer of 1995, 1996, and 1997 (prior to harvesting), the abundance and composition of CWD was measured on each 500-$m^2$ sample plot. Post-harvest measurements of CWD were made in the summer of 1998, 1999, and 2000, so that all sample plots were re-measured three growing seasons after harvest. A total of 7599 pieces of CWD were measured during these inventories.

All down CWD occurring inside each sample plot was inventoried. Measurements included diameter at large and small ends (measured with calipers), length, species (when possible), and decay class (see below). Only pieces >9.5 cm in diameter at the large end were included in the sample. For pieces that crossed the sample plot boundary, only that portion lying within the plot was measured. If the largest end of such pieces lay outside the plot, the piece was measured only if it had a diameter of 9.5 cm or larger at the plot boundary. Leaning snags inclining greater than 45° from vertical were considered as CWD. Each piece was assigned a unique number and marked with an aluminum tag. Although snags and cut stumps were also inventoried as part of the general protocol, we include only down CWD in this analysis.

### Decay classes

Each piece of CWD was assigned to one of four classes based on its state of decay.

(1) Wood is sound and cannot be penetrated with thumbnail; bark is intact; smaller to medium sized branches are present; and log is often suspended by its own branches.

(2) Wood is sound to somewhat rotten; bark may or may not be attached; branch stubs are firmly attached but only larger stubs are present; and log retains round shape and lies on duff.

(3) Wood is substantially rotten, enough that branch stubs pull out easily (softwoods) and thumbnail penetrates readily; wood texture is soft and may be "squishy" if moist; bark is lightly attached, sloughing off or detached; and bole may assume a slightly oval shape and may be partly buried in duff.

(4) Wood is mostly rotten, "fluffy" when dry and "doughy" when wet; branch stubs are rotted down; bark is detached or absent (except *Betula*); and log is decidedly oval in cross section and usually substantially buried in duff. The lower cut-off point for this class occurs when the top of the log has been lowered by decay to the general duff level at its sides making it indistinguishable, except for traces of decayed wood or plant covering, from the surrounding duff.

We recorded the species of all CWD assigned to decay classes 1 and 2. The advanced state of decay of classes 3 and 4 often precluded species identification in the field. When possible, such pieces were assigned to a species group (hardwood or softwood). Many pieces, however, were decayed beyond recognition of species group. When this occurred, these pieces were listed as unknowns.

### CWD volume calculation

Using the measurements from each sample plot, we calculated the volume for each piece of CWD (assuming the shape of a frustum) and the projected area (assuming the shape of a trapezoid), the latter being an estimate of the area available for seedling establishment on logs. Volume calculations assumed a circular cross-sectional shape for all pieces, except those in decay class 4. Logs in this class tended to have elliptical cross-sectional shapes (resulting from their collapse through decomposition) and required adjustment. Without this adjustment, the diameters (actually widths measured with calipers) would have overestimated the volume of decay class 4 pieces. These adjustments were based on a sample of height and width measurements (where height is the log diameter perpendicular to the forest floor, and width the diameter parallel to the forest floor and perpendicular to the long axis of the log) from 31 softwood and 31 hardwood logs in decay class 4 using the following procedure. With the intercept held at zero, linear regression models of height versus width were developed for each species group (hardwood and softwood). Both regressions were highly significant ($p < 0.0001$). When the two data sets were combined and species group entered as an indicator variable (Steel et al. 1997), the slopes did not differ significantly ($p$ = 0.495), indicating that we could pool data from both species groups into a single model ($p = 0.0001$, $r^2 = 0.907$, $n = 62$). The resulting equation was height = 0.575 × width, with both dimensions in centimetres. Therefore, the volumes of all class 4 logs were adjusted by multiplying each by 0.575.

### CWD density, moisture content, and biomass

To calculate the biomass of CWD, we needed to determine density for the various species and decay classes that we measured. We used the following procedures for determining wood density and moisture content of CWD.

During the summer of 1999 we collected CWD samples from unharvested portions of the main plots (but outside of the sample plots). Approximately 20 cross-sectional disks (or "cookies") from logs of decay classes 1 and 2 from each of the four most abundant (based on pre-harvest volume calculations) softwood species (*Abies balsamea*, *Picea rubens*, *Thuja occidentalis*, *Tsuga canadensis*) and the three most abundant hardwood species (*Acer rubrum*, *Betula papyrifera*, *Populus grandidentata*) were collected, for a total of 272 cookies. We determined the appropriate sample size of 20 cookies for each species-by-decay-class combination using the variance in wood densities for *Picea rubens* and *Acer rubrum* samples previously collected at the PEF in an unrelated study (J. Brown, unpublished data). The cookies were cut at least 0.3 m from each log end and assigned a decay class based on the portion of the log from which the cookie was removed. At the same time, we collected ca. 50 samples each of decay class 3 and 4 softwood and hardwood logs (the advanced decay of these logs often precluded identification of species) for a total of 220 samples. These decay class 3 and 4 samples often consisted of friable, spongy, or punky material, rather than intact cookies as with decay class 1 and 2 samples. All samples were placed in sealed plastic bags, labeled, and refrigerated until processed in the laboratory. Because heavy rains could inflate our estimates of CWD moisture content, we avoided collecting samples for laboratory analyses for at least two full days following a rainstorm. August 1999 was an exceptionally dry month, with rain events as follows: 3.86 cm on August 8, 0.61 cm on August 14, 0.48 cm on August 21, and 0.25 cm on August 22 (National Climate Data Center archives for Bangor, Maine). We began our collections on August 24 and finished before the next rain on September 6, 1999.

