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Assessing the role of natural disturbance and forest management on dead wood dynamics in mixed-species stands of central Maine, USA

Joshua J. Puhlick, Aaron R. Weiskittel, Shawn Fraver, Matthew B. Russell, and Laura S. Kenefic

Abstract: Dead wood pools are strongly influenced by natural disturbance events, stand development processes, and forest management activities. However, the relative importance of these influences can vary over time. In this study, we evaluate the role of these factors on dead wood biomass pools across several forest management alternatives after 60 years of treatment on the Penobscot Experimental Forest in central Maine, USA. After accounting for variation in site quality, we found significant differences in observed downed coarse woody material (CWM; ≥7.6 cm small-end diameter) and standing dead wood biomass among selection, shelterwood, and commercial clear-cut treatments. Overall, total dead wood biomass was positively correlated with live tree biomass and was negatively correlated with the average wood density of nonharvest mortality. We also developed an index of cumulative harvest severity, which can be used to evaluate forest attributes when multiple harvests have occurred within the same stand over time. Findings of this study highlight the dynamic roles of forest management, stand development, and site quality in influencing dead wood biomass pools at the stand level and underscore the potential for various outcomes from the same forest management treatment applied at different times in contrasting stands.

Key words: silviculture, tree mortality, spruce budworm, harvest severity index, woody debris.

Résumé : Les réservoirs de bois mort sont fortement influencés par les perturbations, les processus de développement des peuplements et les activités d'aménagement forestier. Cependant, l'importance relative de ces facteurs peut varier dans le temps. Dans cette étude, nous évaluons le rôle de ces facteurs sur les réservoirs de biomasse de bois mort en fonction de plusieurs options d'aménagement forestier après 60 années de traitement à la forêt expérimentale de Penobscot, dans le centre du Maine, aux États-Unis. Après avoir tenu compte de la variation dans la qualité de station, nous avons observé des différences significatives dans les débris ligneux grossiers au sol (DLG; diamètre au fin bout ≥7,6 cm) et la biomasse de bois mort sur pied entre la coupe de jardinage, la coupe progressive et la coupe rase commerciale. Globalement, la biomasse totale de bois mort était corrélée positivement avec la biomasse des arbres vivants et négativement avec la densité moyenne du bois mort non récolté. Nous avons aussi développé un indice d'intensité cumulative de récolte, qui peut être utilisé pour évaluer les attributs de la forêt lorsque de multiples récoltes sont survenues avec le temps dans le même peuplement. Les résultats de cette étude mettent en évidence les rôles dynamiques de l'aménagement forestier, du développement des peuplements et de la qualité de station quant à leur influence sur les réservoirs de biomasse de bois mort à l'échelle du peuplement et souligne la possibilité que le même traitement d'aménagement forestier appliqué à différents moments dans différents peuplements produise différents résultats. [Traduit par la Rédaction]

Mots-clés : sylviculture, mortalité des arbres, tordeuse des bourgeons de l'épinette, indice d'intensité de récolte, débris ligneux.

Introduction

Dead wood is an important component of ecosystem structure and function (Harmon et al. 1986; McComb and Lindenmayer 1999; Siitonen 2001). Specifically, dead wood plays a key role in nutrient cycling, provides habitat for a wide array of organisms, and is incorporated into forest soils where it can exist in various stages of decomposition (Harmon et al. 1994; Moroni et al. 2015; Stokland et al. 2012). Several methods, including estimation of dead wood biomass additions from records of tree mortality, can be used to better quantify dead wood abundance and enhance our understanding of its dynamics. The severity and frequency of live and dead tree biomass removals for forest product utilization or the combustion of biomass during wildfire can also influence dead wood abundance and dynamics (Bradford et al. 2012; Hessburg et al. 2010; Smirnova et al. 2008). Although developing indices of cumulative disturbance severity remains a challenge in ecology and related fields, these indices could also improve our understanding of dead wood dynamics. However, most dead wood studies have limited information on past tree mortality and disturbance, which hinders ability to infer the relationship between stand dynamics and current dead wood biomass pools.

The amount of dead wood on a site at any given time is influenced by additions (mortality) and depletions (decay and combustion). Mortality results from a wide range of natural and anthropogenic disturbance agents. It can also be caused by competition among trees for limited resources (Oliver and Larson 1996), which can be particularly high during the stem-exclusion stage of stand development as trees

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J.J. Puhlick, A.R. Weiskittel, and S. Fraver. School of Forest Resources, University of Maine, Orono, ME 04469, USA.
M.B. Russell. Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA.
L.S. Kenefic. Northern Research Station, USDA Forest Service, Bradley, ME 04411, USA.
Corresponding author: Joshua J. Puhlick (email: joshua.puhlick@maine.edu).

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begin self-thinning (Peet and Christensen 1987). In managed forests, logging residues in the form of branches and tree tops, which include fine woody materials, and portions of harvested tree boles left on site are other sources of dead wood additions. Harvesting also influences the amount of potential dead wood additions by removing live tree biomass from the site (Vanderwel et al. 2006). During harvest operations, existing dead wood pools may also be altered due to the felling of standing dead trees, physical disturbance of downed woody materials, and utilization of dead wood for forest products (Stokland et al. 2012; Vanderwel et al. 2006). The degree to which natural and anthropogenic disturbances affect dead wood pools depends on the intensity, frequency, and spatial pattern of disturbance regimes (Spies and Turner 1999).

Despite the recognized importance of partial disturbance on dead wood pools, most research has been conducted on dead wood attributes following stand-replacing disturbances and in forests with single or a few dominant tree species (Hansen et al. 1991; Siitonen 2001; Spies 1998). Following stand-replacing disturbance, dead wood stocks may follow a U-shaped pattern (i.e., high–low–high) as the stand recovers (Spies et al. 1988). However, this U-shaped pattern may not hold in multi-aged, mixed-species forests with complex disturbance regimes. Such forests are typical in northeastern North America (Lorimer and White 2003), where dead wood additions occur in repeated pulses following moderate-severity natural disturbances and partial harvests (Fraver et al. 2002; Harmon 2009). In the mixedwood (softwood–hardwood) forests of northern New England, USA, and eastern Canada, for example, the prevalent natural disturbance agents are moderate-intensity wind storms and periodic eastern spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreaks (Fraver et al. 2009; Seymour et al. 2002). The degree to which these disturbances affect dead wood dynamics depends on past forest management, as well as the timing and duration of natural and anthropogenic disturbance events. Quantifying the role of these various factors requires a long-term dataset that covers a range of conditions and has detailed records to separate natural disturbance and management effects.

The overall goal of this study was to evaluate how stand development and disturbance have influenced current dead wood biomass pools in mixed-species stands with various forest management histories on a long-term research site in central Maine, USA. Our specific objectives were to (*i*) test for differences in average downed coarse woody material (CWM) biomass (≥7.6 cm small-end diameter), standing dead wood biomass (including the portions of stumps ≥ 15.2 cm), and total dead wood biomass among selection, shelterwood, and commercial clear-cut treatments; (*ii*) evaluate variation in dead wood biomass within and between stands; and (*iii*) assess the potential of various metrics for predicting dead wood biomass using 60 years of inventory data on tree mortality and evaluate their relationship with current dead wood biomass pools.

Methods

Study site and experimental design

The study was conducted on the 1619 ha Penobscot Experimental Forest (PEF) located in central Maine, USA (44°52′N, 68°38′W; mean elevation of 43 m). The PEF is within the Acadian Forest Ecoregion, which is a transitional zone between the eastern North American broadleaf and boreal forests (Halliday 1937). Common tree species include balsam fir (*Abies balsamea* (L.) Mill), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), northern white-cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.), maples (*Acer* spp.), birches (*Betula* spp.), and aspens (*Populus* spp.). Mean annual temperature and annual precipitation are 6.2 °C and 110 cm, respectively. This study was conducted on soils derived from glacial till parent material, which are described in detail by Puhlick et al. (2016*a*, 2016*b*).

