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Impacts of post-harvest slash and live-tree retention on biomass and nutrient stocks in *Populus tremuloides* Michx.-dominated forests, northern Minnesota, USA

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ABSTRACT

Globally, there is widespread interest in using forest-derived biomass as a source of bioenergy. While conventional timber harvesting generally removes only merchantable tree boles, harvesting biomass feedstock can remove all forms of woody biomass (i.e., live and dead standing woody vegetation, downed woody debris, and stumps) resulting in a greater loss of biomass and nutrients as well as more severe habitat alteration. To investigate the potential impacts of this practice, this study examined the initial impacts (pre- and post-harvest) of various levels of slash and live-tree retention on biomass and nutrient stocks, including carbon (C), nitrogen (N), calcium (Ca), potassium (K), and phosphorus (P), in *Populus tremuloides* Michx.-dominated forests of northern Minnesota, USA. Treatments examined included three levels of slash retention, whole-tree harvest (WTH), 20% slash retention (20SR), and stem-only harvest (SOH), factored with three levels of green-tree retention, no trees retained (NONE), dispersed retention (DISP), and aggregate retention (AGR).

Slash retention was the primary factor affecting post-harvest biomass and nutrient stocks, including woody debris pools. Compared to the unharvested control, stocks of biomass, carbon, and nutrients, including N, Ca, K, and P, in woody debris were higher in all treatments. Stem-only harvests typically contained greater biomass and nutrient stocks than WTH, although biomass and nutrients within 20SR, a level recommended by biomass harvesting guidelines in the US and worldwide, generally did not differ from WTH or SOH. Biomass in smaller-diameter slash material (typically 2.5–22.5 cm in diameter) dominated the woody debris pool following harvest regardless of slash retention level. Trends among treatments in this diameter range were generally similar to those in the total woody debris pool. Specifically, SOH contained significantly greater amounts of biomass than WTH while 20SR was not different from either WTH or SOH.

Within *P. tremuloides* systems, we observed high stocks of smaller diameter slash material for all prescribed slash retention treatments. Most notably, WTH retains much more material than anticipated, up to 50% of available slash. These results reflect the high levels of breakage during winter harvest operations in these stands and, consequently, warrant consideration when anticipating the impacts of biomass harvesting on woody debris pools. Further investigation is necessary to understand how deliberate slash retention levels and season-of-harvest impact woody debris in other forest systems.

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1. Introduction

With increasing global demand for cleaner, renewable energy sources, there is considerable and growing interest in utilizing forest-derived biomass as bioenergy feedstocks. The removal of bioenergy feedstocks (biomass harvesting) from forested ecosystems can include typically unmerchantable components of these systems (i.e., saplings, shrubs, deadwood, and stumps) potentially resulting in a much greater impact on organisms and ecosystem functions than traditional roundwood harvests (Benjamin et al., 2010; Janowiak and Webster, 2010). Many plants and animals rely on standing trees and deadwood as a source of habitat and intensive removal of forest structural components may have detrimental impacts on these organisms (Kruys and Jonsson, 1999; Åstrom et al., 2005; Riffell et al., 2011). Moreover, removal of forest structural components can significantly impact carbon and nutrient dynamics within forested ecosystems (Mann et al., 1988; Belleau et al., 2006; Eriksson et al., 2007) potentially resulting in decreased site productivity. As a consequence, several regions have developed formal biomass harvesting guidelines specifying retention

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of post-harvest legacies, including fine and coarse woody debris and live trees (Vanha-Majamaa and Jalonen, 2001; MFRC 2007; Benjamin et al., 2010; Briedis et al., 2011). Little is known, however, about the effectiveness of these management actions at ameliorating the ecological impacts (i.e., effects on site nutrients and habitat) of biomass harvesting.