Laboratory methods for determining mass and volume of CWD subsamples varied by decay class. From each cookie of decay class 1 and 2, we cut a pie-wedge sample (mean of 40 $cm^3$) that included heartwood, sapwood, and bark. Wedges were weighed, and volumes were calculated from direct measurements of radius, depth, and angle of each wedge. From each sample of decay class 3 and 4 debris, we extracted a similar volume (ca. 40 $cm^3$) of wood, which was vacuum packed (Deni Freshlock TurboSeal® model 1630) in polyethylene bags, and weighed. The volume of each sample was determined by water displacement. The mass and volume of the standard-sized polyethylene bag was subtracted from the fresh mass and fresh volume of each sample.

To determine whether the vacuum-packing procedure overestimated volume, owing to imperfect fit between sealer bag and sample that is inherent with vacuum packing, we sealed 25 geometric solids of known volume (range 19.8 to 73.6 $cm^3$) and estimated their volume using the same water displacement method. A linear regression of displaced volume against known volume was highly significant ($p$ = 0.0001, $r^2$ = 0.956, $n$ = 25). The resulting equation was KV = 2.567 + 1.034DV, where KV is the known volume and DV is the displacement volume (both in $cm^3$). Significant deviations of the intercept and slope from 0 and 1, respectively, indicated the need for calibrating all volumes estimated by our displacement method. Therefore, we multiplied each displacement volume by the reciprocal of the slope (thereby reducing it to 1) and subtracted the intercept from each geometric solid (reducing the intercept to 0). These same adjustments were applied to all displacement volume estimates for class 3 and 4 samples.

All samples were oven-dried at 80°C until a constant mass was achieved (minimum of 8 days) and then reweighed. From these data, we calculated density (g dry mass/$cm^3$ fresh volume) and mass moisture content ((sample fresh mass – dry mass)/dry mass) for each wood-type by decay-class combination for all 492 samples. Given the limitations of expressing moisture content as a percentage of sample mass (comparisons among samples with different wood densities become spurious; see Boddy 1983), we also estimated the volumetric moisture content (volume of water in sample/dry volume of sample). The numerator was determined by subtracting sample dry mass from fresh mass (given that 1 g pure water occupies 1 $cm^3$), the denominator by assuming the sample fresh volume shrunk by 9% upon complete drying, a value typical for nondecayed wood of various species (Panshin and de Zeeuh 1980).

For decay class 1 and 2 samples, the mean density and moisture content for each species and decay class were combined with the volume data from the sample plots to estimate total biomass and water storage of CWD on a per-hectare basis. For those species for which we had not determined density and moisture content in the laboratory, we substituted mean densities and moisture contents of congeners where possible; otherwise, we substituted means for the species group (hardwood or softwood) to which they belonged. For decay classes 3 and 4, mean density and moisture content of each species group by decay class was used to estimate biomass and water storage per ha.

### Statistical analyses

Because pre-harvest differences in various characteristics of CWD among the main plots could potentially confound our treatment comparisons, we first compared pre-harvest CWD volume among treatments using ANOVA (model: CWD volume = $f$(treatment)). Given that the gap-harvesting treatments were applied to the main plots (three each per treatment), these served as experimental units. CWD volume was first log transformed to successfully meet the ANOVA assumptions of homogeneity of variance and normality of error terms. In addition, we tested the equality of CWD diameter-class distributions (based on mean volumes of CWD in each class) among planned treatments by Kolmogorov–Smirnov two-sample tests (Sokal and Rohlf 1981), using all three possible pairwise comparisons among treatments. We did not feel it necessary to test for equal distributions across decay classes, because our variable of interest was the difference between pre- and post-harvest volumes in these classes. This difference is unlikely related to initial volumes.

The relationship between wood density and decay class was examined using ANOVA (model: wood density = $f$(decay class)) based on data resulting from laboratory analyses. These data violated ANOVA assumptions, and although various transformations corrected non-normality of error terms, no transformation was found that corrected the heterogeneity of variance. Thus, we analyzed the rank transformations of wood density (Conover and Iman 1981). Conceptually, the ANOVA models would express density as a function of decay class, species group, and the interaction; however, the explicit test for interaction is not recommended for rank-transformed data (see Conover 1999). For this reason, we analyzed hardwoods and softwoods in separate ANOVAs, with decay class as the only independent variable, it being of more interest than differences attributable to species group. Linear contrasts were then used to test differences in ranked mean densities in adjacent decay classes (contrasts of class 1 vs. 2, 2 vs. 3, and 3 vs. 4). In addition we compared, by Wilcoxon rank sum tests, hardwood and softwood densities within each decay class to determine if the species groups became indistinguishable as decay advanced.

Considering the wide fluctuations in CWD moisture content over time (see Discussion), we elected not to perform detailed ANOVAs on these data. We did, however, compare hardwood and softwood moisture contents within decay classes (as was done with the wood-density data), although we acknowledge that these relationships can change substantially over time.

Pre- and post-harvest field data collected on the same permanent plots allowed direct assessments of harvesting effects on CWD volume and biomass. In two separate ANOVAs (one for volume and one for biomass), we used the

**Table 1.** Wood density, mass moisture content, and volumetric moisture content for each species (or species group) for (A) decay classes 1 and 2 and (B) decay classes 3 and 4.