Since the 1950s, the USDA Forest Service, Northern Research Station, has maintained studies on the PEF to investigate forest response to silvicultural treatments and exploitative cuttings (Sendak et al. 2003). Each forest management treatment was assigned to two experimental units (stands) ranging from 7 to 18 ha in size. Each stand has a system of 8–21 permanent sample plots (PSPs) consisting of a nested design with 0.08, 0.02, and 0.008 ha circular plots sharing the same plot center. Trees ≥ 11.4 cm diameter at breast height (dbh; 1.37 m) are measured on the entire 0.08 ha plot, trees ≥ 6.4 cm are measured on the 0.02 ha plot, and trees ≥ 1.3 cm are measured on the 0.008 ha plot.

For the present study, we focus on stands managed according to three prescriptions (single-tree selection cutting on a 5 year cycle, three-stage uniform shelterwood cutting, and commercial clearcutting), and an unmanaged reference stand. The selection stands had been cut 11 times prior to our sampling in 2012; residual structural goals were defined using the BDq method (Guldin 1991; Smith et al. 1997) to specify target residual basal area, maximum diameter, and distribution of trees among size classes. The shelterwood stands were regenerated over a period of 17 years, with final overstory removal in the 1970s; no management has since taken place. The commercial clear-cut stands were harvested twice, once in the 1950s and again in the 1980s. During the commercial clearcuts, all merchantable trees were removed without stand tending or attention to regeneration. The reference stand was not part of the original USDA Forest Service study design but was later added because no harvesting has occurred in the stand since the late 1800s (Brissette and Kenefic 2014). Detailed descriptions and timings of each treatment and stand are presented in Sendak et al. (2003) and Brissette and Kenefic (2014). Also, the timing of harvests across replicates was not synchronized within a given number of years (Sendak et al. 2003), contributing to between-stand variation within treatment.

Before the PEF was established in 1950, repeated partial cutting and forest fires of unknown frequency and severity occurred across the forest (Kenefic and Brissette 2014). Commercial harvesting began in the late 1700s and continued until the late 1800s. In the 1950s, the stands used for this study were dominated by eastern hemlock, balsam fir, red spruce, hardwoods (mostly red maple (*Acer rubrum* L.)), and other softwoods (mostly northern white-cedar) (Sendak et al. 2003). The stands were irregularly uneven aged, with relatively low stem density in the larger size classes (Kenefic and Brissette 2014; Sendak et al. 2003). Since the 1950s, harvesting has been stem only (tree tops and branches left on site) and usually confined to the winter months. Our measurements of dead wood in 2012 were timely because the shelterwood and commercial clear-cut stands have attributes that suggest harvesting could be conducted in these stands (Table 1). For instance, the shelterwood stands had high stem densities and small tree diameters with high height to diameter ratios that indicate regenerating these stands would be more appropriate than thinning, which could result in the windthrow of residual trees. The commercial clear-cut stands could be harvested for a third time since the 1950s, which would emulate repeated partial harvesting every 30 years. This makes these treatments comparable from the standpoint that they are at the end of their harvest intervals.

Data collection

In 2012, we measured dead wood on 85 PSPs across seven stands (two replicates each of selection, shelterwood, and commercial clearcut, and one reference stand). Fine woody material (FWM) was measured along three line transects per PSP according to methods by Brown (1974). Transects were established 4 m from the PSP center and radiated outward to the 0.08 ha plot boundary at 0°, 90°, and 270°. We recorded the number of woody pieces intersecting the plane of each sampling transect. Pieces were recorded separately by size; diameters at transect < 0.6, 0.6–2.5, and 2.5–7.6 cm were recorded in the first 1, 2, and 4 m of transect length, respectively. The number of woody pieces within each size class were summed across all three transects per PSP. Because of the large number of tree species on the PEF, we used the composite average nonhorizontal correction factors and approximations for specific gravities developed

Table 1. Mean (standard deviation (SD)) and range of forest attributes by treatment in 2012 at the Penobscot Experimental Forest in central Maine, USA.

Attribute	Reference (*N* = 10)		Selection (*N* = 32)		Shelterwood (*N* = 16)		Clearcut (*N* = 27)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Live trees								
Tree density (trees·ha^{-1})	833 (287)	432–1359	3538 (2125)	507–8093	8162 (3219)	3897–15 333	7583 (4208)	3286–24 871
QMD (cm)	29.3 (5.7)	20.6–40.6	12.5 (4.7)	7.6–27.5	9.0 (1.6)	5.9–11.7	7.6 (1.3)	4.6–9.9
Total basal area (m^2·ha^{-1})	51.9 (6.1)	45.3–60.5	32.0 (5.4)	20.6–42.1	47.6 (8.0)	33.7–65.3	31.1 (6.0)	21.0–40.5
Conifer basal area (% of total basal area)	89.3 (7.8)	73.4–98.4	89.2 (8.0)	65.0–100	87.8 (11.4)	51.6–97.9	58.3 (21.3)	18.3–87.5
Pine basal area (% of total basal area)	34.4 (10.4)	13.6–45.8	3.1 (6.4)	0–26.4	23.5 (16.5)	0–60.5	3.9 (4.8)	0–17.3
Spruce basal area (% of total basal area)	4.2 (3.7)	0–11.1	21.0 (14.9)	0–60.4	21.0 (19.8)	0–71.3	5.6 (9.5)	0–47.3
Hemlock basal area (% of total basal area)	48.4 (15.6)	32.9–82.8	41.4 (18.4)	9.2–81.4	4.3 (3.2)	0.1–11.3	4.4 (6.5)	0–31.5
Balsam fir basal area (% of total basal area)	0.3 (0.4)	0–1.1	18.5 (11.3)	0.8–39.3	38.5 (17.1)	8.0–71.3	39.1 (17.5)	10.9–70.4
Dead wood (biomass, Mg·ha^{-1})								
FWM	5.2 (2.3)	2.0–8.5	5.2 (3.5)	1.3–15.6	5.2 (2.5)	0.9–10.8	3.1 (1.4)	0.7–7.3
Downed CWM	14.3 (4.6)	9.4–21.5	4.2 (3.7)	0–15.1	0.8 (0.7)	0–2.5	2.5 (3.4)	0.1–15.8
Standing dead wood	16.2 (7.1)	4.1–22.7	3.6 (2.7)	0.6–12.4	7.8 (4.7)	1.9–17.4	2.1 (1.0)	0.5–4.4
Total dead wood	35.7 (9.3)	15.7–45.5	13.0 (5.5)	3.1–26.6	13.8 (6.4)	3.6–24.9	7.7 (3.9)	2.7–21.0

Note: Live tree attributes are based on measurements of trees ≥ 1.27 cm diameter at breast height. QMD, quadratic mean diameter; FWM, fine woody material (<7.6 cm diameter); CWM, coarse woody material (≥7.6 cm small-end diameter); standing dead wood, the portions of snags and stumps ≥ 15.2 cm. *N* is the number of plots.

for the Northern Region of the USDA Forest Service to calculate the oven-dried biomass of FWM for each size class (Brown 1974). The FWM biomass values for each size class were then summed to derive a total FWM biomass estimate for each PSP.