Most nutrients in trees are more highly concentrated in logging slash (i.e., branches and foliage) than other aboveground tree components, most notably the stemwood (Alban et al., 1978; Whittaker et al., 1979; Smith et al., 1986; Wang et al., 1995; Klockow, 2012. Logging slash is typically unmerchantable in conventional harvest (stem-only harvest, SOH) systems and includes tree tops generally above the merchantable diameter on the bole. This material is retained on site following harvest, providing inputs of nutrients and organic matter into the soil (Johnson and Todd, 1998; Belleau et al., 2006). Whole-tree harvesting (WTH) is a common practice for pulp, paper, and fiber production in North America in which the entire tree is harvested with no intentional woody retention on site. This practice results in a greater removal of biomass from a site, specifically the logging slash typically left behind after SOH (Mann et al., 1988). The effects of SOH and WTH on site nutrients and organic matter have been widely studied and several studies have found that SOH results in lower removal of site biomass and nutrients (i.e., roughly 1/3 less material removed) when compared with WTH (Hendrickson et al., 1987; Mann et al., 1988). Results from some longer-term studies of WTH impacts suggest that WTH does not strongly affect soil nutrient stocks over one or more decades following harvest (Alban and Perala, 1992; Johnson and Todd, 1998; McLaughlin and Phillips, 2006; Wall and Hytönen, 2011; Tamminen et al., 2012), whereas others have found that these removals can result in nutrient depletion and declines in forest productivity on certain soil types, including lower fertility soils with sandy textures (Perala and Alban, 1982; Smolander et al., 2008, 2010; Vanguelova et al., 2010; Helmisaari et al., 2011; Jones et al., 2011). Given the recognized importance of slash in maintaining soil nutrient capital and providing habitat, there is a great need for empirical estimates of slash levels immediately following harvest, whether from incidental breakage during harvest operations or prescribed levels of slash retention. Such estimates would be useful for forecasting the impacts of repeated biomass harvests and assessing the effectiveness of recommended slash retention guidelines at mitigating these effects.

In addition to slash retention, variable live-tree retention (green-tree retention) harvest systems in which live mature trees are retained following regeneration fellings have become a common forest management strategy around the globe (Franklin et al., 1997; Vanha-Majamaa and Jalonen, 2001; Gustafsson et al., 2012). Green-tree retention practices were developed in response to concerns over the loss of mature forest habitat and associated biodiversity within managed areas and have been formally integrated into management guidelines for many regions (USDA and USDI, 1994; Anonymous, 1999 (Canada); Aubry et al., 1999; Anonymous, 2006 (Norway); MFRC, 2007). Several studies have demonstrated the benefits of retaining green-trees for promoting regeneration and biodiversity of vegetation, insects, and small mammals (Sullivan and Sullivan, 2001; Sullivan et al., 2001, 2008; Martikainen, 2001; Deans et al., 2003; Macdonald and Fenniak, 2007). These benefits can depend on the patterns of trees on site, which commonly include dispersed trees (DISPs) and aggregate clumps (AGRs) under varying levels of retention (i.e., percentage of basal area) (Vanha-Majamaa and Jalonen, 2001; Beese et al., 2003). Dispersed patterns of retention can provide microclimates for regenerating plants (Macdonald and Fenniak, 2007) while AGR is intended to provide habitat similar to an undisturbed forest (Halpern et al., 1999).

Dispersed and AGR green-tree retention patterns both maintain habitat following harvest and provide woody debris inputs as stands age and retained trees fall and collapse (Franklin et al., 1997). Additionally, retained trees may help or hinder regenerating trees and understory plants by providing more suitable habitat for shade-tolerant species versus shade-intolerant species, including *Populus tremuloides* (Zenner et al., 1998; Puettmann et al., 2008). The pattern of green-tree retention can also influence the distribution of slash and woody debris following harvest (Halpern and McKenzie, 2001). This accumulation of slash following harvest and subsequent litter inputs from retained trees could provide critical nutrients for the regenerating stand, yet few studies have examined nutrient cycling in stands utilizing green-tree retention systems (Titus et al., 2006). Given that green-tree retention is a component of many biomass harvests for meeting administrative and ecological requirements (Vanha-Majamaa and Jalonen, 2001), understanding how these retained trees affect regeneration, biodiversity, and slash accumulation is crucial. There is little empirical evidence, however, for how various green-tree retention patterns affect the abundance of slash and, subsequently, carbon and nutrients retained on site following a harvest.