(A) Decay classes 1 and 2.

| | Wood density[a] | | Mass moisture content (%)[b] | | Volume moisture content (%)[c] | |
|---|---|---|---|---|---|---|
| | Decay class 1 | Decay class 2 | Decay class 1 | Decay class 2 | Decay class 1 | Decay class 2 |
| **Species** | | | | | | |
| *Abies balsamea* | 0.351 (0.067) | 0.273 (0.085) | 36.3 (19.5) | 43.8 (48.0) | 13.8 (7.3) | 12.0 (12.2) |
| *Picea rubens* | 0.406 (0.057) | 0.316 (0.112) | 28.5 (17.7) | 62.6 (81.0) | 12.3 (6.1) | 17.2 (17.8) |
| *Thuja occidentalis* | 0.329 (0.038) | 0.315 (0.053) | 30.5 (25.3) | 35.8 (47.5) | 10.8 (8.2) | 12.5 (16.3) |
| *Tsuga canadensis* | 0.398 (0.059) | 0.325 (0.084) | 51.1 (25.3) | 63.5 (50.9) | 22.1 (11.1) | 20.5 (13.9) |
| *Acer rubrum* | 0.512 (0.057) | 0.342 (0.116) | 27.8 (8.2) | 70.0 (78.2) | 15.6 (4.8) | 18.7 (13.0) |
| *Betula papyrifera* | 0.469 (0.052) | 0.352 (0.128) | 55.2 (17.4) | 126.3 (108.9) | 28.2 (8.6) | 40.9 (25.7) |
| *Populus grandidentata* | 0.336 (0.067) | 0.298 (0.066) | 61.2 (38.6) | 73.7 (81.0) | 21.1 (10.3) | 21.7 (16.4) |
| **Species group** | | | | | | |
| Softwoods | 0.372 (0.064) | 0.308 (0.086) | 37.1 (23.7) | 51.1 (58.5) | 15.0 (9.5) | 15.5 (15.3) |
| Hardwoods | 0.441 (0.094) | 0.331 (0.108) | 48.0 (28.1) | 89.7 (92.4) | 21.8 (9.7) | 27.0 (21.2) |
| All samples | 0.402 (0.085) | 0.317 (0.096) | 41.8 (26.2) | 67.5 (77.0) | 17.9 (10.1) | 20.4 (18.9) |

(B) Decay classes 3 and 4.

| | Wood density[a] | | Mass moisture content (%)[b] | | Volume moisture content (%)[c] | |
|---|---|---|---|---|---|---|
| Species group | Decay class 3 | Decay class 4 | Decay class 3 | Decay class 4 | Decay class 3 | Decay class 4 |
| Softwoods | 0.141 (0.050) | 0.123 (0.031) | 102.4 (101.2) | 206.7 (140.1) | 14.4 (13.7) | 26.5 (16.2) |
| Hardwoods | 0.190 (0.095) | 0.121 (0.044) | 161.1 (150.1) | 233.6 (211.4) | 25.6 (19.1) | 27.3 (20.2) |
| All samples | 0.166 (0.080) | 0.122 (0.038) | 132.6 (131.5) | 220.1 (179.0) | 20.2 (17.6) | 26.9 (18.2) |

**Note:** Standard errors are given in parentheses.
[a]Grams dry mass/$cm^3$ fresh volume.
[b](Sample fresh mass – dry mass)/sample dry mass.
[c]Volume of water in fresh sample/volume of dry sample.

post- minus pre-harvest difference as the dependent variable, with treatment, decay class, block, and the decay-class-by-treatment interaction as independent variables. The volume-difference ANOVA met the assumptions of homogeneity of variance and normality of error terms. The biomass-difference ANOVA required log transformation to satisfy ANOVA assumptions. Species group (hardwood or softwood) could not be included in these analyses because of the large number of class 3 and 4 pieces that could not be identified in the field.

## Results

### CWD density and moisture content

Mean wood densities and moisture contents for each species (or species group) by decay class are presented in Table 1. Wood density decreased with increasing decay class (hardwood ANOVA: $F_{[3,223]} = 154.6$, $p < 0.0001$; softwood ANOVA: $F_{[3,261]} = 217.8$, $p < 0.0001$) (Fig. 1). Results from linear contrasts for hardwoods showed that each decay class differed significantly from its adjacent class in terms of wood density (contrast $p$ values < 0.001; see Fig. 1*a*). Results for softwoods showed the first two pairwise comparisons to be distinct (class 1 vs. 2 and class 2 vs. 3; contrast $p$ values < 0.001); however, decay classes 3 and 4 could not be distinguished from one another in terms of wood density ($p = 0.094$; see Fig. 1*a*). Comparisons within decay classes indicated that upon reaching decay class 4, hardwoods and softwoods had become indistinguishable in terms of wood density (see Fig. 1*a* for statistical results). Oddly, the two species groups showed no significant difference in decay class 2.