We conducted a complete inventory of downed CWM and stumps (<1.37 m tall; otherwise classified as a snag or standing dead tree) on the 0.02 ha plots. For downed CWM pieces that crossed the plot boundary, only the portion lying within the plot was measured. If the largest ends of such pieces were outside the plot, the portion of the piece inside the plot was included in the inventory if it had a diameter ≥ 7.6 cm at the plot boundary. For each piece, large- and small-end diameters (to a minimum small-end diameter of 7.6 cm), length, decay class, and species (when possible; otherwise, softwood, hardwood, or unknown) were recorded (Waskiewicz et al. 2015). The volume of each downed CWM piece was calculated using the conic-paraboloid formula (Fraver et al. 2007*a*). For each stump, the diameter at the top of the stump, height (root collar to top of the stump), decay class, and species were recorded. For the portion of stumps > 15.2 cm from the root collar, volume was calculated using the formula for a cylinder; volume in the lower portion of stumps (i.e., ≤ 15.2 cm) was not estimated because it was not included in estimates of woody biomass additions from trees that died since the 1950s (see Summarization of historical data). Downed CWM and stump biomass was calculated using nondecayed species-specific wood and bark specific gravities and average bark volume as a percentage of wood volume (Miles and Smith 2009), as well as a decay class reduction factor (Harmon et al. 2011).

Snags ≥ 11.4 cm dbh were measured on the entire 0.08 ha plot, snags ≥ 6.4 cm dbh were measured on the 0.02 ha plot, and snags ≥ 1.3 cm dbh were measured on the 0.008 ha plot. Species, dbh, height, and decay class were recorded for each snag. Snags that could not be identified to species were recorded as softwood, hardwood, or unknown. Standing dead trees were classified as snags if their lean was ≤ 45° from vertical; otherwise, they were classified as downed CWM. Diameter–height equations developed by Saunders and Wagner (2008*a*) and Puhlick (2015) were used to estimate tree height at time of death. If the observed height was less than the predicted height, then the snag was assumed to have a broken bole. In this case, predicted height at time of death and observed height were used to estimate diameter at the top of the broken bole (Russell and Weiskittel 2012). For all snags, volume was calculated by (*i*) dividing the snag into 100 sections of equal length, (*ii*) determining the large- and small-end diameters of each section using species-specific taper equations developed by Li et al. (2012), (*iii*) using Smalian's formula to calculate the volume of each section, and (*iv*) summing the section volumes (Husch et al. 2003). The volume in the stump portion of snags was excluded from these estimates because it was not included in estimates of woody biomass additions (see Summarization of historical data). Biomass was calculated using the same methods as for downed CWM. Branch biomass was not estimated for snags, so our estimates of snag biomass are likely conservative.

Live trees and shrubs were measured on PSPs to assess their influence on dead wood biomass. Species and dbh were recorded for each tree and shrub, and biomass in woody portions above a 15.2 cm stump for trees and shrubs ≥ 2.5 cm dbh and above the root collar for smaller trees and shrubs were estimated using equations developed by Young et al. (1980). We refer to live tree and shrub biomass as "live tree biomass" throughout the remainder of the manuscript. On PSPs where we measured tree heights, a soil pit was excavated to estimate depth to redoximorphic features, which was taken as a measure of site quality. These PSPs were selected in a random, stratified process, with stratification according to the proportion of major soil types on glacial till within each replicate (Puhlick et al. 2016*a*). For the remaining PSPs, we used estimates of depth to redoximorphic features made by Olson et al. (2011).

Summarization of historical data

Our methods required that we estimate dead wood inputs since the inception of the treatments at the PEF. Of the 85 PSPs on which dead wood was measured in 2012, 78 of them had tree mortality records dating back to the 1950s (Kenefic et al. 2015); records were only available for 3 of the 10 PSPs in the reference stand. For these 78 PSPs, we tallied the number of trees that had been harvested or died due to nonharvest mortality agents since the 1950s; other plots were not used in the analysis involving tree mortality data (see Models of dead wood biomass using tree mortality data). The USDA Forest Service measured live trees on PSPs every 5 years (every 10 years starting in 2000) and before and after harvest; trees that had died since the previous inventory were recorded as mortality. Prior to 1981, the agent of mortality is unknown for all but harvested trees. Since that time, mortality codes in addition to harvest include spruce budworm, suppression, breakage, uproot, timber stand improvement (used for saplings only, 1987), and animal damage (1992).

Using these data, we developed an index of cumulative harvest severity to be used as a predictor in analyses of current dead wood biomass. The index includes the severity of past harvests (here with biomass removed), as well as a down-weighting to account for harvests more distant in the past, such that a low-severity recent harvest

Table 2. For each treatment and stand number, the mean (standard deviation) and range of observed dead wood biomass and explanatory variables included in models of dead wood biomass are shown.

	Reference 32B (N = 3)		Selection 9 (N = 13)		Selection 16 (N = 19)	
Variable	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
FWM (biomass, Mg·ha^{-1})	3.1 (1.0)	2.0–3.9	3.8 (1.9)	1.3–9.0	6.1 (4.0)	1.9–15.6
Downed CWM (biomass, Mg·ha^{-1})	16.2 (5.8)	9.6–20.2	4.8 (4.5)	0–15.1	3.9 (3.1)	0.2–12.5
Standing dead wood (biomass, Mg·ha^{-1})	9.3 (7.2)	4.1–17.5	4.2 (3.5)	0.6–12.4	3.2 (2.0)	0.7–8.5
Total dead wood (biomass, Mg·ha^{-1})	28.6 (12.3)	15.7–40.3	12.9 (7.0)	3.1–26.6	13.2 (4.3)	6.2–19.8
Additions (since 1950s, Mg·ha^{-1})	59.6 (18.6)	44.2–80.3	49.6 (17.6)	22.9–90.7	51.2 (14.9)	29.8–84.5
Recent additions (since 1980s, Mg·ha^{-1})	37.3 (16.9)	22.4–55.6	17.6 (6.5)	7.4–26.7	16.8 (6.0)	8.9–32.4
Harvest severity index (relative, unit less)	0 (0)	0–0	57.9 (14.8)	35.1–78.1	63.1 (12.9)	32.6–84.9
Harvest severity index (absolute, Mg·ha^{-1})	0 (0)	0–0	49.4 (20.2)	31.0–88.0	49.5 (12.0)	28.8–79.7
dbh (cm)	16.6 (2.7)	15.0–19.8	10.4 (2.9)	7.5–16.2	11.8 (3.7)	6.9–23.2
Time since death (years)	25 (5)	21–30	24 (5)	13–31	25 (6)	16–36
Wood density (kg·m^{-3})	0.37 (0.02)	0.35–0.38	0.36 (0.01)	0.34–0.38	0.36 (0.03)	0.32–0.42
Live tree biomass (Mg·ha^{-1})	248.0 (25.9)	232.7–277.8	127.4 (22.0)	96.0–162.2	115.1 (18.4)	81.1–143.3
Redoximorphic features (cm)	50 (3)	48–53	23 (13)	0–48	41 (10)	15–51

Note: The explanatory variables are the cumulative dead wood biomass additions, cumulative harvest severity index, average diameter at breast height (dbh) of FWM, fine woody material (<7.6 cm diameter); CWM, coarse woody material (≥7.6 cm small-end diameter); standing dead wood, the portions of snags and stumps

could conveniently have the same index as a moderate-severity harvest that occurred further in the past. For each tree that was killed during harvest operations, woody biomass in the bole and tops of trees and branches was estimated using equations developed by Young et al. (1980), who defined the upper portion of the bole as beginning at a diameter of 10.2 cm for trees ≥ 15.2 cm dbh and 2.5 cm or where large branches were encountered for smaller trees. For each PSP and harvest, the biomass in the boles of harvested trees ≥ 12.7 cm dbh was summed to represent biomass removals (woody biomass in the tops and branches of these trees was considered dead wood additions). Then, the percentage of merchantable bole biomass of live trees prior to harvest that was removed during the harvest operation was calculated as the harvest severity. For each PSP, each harvest severity index was then down-weighted by a time metric, which was related to years since harvest and the initiation of the long-term silvicultural study (in 1950; i.e., 62 years prior to our measurement of dead wood pools). Specifically, the weight for each harvest severity index was calculated as follows: (62 – years since harvest)/62. For each PSP, the sum of the weighted harvest severity indices was considered to be the cumulative harvest severity index. We also calculated this index in absolute terms (i.e., for each PSP and harvest, biomass removals were not divided by the biomass of live trees prior to harvest).