This study examined the effects of slash retention and green-tree retention following biomass harvesting on site biomass, carbon, and nutrient stocks. Specifically, harvest treatments were established in a randomized, complete block design including prescribed slash retention levels of 0% retention (WTH), 20% retention (20SR), and 100% retention (SOH) crossed with green-tree retention levels of no trees (NONE), dispersed trees (DISP), and aggregate clumps (AGR). Treatments were applied at four *P. tremuloides* Michx.-dominated sites in northern Minnesota and each site included an unharvested control. The slash retention level of 20SR along with DISP and AGR green-tree retention were based on current forest management guidelines for the state of Minnesota (MFRC, 2007), and are similar to recommendations for other parts of the globe (Vanha-Majamaa and Jalonen, 2001; Briedis et al., 2011). Our specific objectives were to assess the effects of slash retention and green-tree retention on (1) total ecosystem biomass, carbon, and nitrogen stocks; (2) total woody debris biomass, carbon, and nutrient stocks; and (3) woody debris biomass stocks by size class through quantification of pre-harvest and immediate post-harvest forest conditions across treatments.

2. Methods

2.1. Study sites

Study sites were located in St. Louis County, Minnesota, USA near the towns of Independence, Minnesota (47°0′N, −92°24′W); Melrude, Minnesota (47°15′N, −92°19′W); south of Orr, Minnesota (48°1′N, −92°59′W); and north of Orr, Minnesota (48°9′N, −92°59′W) and were named Independence (IND), Melrude (MEL), Pelican Lake (PL), and Lost River (LR), respectively. Elevation at these four sites ranges from 395 to 428 m with slopes between 0% and 8%. Soils are till-derived loams, consisting of stony to very stony loams and sandy loams at IND and silt loams or loams at MEL, PL, and LR. More specifically, the prevalent soil series descriptions at each site included, IND: Brimson soils of coarse-loamy, isotic, frigid Aquic Dystric Eutrudepts; MEL: Dusler soils of fine-loamy, mixed, superactive, frigid Aquic Glossudalfs and Ellsburg soils of fine-loamy, mixed, superactive, frigid Typic Glossaqualfs; and PL and LR: Ashlake soils of fine, smectitic, frigid Aquic Glossudalfs and Suomi soils of fine, smectitic, frigid Oxyaquic Glossudalfs. Climate is continental with mean temperatures of −16 °C in January and 26 °C in July. Mean annual precipitation ranges between 660 and 710 mm, about 75% of which occurs between the months of May and October.

Stands were mesic and generally hardwood dominated, most notably by *P. tremuloides*. Other prevalent hardwoods included *Betula papyrifera* Marshall, *Acer rubrum* L., and *Fraxinus nigra* Marshall. In addition, commonly occurring softwoods included *Abies balsamea* (L.) Mill., *Picea mariana* (Mill.) Britton, and *Picea glauca* (Moench) Voss with occasional *Thuja occidentalis* L. and *Pinus strobus* L. The stands originated from clearcutting and ranged in age from 55 to 68 years. In addition, a few scattered trees were removed from MEL in 1999 following a windthrow event. Site index for all four sites ranges from 22 to 24 m at 50 years for *P. tremuloides*.

2.2. Study design

Each study area was approximately 40.5 ha and harvest treatments were implemented in a randomized complete block design and replicated across four blocks with each site representing one block (IND, MEL, PL, and LR). Each block was setup in a 3 × 3 fully factorial design plus an unharvested control resulting in ten stands per block, each approximately 4.1 ha in area. Treatments were designed to examine the effects of two factors, slash retention and green-tree retention, each comprised of three levels of slash retention (WTH, 20SR, and SOH) and three levels of green-tree retention (NONE, DISP, and AGR). Dispersed green-trees were prescribed with a density of approximately 15–30 trees/ha and 21 m spacing across designated stands. For AGR, two roughly square or rectangular clumps with area approximately 0.1 ha each, representing a similar stand area (5% of stand) as DISP, were located within designated stands. Prior to harvest, six permanent, 0.04 ha circular plots were located within each stand for repeated measurements and sampling. Each plot was randomly located within one of six approximately equal areas of the stand. Plots were selected such that basal area of *P. tremuloides* was determined to be >40% by sighting stems through a wedge prism. In addition, plot centers were located >20 m from stand boundaries, AGR boundaries, other plots, and wetlands; >10 m from roads or trails; and without cuttings or large anthropogenic debris within plot boundaries. For AGR stands, a single plot was setup roughly within the middle of each retained clump and plot boundaries were within clump boundaries. Plots in AGR clumps were used to capture the presence of retained biomass following harvest based on the weighted average of stand area these clumps occupied. Harvests were implemented in February of 2010.