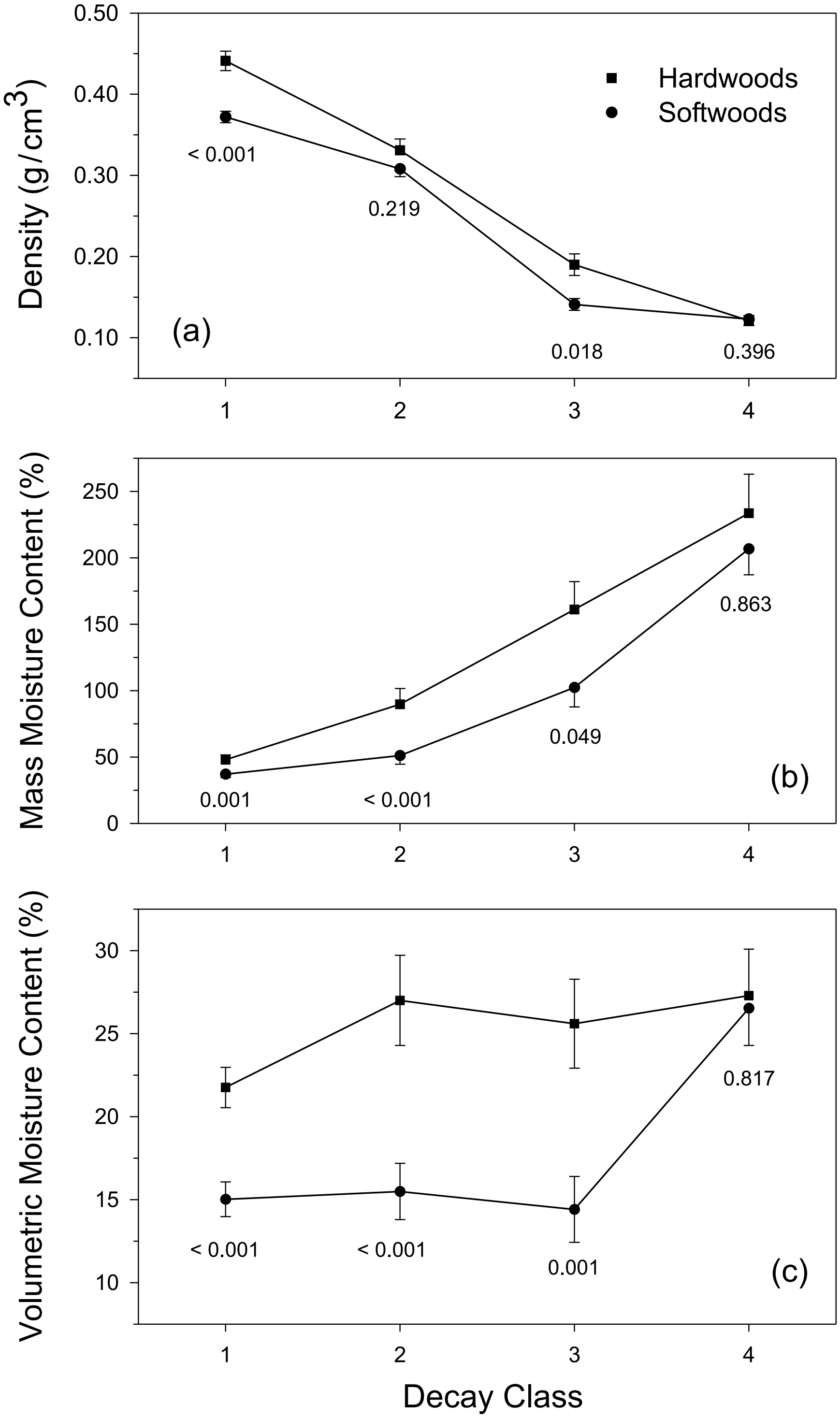
Although ANOVAs of moisture-content data were deemed inappropriate (see Discussion), data summaries suggest that mass moisture content increased with increasing decay for both hardwoods and softwoods (Fig. 1*b*). Different densities across species groups and decay classes, however, can confound the interpretation of mass moisture content. As an alternative, we calculated the volumetric moisture content of samples to remove the effect of density differences (Fig. 1*c*). Volumetric moisture content tended to increase with increasing decay (Fig. 1*c*) but not as dramatically as mass moisture content (Fig. 1*b*). For both moisture-content measures, hardwoods exceeded softwoods in the first three decay classes, but the two species groups were indistinguishable in the most advanced state of decay (see Figs. 1*b* and 1*c* for statistical results).

### Pre-harvest CWD measures

We found no evidence for differences in CWD volumes among the main plots before harvest ($F = 0.16$, $p = 0.849$, model df = 2), nor did the pre-harvest diameter-class distributions differ among main plots (Kolmogorov–Smirnov tests, $p > 0.05$). This finding suggests that CWD volumes and distributions were similar at the start of study and not likely to influence our subsequent interpretations concerning the effect of harvest treatments.

Pre-harvest CWD volume across all nine main plots was 109.1 ± 18.5 $m^3$/ha (mean ± SD); biomass, 23.2 ± 5.78 Mg/ha; water storage, 18.5 ± 3.33 $m^3$/ha; and projected area, 252.2 ± 42.1 $m^2$/ha. Snag basal area was 3.45 ± 0.57 $m^2$/ha, and snag number was 136 ± 18/ha. Pre-harvest living basal area was 36.2 ± 3.8 $m^2$/ha.