We also developed a metric for dead wood additions. For trees that had died due to mortality agents other than harvest since the 1950s, bole and branch biomass above the stump were estimated with Young et al.'s (1980) equations. For each PSP, the biomass from harvest residues (the tops and branches of all trees killed during harvest plus the boles of trees < 12.7 cm dbh that were killed during harvest) and trees that died due to nonharvest mortality agents was summed to represent "cumulative dead wood biomass additions". Biomass additions due to tree mortality before the 1950s and annual and episodic litter inputs from live trees were not included in our estimate of dead wood biomass additions. Our estimate does not include the boles of merchantable trees that were cut during harvests but left on plot for various reasons including excessive defect or failure to transport cut trees to the landing site.

Testing for a treatment effect on dead wood biomass

The influence of treatment on dead wood biomass was tested using linear mixed effects modeling using data collected on 85 PSPs in 2012. The response variables included (*i*) downed CWM biomass, (*ii*) standing dead wood biomass including the portions of snags and stumps ≥ 15.2 cm, and (*iii*) total dead wood biomass including all downed woody material and standing dead wood biomass. Treatment, depth to redoximorphic features, and their interaction were modeled as fixed effects, and only data from the replicated treatments (selection, shelterwood, and commercial clearcut) were evaluated. "Stand" (i.e., experimental unit) was used as a random effect to account for the nested structure of the data and potential correlation between observations from the same stand. Logarithmic transformations were applied to downed CWM biomass ($\log_{10}(x + 0.1) + 1$), standing dead wood biomass ($\log_{10}(x + 1)$), and total dead wood biomass ($\log_{10}x$) to linearize the relationship between the response and explanatory variables. Likelihood ratio tests using maximum likelihood estimation were used to determine the optimal models in terms of fixed effects. The lme function in the nlme package in R (Pinheiro et al. 2014) was used to fit the linear mixed-effects models.

Least-squares (LS) means were used to summarize the effects of the treatments on dead wood biomass and for pairwise comparisons among LS means. In this study, LS means are averages of biomass predictions over the predictors of the linear mixed-effects model. The LS means and pairwise comparisons were calculated using the lsmeans and cld functions in the lsmeans (Lenth 2014) and multcompView (Graves et al. 2012) packages, respectively, in R. For the pairwise comparisons, after applying a Tukey's honestly significant difference multiplicity adjustment, differences between dead wood biomass LS means were considered significant at $P < 0.05$.

Models of dead wood biomass using tree mortality data

This analysis focused on factors affecting downed CWM biomass, standing dead wood biomass, and total dead wood biomass on PSPs within stands. PSPs from the reference and managed stands with long-term records of tree mortality data (78 PSPs) were included in the analysis because of the emphasis on stand dynamics as opposed to specific treatment effects. In this respect, stands can be viewed as having unique stand development and disturbance histories. Mixed-effects modeling was conducted using "stand" as a random effect, and the same transformations were applied to the response variables as in the test for a treatment effect. The following explanatory variables were evaluated for inclusion in the models as fixed effects: cumulative dead wood biomass additions from the 1950s to 2012, cumulative harvest severity index, average dbh of trees ≥ 1.3 cm that had died due to mortality agents other than harvest since the 1950s (henceforth, nonharvest mortality), average time since death of nonharvest mortality, average wood density of nonharvest mortality, live tree biomass in 2012, and depth to redoximorphic features (Table 2). Recent (since the 1980s) dead wood biomass additions, average dbh of nonharvest mortality, average time since death of nonharvest mortality, and average wood density of nonharvest mortality were also evaluated for inclusion in the model of standing dead wood biomass. For correlated explanatory variables ($r \geq |\pm 0.3|$), the variable with the best bivariate fit with the response variable (in terms of R^2, root

Shelterwood 23B (N = 9)		Shelterwood 29B (N = 7)		Clearcut 8 (N = 17)		Clearcut 22 (N = 10)	
Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
6.5 (2.4)	3.0–10.8	3.6 (1.5)	0.9–5.2	3.1 (1.6)	0.7–7.3	3.2 (1.1)	1.1–4.7
0.8 (0.9)	0–2.5	0.8 (0.6)	0.1–2.1	1.9 (3.7)	0.1–15.8	3.4 (2.5)	0.3–7.5
10.7 (3.4)	5.6–17.4	4.0 (3.1)	1.9–10.6	1.9 (0.9)	0.5–3.4	2.4 (1.3)	0.7–4.4
17.9 (4.3)	12.2–24.9	8.4 (4.0)	3.6–16.2	6.9 (4.1)	2.7–21.0	9.0 (3.4)	4.3–13.8
56.6 (15.4)	29.5–81.2	49.3 (11.4)	35.4–72.0	65.8 (13.3)	44.3–85.3	67.4 (13.1)	49.2–93.2
25.8 (7.1)	15.9–37.1	13.3 (6.4)	6.5–25.7	7.7 (3.8)	2.1–15.6	10.1 (4.9)	3.6–18.1
58.5 (3.2)	52.6–64.4	59.9 (4.2)	54.6–67.0	55.3 (1.2)	52.1–58.0	61.5 (11.5)	30.8–68.9
26.6 (8.0)	8.0–32.4	33.3 (6.7)	24.6–46.0	43.0 (11.5)	26.2–62.7	49.6 (18.3)	13.8–77.6
4.5 (1.0)	3.5–6.5	4.9 (2.1)	3.3–9.0	6.1 (2.1)	3.3–10.4	9.0 (2.3)	5.9–12.7
18 (1)	16–20	15 (3)	12–22	21 (3)	15–27	24 (4)	17–30
0.37 (0.02)	0.34–0.42	0.38 (0.01)	0.37–0.40	0.41 (0.02)	0.36–0.45	0.38 (0.03)	0.34–0.44
142.6 (10.1)	129.0–155.0	117.0 (31.6)	86.5–183.2	94.1 (16.6)	56.2–127.2	85.1 (16.8)	62.2–113.4
40 (7)	30–53	34 (17)	8–53	19 (11)	0–36	25 (12)	8–43

nonharvest mortality, time since death of nonharvest mortality, wood density of nonharvest mortality, live tree biomass in 2012, and depth to redoximorphic features. ≥ 15.2 cm. N is the number of plots.

mean square error, and F ratio) was included in the mixed-effects model.

Results

Dead wood attributes

The unmanaged reference stand had, on average, greater total dead wood volume and biomass than the managed stands (Table 2). Downed CWM and standing dead wood volumes were 53.8 ± 17.1 and 50.3 ± 21.3 $m^3 \cdot ha^{-1}$ (mean ± SD), respectively, in the reference stand and 12.7 ± 14.9 and 12.8 ± 10.6 $m^3 \cdot ha^{-1}$, respectively, in the managed stands. Across managed stands, FWM biomass averaged 4.4 ± 2.8 $Mg \cdot ha^{-1}$, downed CWM biomass averaged 2.9 ± 3.4 $Mg \cdot ha^{-1}$, standing dead wood biomass averaged 4.0 ± 3.5 $Mg \cdot ha^{-1}$, and total dead wood (all downed woody material and standing dead wood) biomass averaged 11.3 ± 5.8 $Mg \cdot ha^{-1}$.