2.3. Field-sampling methods

A number of forest components were measured and sampled within the 0.04 ha plots to assess the effects of treatments on biomass and nutrient stocks. These included large woody stems (trees), smaller woody stems (saplings and shrubs/advance regeneration), litterfall (for nutrient analyses), fine woody debris (FWD, ⩽7.5 cm dia.), coarse woody debris (CWD, >7.5 cm dia.), herbaceous vegetation, forest floor material, mineral soil, fine roots, and coarse roots (for nutrient analyses). Each component was measured prior to the harvest (summer 2009) and during the first growing season post-harvest (summer 2010).

2.3.1. Woody vegetation (trees, saplings, shrubs/advance regeneration)

Diameter at breast height (DBH), species, condition (live or dead), and, if snapped, stem height were recorded for all trees (large woody stems ⩾10 cm DBH) rooted within the 0.04 ha area of each main plot. Smaller woody stems (saplings and shrubs/advance regeneration) were measured within three nested subplots located at azimuths of 30°, 150°, and 270° with centers located 5.5 m from main plot center. DBH, species, condition (live or dead), and, if snapped, sapling stem height (woody stems ⩾2.5 cm and <10 cm DBH) were measured in 25 m^2 subplots. Species and stem diameter at 15 cm height of shrubs/advance regeneration (woody stems >15 cm height and <2.5 cm DBH) were measured in 3.14 m^2 subplots. Dead shrubs/advance regeneration were assessed via diameter measurements at 15 cm height in one subplot per plot.

2.3.2. Woody debris (FWD and CWD)

Sampling of downed FWD and CWD was based on the line-intercept method (Brown, 1974). CWD was measured along 20 m transects originating from plot center at azimuths of 30°, 150°, and 270° and included all logs >7.5 cm in diameter. Measurements included species and decay class based on a 5-class system of decay as described by Sollins (1982). Following harvest, the magnitude of slash levels removed from MEL in certain plots varied substantially as a result of operations. Consequently, woody debris levels in WTH stands (outside of the AGR clumps) were manipulated to ensure that the slash retention levels in these treatments were more consistent with the other three sites. Specifically, slash within a 20 m radius of each plot center was moved >20 m away from plot center if the slash was (a) >7.5 cm in diameter (at large end) and (b) derived from trees felled during harvest.

Smaller diameter FWD was tallied within three size classes (⩽0.6 cm, >0.6 cm to ⩽2.5 cm, and >2.5 cm to ⩽7.5 cm) along 1 m, 2 m, and 4 m transects, respectively, located along the three longer CWD transects and originating near the edge of the circular plots. Size classes were based on estimates of fuel burning times of 1-, 10-, and 100-h for the smallest to the largest size classes, respectively, and permitted a higher resolution of estimating stocks of FWD (Brown, 1974). Due to the high variability in FWD in post-harvest stands, a fourth FWD sampling transect was added, originating near plot center and oriented along the 30° azimuth CWD transect.

2.3.3. Herbaceous vegetation, forest floor, mineral soil, and roots

Samples of litterfall, herbaceous vegetation, forest floor, mineral soil, and fine and coarse roots were collected for measurement of biomass stocks as well as carbon and nutrient concentrations. Litterfall was collected in a single 45 cm diameter circular littertrap at each plot with centers located 2 m from plot center at a random azimuth. Littertraps were placed in the field before leaf-out in the spring and were collected following leaf-off in autumn of each sampling year. Herbaceous vegetation, forest floor, and soil were collected within nested subplots in the main plot centered approximately 5.5 m from main plot center. Herbaceous vegetation was sampled once within each plot by clipping at ground level within a 15 cm diameter PVC ring. The forest floor was sampled within three 15 cm diameter PVC rings nested within the main plot. Forest floor included all dead material to the surface of the mineral soil and excluded any woody debris. Three mineral soil cores of 6.35 cm diameter and 20 cm depth were collected within the same sampling area as forest floor. Soil samples were divided into two classifications by depth (not horizon depth) to quantify nutrient concentrations in shallow and deeper soils (0–5 cm, 5–20 cm depth). Fine roots with diameter ⩽5 mm at the large end and coarse roots with diameter >5 mm were removed from soil samples, dried, and weighed.