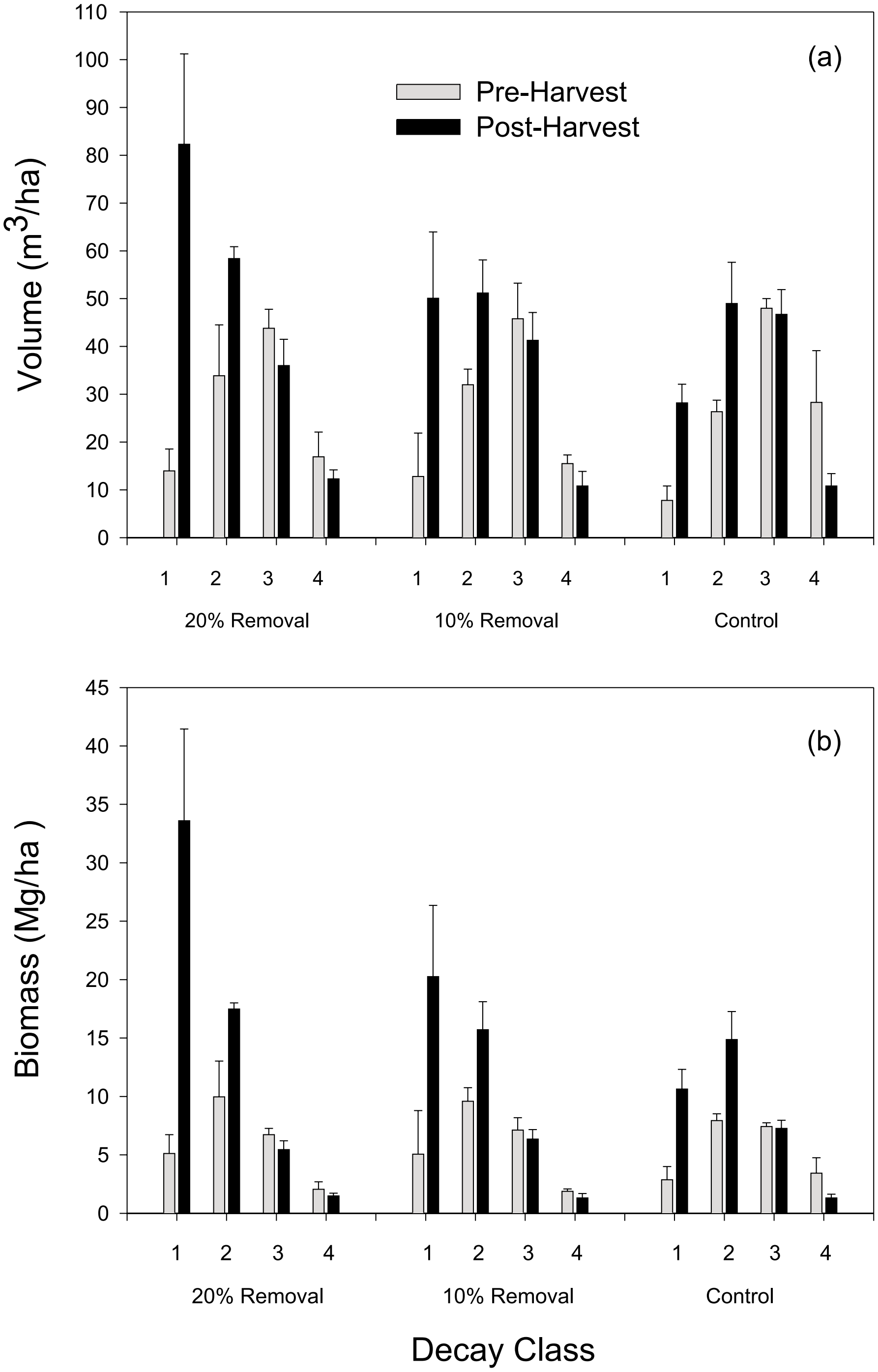
**Fig. 1.** Mean (*a*) wood density (grams dry mass/cm$^3$ fresh volume), (*b*) mass moisture content ((sample fresh mass – dry mass)/sample dry mass), and (*c*) volumetric moisture content (volume of water in fresh sample/volume of dry sample) for each species-group by decay-class combination. Results are based on laboratory analyses of 492 CWD samples. Sample sizes range from 48 to 83 for each data point. *P* values shown for each decay class reflect comparisons between hardwoods and softwoods. Error bars are SEs.




**Effect of harvest treatments**

Pre-harvest CWD volume was greatest in decay class 3 (Fig. 2*a*), while biomass tended to be greatest in decay class 2 (Fig. 2*b*). Both harvest treatments increased the volume and biomass of decay class 1 CWD in the form of logging slash, with the 20% treatment showing a greater increase than the 10% treatment and both harvest treatments showing greater increases than the control (Fig. 2). Decay class 2 CWD increased similarly in both harvest treatments and the control. Overall increases in decay class 1 and 2 CWD during the 3 years include contributions from a severe ice storm in 1998 (Irland 1998). Therefore, assessing the

**Fig. 2.** Mean (*a*) volume and (*b*) biomass of CWD according to decay class and silvicultural treatment. Volumes were based on direct measure of 7599 pieces; biomass was estimated from species- (or species group) and decay-class-specific densities determined in the laboratory and applied to field measures. Error bars are SEs.




true effect of harvesting on CWD requires subtracting off the ice-storm contributions, which represent about 75% of the volume increase in the 10% treatment and about 45% in the 20% treatment, based on increases evident in the control.

These treatment effects were reflected in ANOVAs addressing changes in CWD volume and biomass from pre- to post-harvest (Table 2). Significant decay class, harvest treatment, and the decay class × treatment interaction terms each reflect the results shown in Fig. 2; however, the presence of an interaction suggests caution in drawing conclusions concerning the main effects (Sokal and Rohlf 1981). The significant interaction indicates that harvesting treatment influenced the amount of CWD, but this influence was not consistent across decay classes. Harvest-related increases in decay class 1 CWD likely account for the significant interaction.

The declines in the volume of CWD in decay classes 3 and 4 across the treatments likely reflect a limitation in our tagging and re-measurement procedures. We initially used aluminum tags and nails for marking all CWD. This system worked well for class 1 and 2 material; however, given the soft consistency of the class 3 and 4 material, nails did not hold well, and tags were occasionally lost during the 3 years between inventories. The advanced state of decay (pieces being incorporated into the soil in many cases) limited our recovering such pieces that were tagged in the pre-harvest sample. This limitation occurred on both treatment and control plots, so was not related to harvesting activities. During the post-harvest sampling, we improved the marking of well-decayed CWD by affixing an aluminum tag to a PVC pipe driven into each piece.