The selection treatment had numerous downed CWM pieces with large diameters and lengths (Supplementary Fig. S1[1]). In the selection stands, dead wood biomass additions have been relatively consistent since the 1950s, whereas the shelterwood stands have experienced a relatively high amount of recent additions (Fig. 1). In the shelterwood stands, most of the recent dead wood was in the form of small-diameter snags that have yet to be transferred to the downed CWM pool (Fig. 2). Although the commercial clear-cut stands experienced a pulse of dead wood during the ca. 1972–1986 budworm outbreak, these stands have had minimal dead wood recruitment since that time (Fig. 1). Also, though mean basal area of balsam fir at the beginning of the budworm outbreak was similar between these stands (Supplementary Table S1[1]), timing of the commercial clearcuts increased the amount of balsam fir added to the dead wood biomass pools of stand 22 (Fig. 1).

Forest management effects on dead wood biomass pools

The best model of current downed CWM biomass included forest management treatment and depth to redoximorphic features as significant fixed effects ($P < 0.05$), which explained 26% of the variation in downed CWM biomass (Table 3). A likelihood ratio test indicated that stand-level variation in downed CWM biomass was not significant (df = 1, L = 2.208, P = 0.069), but the stand random effect was retained in the model to account for nested structure of the data. Across all managed stands, depth to redoximorphic features was negatively correlated with downed CWM biomass. Pairwise comparisons indicated that the selection treatment had a greater amount of downed CWM biomass than the shelterwood (P = 0.025), whereas downed CWM biomass was similar between the selection and commercial clearcut (P = 0.168) and between the shelterwood and commercial clearcut (P = 0.691) (Fig. 3).

The best models of standing and total dead wood biomass included forest management treatment, depth to redoximorphic features, and their interaction as fixed effects. These variables explained 39% and 26% of the original variation in standing and total dead wood biomass, whereas variation in biomass between stands where the same treatment was applied accounted for 33% and 42% of the observed variance, respectively (Table 3). For both pools, the strongest correlation between depth to redoximorphic features and dead wood biomass was for the shelterwood, which was positive (Supplementary Fig. S2[1]). Pairwise comparisons suggested that the shelterwood had a greater amount of standing dead wood biomass than the commercial clearcut (P = 0.049), whereas standing dead wood biomass was similar between the shelterwood and selection (P = 0.399) and between the selection and commercial clearcut (P = 0.499) (Fig. 3). Pairwise comparisons suggested no differences between total dead wood biomass means for the managed treatments at the mean value for depth to redoximorphic features (30 cm) (Fig. 3).

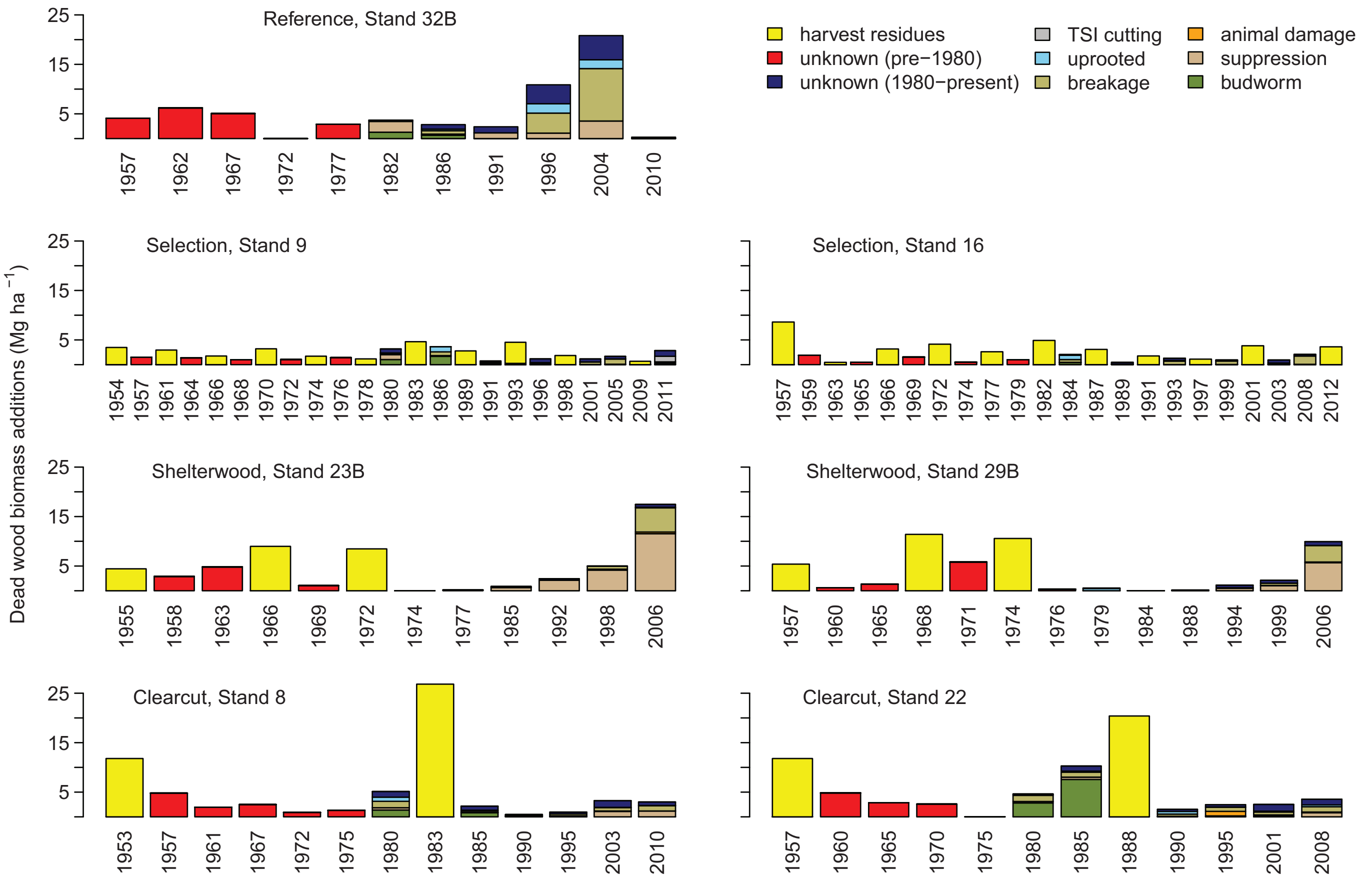
Models of dead wood biomass using tree mortality data

The following models utilized data from PSPs within the reference and managed stands and explanatory variables other than forest management treatment. Although many variables were significantly correlated with the various dead wood biomass pools (Table 4), only uncorrelated explanatory variables were used in the mixed-effects models. Relative and absolute cumulative harvest severity indices were not significantly correlated with any of the biomass pools. Only average dbh of nonharvest mortality, live tree biomass, and their interaction were considered for inclusion in the model of downed CWM biomass because average dbh of nonharvest mortality was correlated with average years since death of nonharvest mortality (r = 0.66) and average wood density of nonharvest mortality (r = −0.42); average dbh of nonharvest mortality also had the strongest correlation with downed CWM biomass (Table 4). The best model of downed CWM biomass included average dbh of nonharvest mortality as a significant fixed effect ($P < 0.05$), which explained 46% of the original variation in downed CWM biomass (Table 5). A likelihood ratio test indicated that the stand random effect was not significant (df = 1, $L < 0.001$, P = 0.5), but it was retained in the model to account for nested structure of the data.