2.4. Biomass calculations

Biomass estimates of living trees and saplings were calculated using species-specific allometric biomass equations based on DBH from Jenkins et al. (2003). In addition to calculating total biomass for each tree or sapling, ratios of each tree component (i.e., coarse roots, stemwood, stembark, foliage, and branches) were used to calculate biomass estimates of the specific components of each tree (Jenkins et al., 2003). Biomass estimates of dead trees and saplings were calculated using the same equations as live individuals, excluding foliage. To calculate biomass of broken stems, stems were assumed to be parabolic and volume was calculated based on DBH and stem height following Duvall (1997), excluding bark volume. Mass of each snapped dead tree and sapling was estimated using wood specific gravities from Harmon et al. (2008), which were converted to density and multiplied by stem volume. Coarse roots of snapped dead trees and saplings were calculated from ratios derived in Jenkins et al. (2003) and were added to stem biomass estimates to create estimates of total snapped, dead tree and sapling biomass. Since no decay classes were recorded for dead trees or saplings, all densities were assumed to be within decay class 1 as defined by Harmon et al. (2008). Thus, estimates of dead tree and sapling biomass are likely overestimates of actual biomass, even with bark excluded from broken stem biomass, as stems were not exact paraboloids in volume and were likely in varying stages of decay. All pre-harvest coarse root stocks were assumed to exist immediately post-harvest.

Post-harvest woody debris biomass was estimated for five size classes. Specifically, FWD was divided into three size classes, small (FWD-S, ⩽0.6 cm), medium (FWD-M, >0.6–⩽2.5 cm), and large (FWD-L, >2.5–⩽7.5 cm), corresponding to 1-, 10-, and 100-h burning times and CWD was divided into two size classes, unmerchantable (CWD-U, >7.5–<22.5 cm) and merchantable (CWD-M, ⩾22.5 cm) sizes representing stems that were too small to be sawlogs (i.e., minimum pulpwood diameters) and those of sawlog size, respectively.

Biomass estimates for shrubs/advance regeneration were calculated using species-specific allometric biomass equations from Perala and Alban (1993) based on diameter at 15 cm height. Roots of shrubs/advance regeneration were accounted for in fine root stocks as described below. Estimates of FWD and CWD biomass were calculated using volume equations from Brown (1974) and densities derived from Harmon et al. (2008). Woody debris volume estimates were multiplied by densities specific to each species and decay class in order to obtain mass estimates. Oven-dry biomass of herbaceous vegetation, forest floor, mineral soil, and fine roots were scaled, based on sampled area, to Mg ha^{-1} or kg ha^{-1}.

2.5. Nutrient analyses and calculations

Nutrient analyses facilitated assessment of treatment impacts on post-harvest carbon (C) and nitrogen (N) pools. Litterfall, herbaceous vegetation, forest floor material, coarse and fine roots, and mineral soil were all analyzed for percent total C and N and the results were used to determine C and N stocks within each pool (i.e., foliage, herbaceous vegetation, forest floor material, coarse and fine roots, and mineral soil) by multiplying nutrient concentrations by biomass or, for mineral soil, mass. Litterfall nutrient concentrations were used to estimate nutrient stocks within foliage. This method likely underestimates foliage nutrient concentrations due to leaf senescence in hardwood species and collection of litter through leaf-off in autumn. However, these translocated nutrients were present in the smaller branch material following senescence and are represented in the woody debris nutrient pools. Pre-harvest samples were used to estimate pre- and post-harvest C and N concentrations, with the exception of mineral soil, which was collected both pre- and post-harvest. Samples were dried at 70 °C to a constant mass, ground and homogenized in Wiley mills, and analyzed for percent total C and N on a LECO Truspec CHN Macro analyzer (LECO Corporation, St. Joseph, Michigan).

Nutrient stocks in trees, saplings, shrubs, FWD, and CWD were based on intensive destructive sampling from a separate study conducted within and around the harvest sites (see Klockow, 2012). This work generated species-specific nutrient concentrations for woody debris of the predominant tree species on this site, as well as across a range of decay classes for both FWD and CWD. Nutrient concentrations were used to calculate nutrient stocks for trees, saplings, shrubs, FWD, and CWD. Calculated nutrient stocks included C and N for trees, saplings, shrubs, FWD, and CWD as well as calcium (Ca), potassium (K), and phosphorus (P) for FWD and CWD (Klockow, 2012).