To evaluate the effects of harvesting on size-class distributions of CWD, we examined both volume and abundance (number of pieces) by diameter class (Fig. 3). Both harvest treatments contributed disproportionately more to the smaller size classes (12.5 and 17.5 cm diameter), although marginal increases were evident in the 27.5 and 32.5 cm diameter classes.

**Table 2.** Analysis of variance for pre- and post-harvest differences in CWD volume and biomass.

| Source | df | MS | *F* | *p* |
|---|---|---|---|---|
| **Volume difference** | | | | |
| Decay class | 3 | 14.04 | 28.82 | <0.0001 |
| Harvest treatment | 2 | 1.48 | 3.03 | 0.069 |
| Block | 2 | 0.48 | 0.99 | 0.387 |
| Decay class × treatment | 6 | 1.09 | 2.24 | 0.078 |
| Error | 22 | | | |
| **Biomass difference (log transformed)** | | | | |
| Decay class | 3 | 0.170 | 55.81 | <0.0001 |
| Harvest treatment | 2 | 0.012 | 3.91 | 0.035 |
| Block | 2 | 0.003 | 1.07 | 0.360 |
| Decay class × treatment | 6 | 0.009 | 3.23 | 0.020 |
| Error | 22 | | | |

## Discussion

### CWD density and moisture content

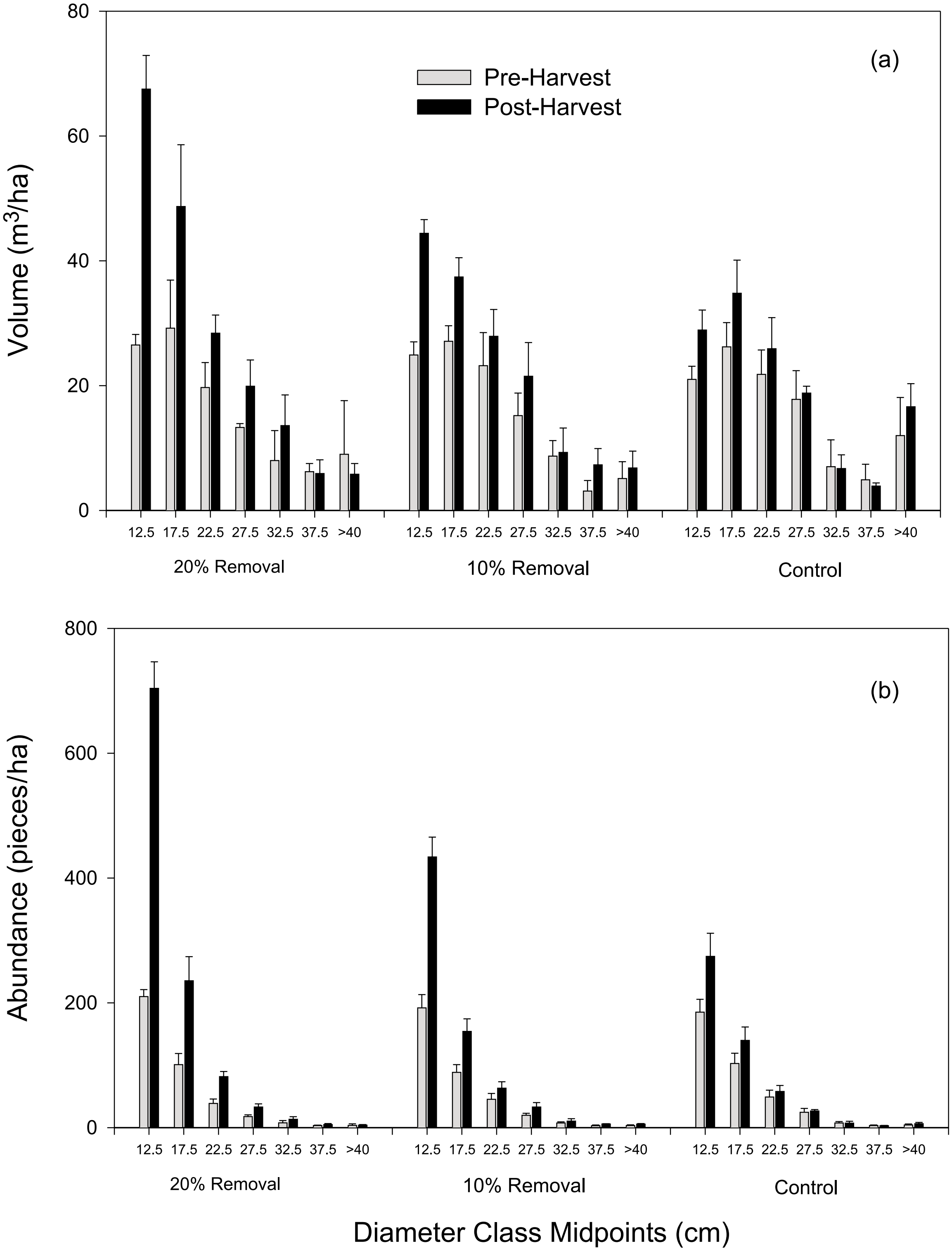
The densities of CWD in our study are similar to those previously reported for comparable decay classes and species in this region (McFee and Stone 1966; Lambert et al. 1980; Foster and Lang 1982; McGee et al. 1999). Declines in wood density for both hardwoods and softwoods as decay advances is not surprising given that many of the tactile traits used to assign decay class are implicit assessments of wood density. Following tree death, density decreases (i.e., pore volume increases) through leaching and increasing activity of microbes and channelizing invertebrates (Graham 1925; Shigo 1969; Ausmus 1977; Harmon et al. 1986). Our results indicate that upon reaching decay class 4, hardwoods and softwoods become indistinguishable in terms of wood density (Fig. 1*a*).