Standing dead wood biomass was significantly correlated with several long-term (since the 1950s) and recent (since the 1980s) metrics, but the latter generally had higher correlations with standing

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0177.

Fig. 1. Mean woody biomass additions (Mg·ha⁻¹; above a 15.2 cm stump) resulting from tree mortality. Year of biomass additions represents the midpoint between permanent plot inventories; in years when harvests were conducted, inventories occurred immediately before and after the harvest. Although inventories were usually conducted every 5 years, the longer time period between the 1999 and 2009 inventories in stand 32B corresponds to the 2004 bar. For stands 32B, 23B, and 22, no mortality data exist for the time periods 1970–1975, 1972–1975, and 1973–1977, respectively. TSI = timber stand improvement (mainly, the release of desirable saplings by cutting other saplings with brushsaws). Figure is provided in colour online.



dead wood biomass. Recent dead wood biomass additions were correlated with average dbh of the three largest trees that had died due to recent nonharvest mortality agents (r = 0.61), average years since death of recent nonharvest mortality (r = 0.36), average wood density of recent nonharvest mortality (r = −0.35), and live tree biomass (r = 0.67). The best model of standing dead wood biomass included recent dead wood biomass additions as a fixed effect, which explained 52% of the original variation in standing dead wood biomass (Table 5), indicating that standing dead wood biomass was positively correlated with recent dead wood biomass additions. Variation in standing dead wood biomass between stands where the same treatment was applied accounted for 24% of the observed variance.

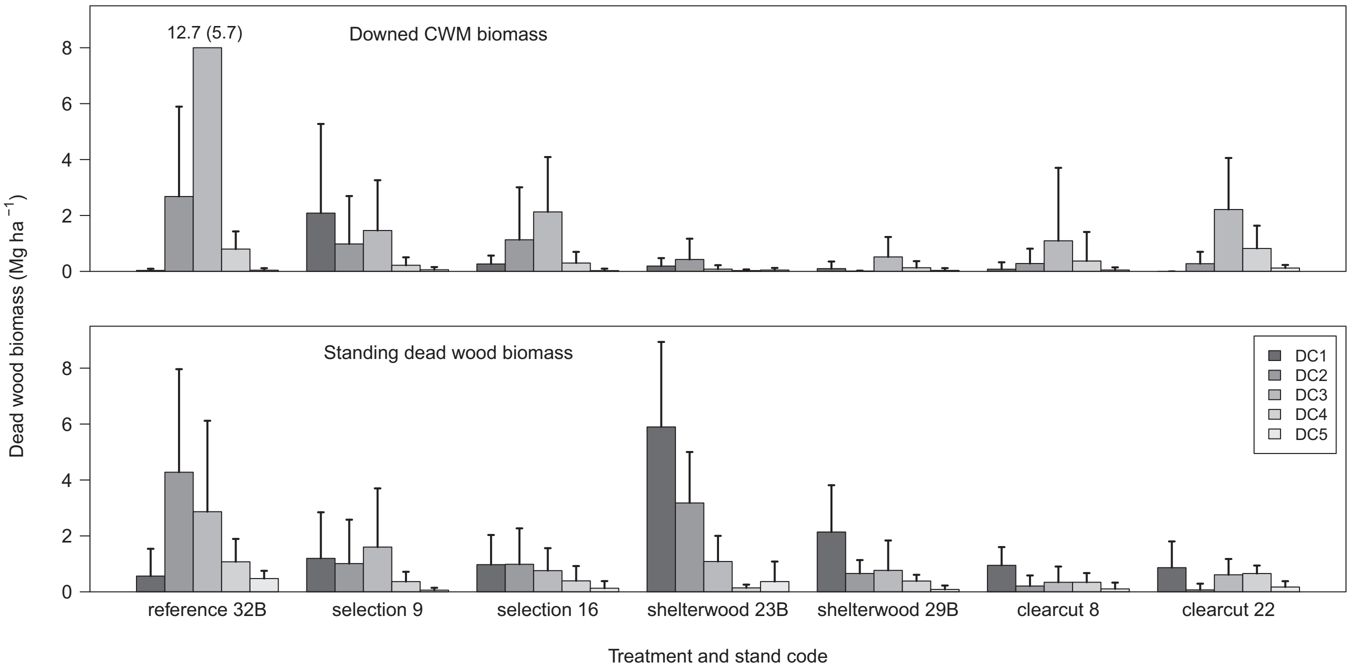
Only average wood density of nonharvest mortality, live tree biomass, and their interaction were considered for inclusion in the model of total dead wood biomass because average wood density of nonharvest mortality was correlated with average dbh of nonharvest mortality (r = −0.42), and live tree biomass was correlated with depth to redoximorphic features (r = 0.43). The best model of total dead wood biomass included average wood density of nonharvest mortality and live tree biomass as fixed effects. These variables explained 35% of the original variation in dead wood biomass, whereas the stand random effect accounted for 11% of the observed variance (Table 5). Total dead wood biomass was positively correlated with live tree biomass and was negatively correlated with average wood density of nonharvest mortality.

Discussion

Dead wood attributes

Comparison of dead wood volume or biomass estimates between studies is often confounded by the use of different inventory techniques, site productivities, disturbance histories, and dead wood decomposition rates, which vary by species, dead wood type, climate, and region. With this caution in mind, our average estimate of downed CWM biomass in the managed stands (2.9 Mg·ha⁻¹) was lower than the estimate reported for Maine (9.79 Mg·ha⁻¹) by Woodall et al. (2013), which was based on a state-wide inventory. Although the inventory of downed CWM was different between studies (i.e., fixed area plots were used in our study, whereas line-intercept transects were used in the state-wide inventory), both methods generally provide consistent estimates with a sufficient sample size. Our study was restricted to soils derived from glacial till; on other soils such as those derived from marine deposits and with poor drainage (e.g., Biddeford soil series), downed CWM biomass may be greater, particularly if species with long residence times are present (e.g., northern white-cedar). Also, in other stands across Maine, tree mortality due to eastern spruce budworm (in the 1970s and 1980s) was greater than that observed on the PEF (see Trends in dead wood dynamics), which could partially explain the difference in average downed CWM estimates between studies.

Fig. 2. Mean downed coarse woody material (CWM; Mg·ha⁻¹; small-end diameter ≥ 7.6 cm) and standing dead wood (Mg·ha⁻¹; above a 15.2 cm stump) biomass, with standard deviations in various decay classes (DC) for the managed stands.



Estimates of standing dead wood biomass in managed stands are less common but are generally lower than those of unmanaged stands (Jonsson et al. 2005; Lassauce et al. 2011; Lonsdale et al. 2008). The unmanaged reference stand, which was dominated by large pine and hemlock trees, had downed CWM and standing dead wood biomass pools similar to old-growth stands in northern New England, USA (Hoover et al. 2012), and volumes similar to old-growth, pine-dominated forests in Fennoscandia and northern Russia (Siitonen 2001). The average biomass of downed CWM in the reference stand (14.3 Mg·ha⁻¹) was near the lower range of estimates for stands at the Big Reed Forest Reserve in northern Maine (17.3–46.3 Mg·ha⁻¹; S. Fraver, unpublished data). However, our estimate of downed CWM biomass was higher than pretreatment estimates (5.81 ± 1.45 Mg·ha⁻¹) made in 1995–1997 for other stands on the PEF that have since been harvested (Fraver et al. 2002, 2007*b*). The contribution of standing dead wood to the total CWM pool of the reference stand was higher than that reported by D'Amato et al. (2008) for hemlock-dominated forests in New England, USA. These differences may be partially due to the longer residence times of pine snags in comparison with snags of other species (Siitonen 2001); however, few studies report the residence times of hemlock snags.