Within each plot, one litterfall and one herbaceous vegetation sample was collected for a total of 240 samples of each across all sites. Nutrient concentrations in litterfall were used to estimate total nutrients in foliage for each plot. Herbaceous vegetation nutrient concentrations were generated by homogenizing samples within each treatment and using the resulting concentration value for each plot within each respective treatment. A total of 720 forest floor and mineral soil samples (three per plot) were collected and homogenized within each plot. Mineral soil samples were split by depth (0–5 cm, 5–20 cm) and roots were removed from soil samples and divided by size to represent coarse roots (>5 mm diameter) and fine roots (2–⩽5 mm diameter). Root samples were homogenized by plot (240 total homogenized root samples) within each size class and nutrient concentrations determined for calculating nutrient stocks for each root size class within a given plot.

2.6. Statistical analyses

Analysis of covariance (ANCOVA) was used to determine the effects of slash-retention and green-tree retention on post-harvest biomass, C, N, Ca, K, and P stocks using PROC MIXED in SAS (SAS Institute, Inc.). Initial ANCOVA analyses indicated no significant effect from green-tree retention so we focused exclusively on slash retention effects. Subsequently, the fixed effect within the model included slash retention and the random effect was slash retention nested within site. For all components analyzed, the dependent variable and covariate consisted of post-harvest and pre-harvest data, respectively. Accordingly, the covariate served as a control to further refine explanations of variation in post-harvest data. Diagnostics were conducted to examine whether data met the assumptions of ANCOVA, specifically, normally distributed residuals and homogeneous variances. When these assumptions were violated, data were transformed using mathematical functions commonly used for data transformations, including natural logarithm, square root, and inverse. These transformations were first tested on the dependent variable alone and when data still violated the assumptions both the dependent variable and the covariate were transformed and tested. If data still did not meet the necessary assumptions for ANCOVA, rank transformations were applied (Conover and Iman, 1982). The rank transformed data met the assumptions of ANCOVA and allowed for the use of common Post Hoc pairwise comparisons on the ranked data.

Once initial diagnostics were complete, the effect of the covariate was tested to determine its relevance in explaining variation in the dependent variable. Slopes for each treatment group in the model were estimated, and the data were examined for significant differences in the estimates of the slopes for each group and whether a common slope for all groups was significantly different from zero. If a common slope different from zero was appropriate then the covariate was included in the model to account for any pre-harvest variation in the dependent variable. If a common slope for all groups was not different from zero the covariate was dropped and analysis of variance (ANOVA) was conducted instead with transformations applied when necessary as described above. The Tukey–Kramer method was used to test for significant differences between the slash retention treatments for both ANCOVA and ANOVA. The unharvested control was not included in analyses but is presented for comparison. Significance testing was at $\alpha = 0.05$ level and data is presented in non-transformed format and prior to being adjusted for the covariate in cases in which ANCOVA was used.

3. Results

3.1. Total ecosystem biomass, carbon, and nitrogen

3.1.1. Biomass and carbon

Initial analyses indicated that green-tree retention did not significantly affect the variables analyzed in this study. Consequently, all results correspond to analyses of slash retention only which were grouped across GTR treatments within each block. Slash retention significantly affected total post-harvest biomass stocks and total post-harvest C stocks without mineral soil pools included (Table 1). Slash retention had a marginally significant effect on C stocks with mineral soil pools included (Table 1). Carbon stocks were roughly half the magnitude of biomass stocks (Tables 2 and 3). More specifically, for stocks of biomass, C with mineral soil, and C without mineral soil, SOH was significantly higher than WTH, whereas 20SR was not significantly different from WTH and SOH (Table 3). Compared to the unharvested control, all treatments resulted in substantial reductions in stocks of biomass and C in aboveground overstory vegetation (Table 2). In addition, stocks of FWD and CWD biomass and C were substantially greater in all treatments than in the unharvested control, reflecting the prescribed slash retention levels (Table 3). Stocks of C within the mineral soil were far greater than any other pool of C within the forest systems examined (Table 3). Specifically, in the unharvested control mineral soil C represented 35% of total ecosystem C while in WTH, 20SR, and SOH, mineral soil C represented 53%, 51%, and 48% of total ecosystem C, respectively.