Linear contrasts showed that for hardwoods, all decay classes were distinct in terms of wood density. Results from softwoods were similar but showed that decay classes 3 and 4 could not be distinguished from one another. The similarity between these two classes suggests difficulty in assigning advanced decay classes to softwoods in the field. This problem likely results from the distinct decay processes observed in *Abies balsamea* and *Thuja occidentalis*. In contrast to other softwoods in this forest type, sizeable individuals of these two species often have punky or pocket-rotted heartwood, even when alive, suggesting an inside-out sequence of decay. The remaining softwoods have a more typical decay process where sapwood is decayed first, owing to its lack of decay-resistant extractives (Panshin and de Zeeuh 1980). Although assignment of decay classes emphasizes surface conditions of the log, pieces in advanced decay states may have decayed heartwood exposed, thus complicating decay-class assignments for softwoods. Stewart and Burrows (1994) also commented on the difficulty of applying decay classes to species that rot inside-out. Our field experience has indicated that hardwood logs may also present this problem, but such logs are far less common and do not appear to complicate the assignment of decay classes in this study. Nevertheless, the four-class system of assessing decay used in this study provided a reasonably reliable method of estimating wood density, which is strongly correlated with many important ecological functions of CWD.

As mentioned above, detailed ANOVAs were deemed inappropriate for the moisture-content data, given that moisture in CWD fluctuates considerably with changes in temperature, rainfall, and season (Savely 1939; Graham 1925; Boddy 1983; Maser and Trappe 1984; Harmon and Sexton 1995; Chueng and Brown 1995). The values presented here represent only a single point in a continuous cycle of hydration and dehydration experienced by CWD. Although we acknowledge the limitations of these data, they do suggest that well-decayed material holds more water than non-decayed material, and that hardwoods hold more water than softwoods in the first three decay classes (see Figs. 1*b* and 1*c*). A key factor influencing water-holding capacity, but not quantified in this study, is contact with the forest floor. CWD pieces resting on the forest floor are significantly wetter than elevated pieces (Graham 1925). This factor may outweigh the influence of species group or decay class.

Further, the volume of stored water per unit area reported here (18.5 $m^3$/ha or 1.85 L/$m^2$), even in an exceptionally dry period, provides evidence of substantial water storage capacity in CWD. The high water-holding capacity of CWD makes it an extremely important structural feature of the forest. Although moisture in CWD fluctuates through time, CWD still provides a large and relatively stable source of moisture when compared with leaf litter or mineral soil. While mineral soil adsorbs 20–40% of its dry mass in water (Brady 1990), CWD in this and other studies holds well over 200% (Savely 1939; Sollins et al. 1987; Chueng and Brown 1995; Harmon and Sexton 1995; Takahashi et al. 2000). Well-decayed CWD is particularly important in this regard, as it has the highest moisture content (Savely 1939; Lampert and Lang 1980; Maser and Trappe 1984; Sollins et al. 1987; Takahashi et al. 2000). Indeed, the moisture thus stored facilitates the process of wood decomposition, as the activity of wood-decaying fungi becomes negligible below mass moisture contents of 25–30% (Panshin and de Zeeuw 1980). Further, the water storage and spongelike structure of well-decayed logs makes them ideal habitat for moisture-sensitive amphibians, especially salamanders whose body form allows them to travel under logs and through well-decayed debris (Heatwole 1962; Jaeger 1980; Petranka et al. 1994).

**Fig. 3.** Mean (*a*) volume and (*b*) abundance (number of pieces) of CWD according to diameter class and silvicultural treatment. Diameters were measured at the largest end. Error bars are SEs.




## Pre-harvest CWD measures

The pre-harvest CWD volume and biomass reported here are slightly higher than those of other studies of managed, uneven-aged stands in central or eastern North America (Gore and Patterson 1986; Tyrrell and Crow 1994; Goodburn and Lorimer 1998; McGee et al. 1999). The higher values are likely the result of *Abies balsamea* mortality following the spruce budworm outbreak of 1972–1986 (although named the spruce budworm, it causes greatest damage to *Abies balsamea* (Seymour 1992)). These outbreaks occur in cycles of ca. 35 years in the Acadian region (Royama 1984; Krause 1997), possibly producing cyclic pulses of *Abies balsamea* dominated CWD that lag behind the outbreak by one to several decades, as snags are gradually converted to

CWD. The proportion of CWD attributable to the recent outbreak is difficult to assess in this study, but its importance can be seen in the relative ranking of *Abies balsamea* in the overstory and CWD components: *Abies balsamea* ranked fifth in living volume but first in CWD volume. *Abies balsamea* snags also represented 53% of the individuals in decay classes 2 and 3.

The projected area of CWD (an estimate of log surface area potentially available for seedling establishment) of 252.2 $m^2$/ha (2.52% of ground surface) found in this study is similar to that reported from forests of the central or eastern North America (MacMillan 1981; Shifley et al. 1997), yet is substantially lower than that reported from northwestern North America, where CWD can cover from 10 to 25% of the forest floor (see Harmon and Sexton 1995; Clark et al. 1998).