Forest management and site quality effects on dead wood biomass pools

After accounting for depth to redoximorphic features, which was used as an indicator of site quality, we found differences in average downed CWM biomass among the selection, shelterwood, and commercial clear-cut treatments. The greater amount of downed CWM biomass in selection stands compared with the shelterwood stands may be partially due to the frequent recruitment of large diameter trees into the dead wood pool of the selection stands and the small size of live trees in the shelterwood stands. Large trees incorporated into dead wood pools naturally result in high downed CWM biomass. The similar amount of downed CWM biomass in the selection and commercial clear-cut stands was likely due, in part, to the incorporation of trees killed by the budworm into the dead wood pools of these stands during the well-documented ca. 1972–1986 budworm outbreak. In contrast, the shelterwood stands were relatively young at the time of the outbreak, and no tree mortality pulse due to budworm was detected.

The greater biomass of downed CWM on soils with poor drainage could be related to stand composition, which has been relatively stable over at least the last 60 years (Saunders and Wagner 2008*b*), and longer residence times of conifers when compared with hardwoods (Russell et al. 2014). We tested this hypothesis by evaluating the correlation between conifer dominance (i.e., the percentage of total basal area represented by conifers in 2012) and depth to redoximorphic features; however, the correlation was not significant. Also, when soils are intermittently ponded (i.e., standing water is present above the organic horizon during portions of growing season), the moisture content of downed CWM can increase, which in turn can slow decay rates and lead to the accumulation of CWM (Harmon et al. 1986). However, field observations between May and November 2012 indicated that the saturated zone was almost always below the organic horizon for all soils. Even so, Bond-Lamberty et al. (2002) found that woody material with modest moisture levels had lower average decay rates on poorly drained soils in comparison with well-drained soils. Russell et al. (2012) also hypothesized that snags on poorly drained soils have poor mechanical stability, which could lead to transfers of woody material to the downed CWM pool. Although these findings may partially explain the higher biomass of observed downed CWM on soils with poor drainage in this study, further research on the role that soil drainage has on dead wood biomass and dynamics is needed.

In the shelterwood stands, stand 23B had more standing and total dead wood biomass than stand 29B, likely due to differences in the onset of competition-induced mortality. Even-aged red spruce and balsam fir stands generally begin self-thinning when relative densities reach 0.67 (Wilson et al. 1999). In 2011, the relative densities for stands 23B and 29B were 0.76 and 0.64, respectively, which suggests that stand 23B was experiencing competition-induced mortality and 29B had yet to experience competition-induced mortality in all areas within the stand. Site quality can also influence the onset and progression of self-thinning. Though 23B and 29B are approximately the same age, current dominant height values suggest that stand 23B is on a more productive site and that site quality partially

Table 3. Model fit statistics for mixed-effects models of dead wood biomass pools (Mg·ha^{-1}) that contained treatment and depth to redoximorphic features (DRF; cm) as fixed effects and "stand" as a random effect (b_i).

Biomass pool	a_i (SE) Selection	a_i (SE) Shelterwood	a_i (SE) Clearcut	x_i (SE) Selection	x_i (SE) Shelterwood	x_i (SE) Clearcut	Marginal R^2	Conditional R^2	Residual SE (Mg·ha^{-1})	b_i SE (Mg·ha^{-1})
Log_{10} (downed CWM + 0.1) + 1	1.810 (0.208)	1.222 (0.225)	1.416 (0.218)	−0.011 (0.005)	−0.011 (0.005)	−0.011 (0.005)	0.259	0.336	0.445	0.178
Log_{10} (standing dead wood + 1)	0.809 (0.142)	0.666 (0.238)	0.527 (0.193)	−0.006 (0.003)	0.005 (0.005)	−0.003 (0.005)	0.387	0.502	0.194	0.138
Log_{10} (total dead wood)	1.308 (0.148)	0.842 (0.242)	0.945 (0.202)	−0.008 (0.003)	0.006 (0.005)	−0.004 (0.004)	0.261	0.466	0.184	0.156

Note: CWM, coarse woody material; SE, standard error. Dead wood biomass = $a_i + (>x_i)(\mathrm{DRF}) + b_i$.

affected the onset of self-thinning, which in turn influenced standing dead wood biomass. On average, stand 23B also had more FWM biomass than stand 29B, which influenced differences in total dead wood biomass between the shelterwood stands. Differences in the amount of recent mortality and degree of crown abrasion between the two stands due to the onset of self-thinning could have affected the amount of broken twigs and small branches transferred to the FWM pool.

In the commercial clear-cut stands, stand 8 had less total dead wood biomass, on average, than stand 22, likely related to the timing of harvest entries during the ca. 1972–1986 budworm outbreak. Stand 8 was harvested in 1983, which reduced the amount of living biomass that could have been a potential source of dead wood if killed by the spruce budworm or secondary stressors. It is also likely that budworm-killed trees were salvaged in stand 8 before substantial decay occurred. In contrast, by the time stand 22 was harvested (in 1988), many trees had been killed by the budworm and were unlikely to be salvaged due to advanced decay. Evidence of this can be seen in the large amount of downed CWM biomass in decay class 3 and 4 materials observed in stand 22 in 2012. Furthermore, our estimates of merchantable spruce and balsam fir volume harvested from live trees in stand 22 in 1988 are in agreement with harvest records (USDA Forest Service, unpublished data) for the entire stand (32.8 m^3·ha^{-1} compared with 31.2 m^3·ha^{-1} of spruce and fir pulpwood; 13.3 m^3·ha^{-1} compared with 13.6 m^3·ha^{-1} of spruce sawlogs).

Models of dead wood biomass using tree mortality data

The positive correlation between the average diameter of nonharvest mortality (referred to as "size" hereafter) and downed CWM biomass was likely because large (both in diameter and length) downed CWM pieces have longer residence times (Russell et al. 2014). The recent death of many small-diameter trees in the shelterwood stands may also partially explain this correlation. These stands have low downed CWM biomass, and trees that have recently died are in the form of standing dead wood and have yet to be transferred into the downed CWM pool. Large live trees also have a greater potential of being blown over and incorporated into the downed CWM pool than do smaller trees (Foster 1988; Foster and Boose 1992; Peterson 2007). For example, several of the recently uprooted trees on PSPs in the reference stand were large-diameter trees that contributed to the downed CWM biomass pool.

The average wood density of nonharvest mortality and live tree biomass were significant predictors of total dead wood biomass. The negative correlation between dead wood biomass and the average wood density of nonharvest mortality was likely related to differences in the decay rates of conifer and hardwood dead wood. Conifer wood of forests in the eastern United States exhibits lower decay rates and longer residence times than hardwoods (Russell et al. 2014); in our study, species with low to intermediate nondecayed wood densities were mostly conifers (northern white-cedar, balsam fir, eastern white pine, red spruce, and eastern hemlock), whereas species with high wood densities were hardwoods (gray birch, paper birch, and red maple). Given slower decay of conifer wood, these results suggest that it accumulates on site, despite its generally lower densities. The positive correlation between dead wood biomass and live tree biomass is partially due to the relatively large amount of recent dead wood additions in stands with high live tree biomass (e.g., stands 32B and 23B).

Trends in dead wood dynamics

Our results indicate that frequent, low-severity, natural disturbances have occurred on the PEF over the last 60 years. These disturbances include the well-documented ca. 1972–1986 budworm outbreak that created a pulse of dead wood in some stands, as reported by Fraver et al. (2002) for other stands on the PEF. However, tree mortality due to the budworm was low compared with other areas in Maine during the 1970s. On the PEF, the mixed-species composition

Fig. 3. Least-squares (LS) means and standard errors of various dead wood biomass pools by treatment at the mean depth to redoximorphic features (30 cm). CWM is coarse woody material in Mg ha⁻¹ and was defined as material with a small-end diameter ≥ 7.6 cm. Different letters indicate significantly different LS means at $P < 0.05$.