Table 1
ANOVA/ANCOVA table representing the effect of slash retention on post-harvest values of each variable listed. Woody debris by size class variables represented five diameter classes for both fine woody debris (FWD) and coarse woody debris (CWD). Size classes for FWD included small (⩽0.6 cm; FWD-S), medium (>0.6 cm to ⩽2.5 cm; FWD-M), and large (>2.5 cm to ⩽7.5 cm; FWD-L) and, for CWD, size classes included unmerchantable (>7.5 cm to <22.5 cm; CWD-U) and merchantable (⩾22.5 cm; CWD-M) diameters. For ANCOVA analyses, each variable analyzed was controlled for using pre-harvest values of the same variable.

Variable	ANOVA			ANCOVA		
	df	*F*	*p*	*df*	*F*	*p*
Total ecosystem						
Biomass	–	–	–	(2, 32)	3.53	0.0410
Carbon (w/o Soil)	–	–	–	(2, 32)	4.19	0.0241
Carbon (w/Soil)	–	–	–	(2, 32)	3.29	0.0504
Nitrogen (w/o Soil)	–	–	–	(2, 32)	0.89	0.4187
Nitrogen (w/Soil)	–	–	–	(2, 32)	1.10	0.3451
Total woody debris						
Biomass	–	–	–	(2, 32)	13.06	<0.0001
Carbon	–	–	–	(2, 32)	13.26	<0.0001
Nitrogen	–	–	–	(2, 32)	0.28	0.7580
Calcium	–	–	–	(2, 32)	9.72	0.0005
Potassium	–	–	–	(2, 32)	14.84	<0.0001
Phosphorus	–	–	–	(2, 32)	6.88	0.0033
Woody debris by size class[a]						
FWD-S	(2, 33)	0.45	0.6394	–	–	–
FWD-M	(2, 33)	3.75	0.0341	–	–	–
FWD-L	(2, 33)	7.16	0.0026	–	–	–
CWD-U	–	–	–	(2, 32)	4.45	0.0198
CWD-M	–	–	–	(2, 32)	0.76	0.4749

n = 36 for all variables.
[a] Each variable represents biomass stocks for that particular size class.

3.1.2. Nitrogen

Slash retention did not significantly affect total post-harvest N stocks without mineral soil or with mineral soil included (Table 1 and 3). Stocks of N within the mineral soil were by far the greatest in magnitude among all pools of N (Table 3) and represented similar proportions, approximately 83%, of total N stocks. Nitrogen in standing trees and saplings was very low (Table 2) and the unharvested control had similar stocks of total N as in the slash retention treatments (Table 3). Excluding mineral soil, N stocks in pools of coarse roots and forest floor were substantially greater than any other pool of N (Tables 2 and 3, respectively). Other pools with relatively high levels of N included understory vegetation, particularly herbaceous material, and FWD.

3.2. Woody debris (FWD and CWD) biomass and nutrients

3.2.1. Biomass and carbon

Slash retention influenced both biomass and C of total post-harvest woody debris (Table 1). Biomass and C in SOH were significantly greater than WTH and 20SR while WTH and 20SR did not significantly differ (Fig. 1a and b). Biomass and C stocks in FWD were roughly similar in magnitude to stocks in CWD within each slash retention treatment following harvest (Fig. 1a and b). However, if legacy woody debris (stocks in unharvested control) were excluded from post-harvest stocks, FWD would tend to have a greater magnitude of biomass and C than CWD following harvest.

3.2.2. Other nutrients (N, Ca, K and P)

Slash retention influenced Ca, P, and K stocks in total post-harvest woody debris (Table 1). For Ca and P, SOH had significantly greater stocks than WTH while 20SR was similar to both WTH and SOH (Fig. 1d and f). For K, SOH displayed the highest stocks, WTH the lowest, and K stocks in 20SR were intermediate between these two (Fig. 1e). In contrast, slash retention had no significant effect on stocks of N (Table 1) in total post-harvest woody debris (Fig. 1c). Across all slash retention treatments, stocks of N and P were substantially greater in FWD than in CWD (Fig. 1c and f) while stocks of Ca and K were relatively similar in magnitude within both the FWD and CWD pools (Fig. 1d and e). If legacy woody debris (stocks in unharvested control) were excluded, all nutrient stocks (N, P, Ca, and K) would be greater in FWD than in CWD.