### Harvesting effects and CWD dynamics

Most harvesting systems, including uneven-aged management systems, eventually cause reductions in large-diameter, advanced-decay CWD (Hansen et al. 1991; Freedman et al. 1996; Fridman and Walheim 2000). Comparison of our results of CWD abundance with those from old-growth, mixed-species stands (of similar species composition to our site) in the Acadian forest shows a deficit in large (>35 cm diameter) CWD from a mean of 33.7 pieces/ha in old growth (Chokkalingham 1998) to 9.8 pieces/ha in this study (post-harvest treatments). Similar reductions have been found in uneven-aged forest stands in central and eastern North America (Goodburn and Lorimer 1998; Hale et al. 1999; McGee et al. 1999). These authors report CWD volume of uneven-aged stands under selection management to be intermediate between that of even-aged stands (age range 65–103 years) and old-growth stands of similar species compositions, the additional CWD in selection stands originating from fallen snags and large cull trees left after harvesting. To replenish what may be a current deficit of large-diameter CWD at this study site, the FERP treatments have allocated 10 and 30% of the initial stand basal area to permanent reserve trees, which have a mean diameter at breast height (DBH) of 47.9 cm. As these reserve trees die and become CWD, they will provide important functions as biological legacies (sensu Franklin et al. 2000) intended to persist through many cutting cycles.

Natural disturbances generally add CWD in all size classes, while harvesting activities as shown in this study, typically add smaller diameter debris or slash (although cull trees may contribute some larger diameter debris). Periodic additions of logging slash, which tend to decompose rapidly (Edmonds et al. 1986; Harmon et al. 1986; Mattson et al. 1987; Siitonen et al. 2000), do not result in persistent shifts in diameter- or decay-class distributions of CWD. Although fine woody debris or logging slash may contribute to the richness of wood-inhabiting cryptogams (Kruys and Jonsson 1999), saproxylic insect diversity (Schiegg 2001), or conifer seedling survival (McInnis and Roberts 1995), when compared with large-diameter CWD, it likely has less ecological value because of its rapid decomposition.

Large-diameter, well-decayed CWD provides the greatest benefits in terms of water retention and suitable substrates for cryptogam and seedling establishment. Research from Sweden has shown that logs in intermediate to advanced states of decay are most suitable for the persistence of cryptogams (Andersson and Hyttebron 1991; Bader et al. 1995; Kruys et al. 1999). Further, the scarcity of decayed CWD in Swedish forests has been implicated in that country's decline in abundance of fungal species (Rydin et al. 1997). Many studies have identified the importance of well-decayed wood in tree-seedling establishment (Harmon and Franklin 1989; Hofgaard 1993; Szewczyk and Szwagrzyk 1996; Timoney and Robinson 1996; Takahashi et al. 2000), as the substrate is thought to provide a moist, stable seedbed.

We had expected a reduction in class 4 CWD volume and biomass following harvesting, owing to the mechanical crushing from harvesting equipment (see Freedman et al. 1996). The greatest post-harvest reduction, however, was observed in the control plots that experienced no harvesting (Fig. 2). As indicated in the Materials and methods, our data were somewhat limited by tagging techniques used in the pre-harvest sampling of advanced-decay material; however, we can offer no explanation for the disproportionate reduction in class 4 material in the control plots.

Although preliminary data from this study are insufficient to reveal a long-term temporal trend resulting from this harvesting system, we would expect to see periodic pulses (concomitant with the cutting cycle) of small-diameter, rapidly decaying logging debris and a slow increase in large diameter debris as retention trees die. In areas with abundant *Abies balsamea*, this species would likely be added to the CWD pool in cycles equivalent to, but lagging behind, spruce budworm outbreaks.

The majority of the literature addressing CWD temporal trends comes from even-aged stands. Early in their development, such stands contain relatively large CWD volumes as a result of disturbance-generated debris plus residual CWD from the pre-disturbance stand. As the stand matures, CWD decreases, both from decomposition and the lack of new additions. Over time, volume again increases from natural mortality in the maturing stand. This U-shaped pattern, evident in both volume and biomass, has been reported throughout North America (Bormann and Likens 1979; Gore and Patterson 1986; Spies et al. 1988; Hansen et al. 1991; McCarthy and Bailey 1994; Sturtevant et al. 1997; Clark et al. 1998; Herbeck and Larsen 1999; Spetich et al. 1999; Idol et al. 2001). Forests of the Acadian region of Maine, however, are rarely found to be even aged. Here, stand-replacing natural disturbances occur infrequently (Lorimer 1977; Chokkalingam 1998; Seymour et al. 2002). For example, Lorimer (1977) estimated a return interval for large-scale windthrow at 1150 years. Much more common are small-scale or patchy disturbances, such as wind and ice storms, spruce budworm outbreaks, and selective logging activities, resulting in forests with uneven-aged structures (Cary 1894; Westveld 1931; Seymour 1992; Chokkalingam 1998). Forests of this region are more likely to receive additions of CWD episodically (as in most disturbances) or periodically (as in the ca. 35-year cycle of spruce budworm outbreaks or in silvicultural systems using a regular cutting cycle). As a result, CWD volume and biomass in these forests would likely achieve neither a steady-state condition nor a U-shaped pattern evident in even-aged forests.

Understanding the complexity of CWD temporal trends in the Acadian forest requires long-term study on permanent plots; the shortcomings of space-for-time substitutions (see Introduction) mentioned by Pickett (1989) become especially evident when such chronosequences are applied to these systems. The controlled experimental approach used here provides a direct assessment of harvesting and other disturbance effects on the abundance, volume, biomass, composition, and decay- and size-class distributions of CWD in the Acadian forest.

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