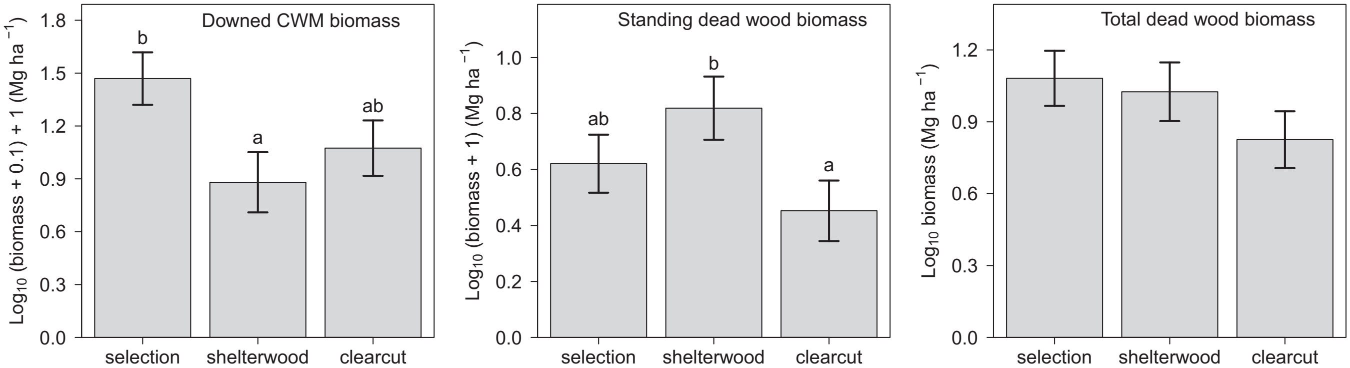


Table 4. Significant ($P < 0.05$) bivariate correlations between response variables (bold headings) and explanatory variables.

Explanatory variable	r	RMSE	F ratio
Downed CWD biomass			
Average dbh of nonharvest mortality[a]	0.68	0.41	65.91
Average years since death of nonharvest mortality	0.34	0.52	9.70
Average wood density of nonharvest mortality	−0.33	0.52	9.59
Live tree biomass[a]	0.21	0.54	3.60
Standing dead wood biomass			
Dead wood biomass additions since the 1980s[a]	0.73	0.19	84.48
Average dbh of nonharvest mortality (three largest trees)	0.42	0.24	16.40
Average years since death of nonharvest mortality	0.30	0.26	7.46
Average wood density of nonharvest mortality	−0.31	0.26	8.12
Live tree biomass	0.54	0.23	31.49
Total dead wood biomass			
Average dbh of nonharvest mortality	0.42	0.23	16.35
Average wood density of nonharvest mortality[a]	−0.44	0.23	18.03
Live tree biomass[a]	0.49	0.22	24.44
Depth to redoximorphic features	0.25	0.24	4.92

Note: For downed coarse woody material (CWD) and total dead wood, nonharvest mortality included trees ≥ 1.3 cm that had died since the 1950s; for standing dead wood, nonharvest mortality included trees that had died since the 1980s. RMSE, root mean square error; dbh, diameter at breast height.

[a]Explanatory variables that were not highly correlated ($r < |\pm 0.3|$) with one another were included in preliminary mixed-effects models.

Table 5. Model fit statistics for mixed-effects models of dead wood biomass pools that contained various fixed effects and "stand" as a random effect (b_i).

Biomass pool	Model of biomass (Mg·ha⁻¹)	Intercept SE	Slope SE	Marginal R^2	Conditional R^2	Residual SE (Mg·ha⁻¹)	b_i SE (Mg·ha⁻¹)
Log_{10} (downed CWM + 0.1) + 1	0.434 + 0.092(dbh) + b_i	0.108	0.011	0.464	0.464	0.407	<0.001
Log_{10} (standing dead wood + 1)	0.346 + 0.019(recent additions) + b_i	0.062	0.003	0.518	0.630	0.169	0.095
Log_{10} (total dead wood)	1.527 − 2.172(wood density) + 0.003(live tree biomass) + b_i	0.366	0.910, 0.001	0.347	0.427	0.196	0.070

Note: The fixed effects were live tree biomass (Mg·ha⁻¹) in 2012, recent dead wood biomass additions (since the 1980s; Mg·ha⁻¹), average diameter at breast height (dbh; cm) of nonharvest mortality, and average wood density (kg·m⁻³) of nonharvest mortality. CWM, coarse woody material; SE, standard error.

of stands made them less vulnerable to the budworm compared with 50- to 60-year-old, pure-fir stands in other areas of Maine (Seymour 1992). Also, the timing of timber harvesting relative to the onset of the budworm outbreak had a long-lasting influence on dead wood biomass pools. For example, overstory removals in the shelterwood stands occurred around the onset of the outbreak. Our results indicate that no large tree mortality due to the budworm and associated dead wood recruitment occurred in these stands. In contrast, low to moderate levels of tree mortality due to the budworm were detected in the reference, selection, and commercial clear-cut stands. Currently, trees that were killed due to the budworm (primarily balsam fir) mainly exist as downed CWM in advanced stages of decay.

Tree mortality due to tree-to-tree competition and senescence has also contributed to dead wood biomass additions on the PEF. Competition-induced mortality is most apparent in the shelterwood stands, which are undergoing self-thinning. Dead wood additions in these stands are generally in the form of small-diameter snags, so dead wood transferred to the downed CWM pool will likely have low residence times. In the reference and selection stands, senescence has likely contributed to dead wood additions. For example, we observed many weakened larger, live spruce and recently recruited snags in these stands. However, larger trees are often subject to a wide range of other mortality agents, including wind and insects (Fraver et al. 2008; Lorimer et al. 2001; Taylor and MacLean 2007).

Although our indices of relative and absolute cumulative harvest severity were not correlated with dead wood biomass pools in 2012, they could be used to evaluate dead wood biomass pools or other forest attributes at different points in time. In 2012, the average cumulative harvest severity indices were similar among the managed stands (Table 2). Puhlick (2015) also found no difference in long-term harvested wood product carbon storage among the same managed treatments, which indicates a similar cumulative impact on a related response variable. Unlike the cumulative severity index proposed by Peterson and Leach (2008), our indices include a time element to weight individual disturbances according to years since disturbance and the start of the long-term silvicultural study in 1950. The temporal weighting can be adjusted for the desired emphasis placed on more recent disturbances compared with those that occurred in the distant past. For example, dividing each harvest's severity (e.g., the percentage of preharvest biomass removed) by years since harvest would place less emphasis on recent harvests compared with the time element that we used. Ultimately, the severity and time metrics should be based on ecological knowledge about the specific variables being evaluated.

Conclusion

Overall, this study highlights the relationships between forest management, stand dynamics, and site quality with regard to dead wood biomass pools at the stand level. In addition to type of forest management treatment, timing of harvest relative to natural disturbance events and site factors related to rates of stand development and composition have important effects on dead wood dynamics. The unmanaged reference stand had greater total dead wood volume and biomass than the managed stands. Across forest management treatments, dead wood biomass pools were correlated with dead wood biomass additions, average size of nonharvest mortality, the average wood density of nonharvest mortality, and current live tree biomass. Our index of cumulative harvest severity can also be used to evaluate the impact of disturbances on a variety of forest attributes. This study also highlights the value of long-term silvicultural studies that track tree mortality and dead wood attributes throughout time to improve our understanding of dead wood dynamics in multi-aged, mixed-species forests with complex disturbance regimes.

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