3.3. Woody debris biomass by size and treatment

Biomass in woody debris by size class was significantly different among slash retention treatments for FWD-M, FWD-L, and CWD-U but not for FWD-S or CWD-M (Table 1). For FWD-M and CWD-U, SOH treatments had significantly greater stocks of biomass than WTH treatments while 20SR treatments were similar to both (Fig. 2). For FWD-L, both 20SR and SOH treatments were similar and had significantly greater stocks of biomass than WTH treatments (Fig. 2). The smallest and largest size class groupings, FWD-S and CWD-M, did not differ significantly between each level of slash retention (Fig. 2). Within each size class, the magnitude of biomass stocks within slash retention treatments appear larger than stocks in the unharvested control, most notably for FWD-M, FWD-L, and CWD-U.

4. Discussion

Given the growing interest in forest-derived biomass as a source of bioenergy and associated concerns regarding ecological impacts, there is an urgent need for empirical studies of the impacts of operational biomass harvesting on post-harvest nutrient stocks and forest structure. Although a number of US states and

Table 2
Post-harvest overstory and understory vegetative biomass in Mg ha^{-1}, C in Mg ha^{-1}, and N in kg ha^{-1} by ecosystem component and slash retention treatment (WTH – whole-tree harvest, 20SR – 20% slash retention, SOH – stem-only harvest). Table shows means and standard errors that have not been adjusted for the respective covariates.

Treatment	Overstory vegetation					Understory vegetation			
Slash	Live trees	Dead trees	Live saplings	Dead saplings	Coarse roots[a]	Live shrubs	Dead shrubs	Herbs	Fine roots[b]
Biomass									
Control	121.48 (7.48)	11.49 (1.57)	4.44 (1.23)	0.76 (0.13)	32.84 (1.73)	0.74 (0.24)	0.21 (0.13)	1.02 (0.05)	1.87 (0.22)
WTH	1.73 (0.40)	0.19 (0.11)	0.10 (0.04)	0.01 (0.00)	29.67 (2.22)	1.13 (0.15)	0.20 (0.05)	1.88 (0.22)	2.35 (0.34)
20SR	1.67 (0.35)	0.17 (0.03)	0.03 (0.01)	–	32.87 (1.70)	1.23 (0.19)	0.08 (0.03)	1.90 (0.21)	1.99 (0.06)
SOH	3.07 (0.98)	0.08 (0.05)	0.06 (0.03)	0.01 (0.01)	30.85 (2.78)	1.24 (0.15)	0.16 (0.05)	1.69 (0.26)	1.74 (0.15)
Carbon									
Control	59.70 (3.69)	5.65 (0.77)	2.20 (0.62)	0.38 (0.06)	15.27 (0.81)	0.60 (0.22)	0.11 (0.07)	0.44 (0.02)	0.87 (0.11)
WTH	0.85 (0.19)	0.09 (0.05)	0.05 (0.02)	–	13.45 (1.01)	0.62 (0.07)	0.10 (0.03)	0.83 (0.10)	1.06 (0.16)
20SR	0.82 (0.17)	0.08 (0.01)	0.02 (0.01)	–	14.85 (0.70)	0.66 (0.11)	0.04 (0.02)	0.84 (0.09)	0.90 (0.02)
SOH	1.49 (0.47)	0.04 (0.02)	0.03 (0.02)	–	13.85 (1.25)	0.66 (0.08)	0.08 (0.02)	0.74 (0.11)	0.78 (0.08)
Nitrogen									
Control	86.69 (6.01)	2.58 (0.18)	9.43 (3.53)	1.04 (0.17)	238.97 (25.10)	5.78 (1.98)	0.38 (0.24)	16.62 (1.51)	14.01 (1.14)
WTH	1.37 (0.35)	0.03 (0.01)	0.21 (0.10)	0.01 (0.00)	221.69 (20.51)	9.15 (1.26)	0.36 (0.10)	33.68 (4.47)	18.52 (3.28)
20SR	1.42 (0.35)	0.03 (0.00)	0.07 (0.03)	–	265.92 (24.25)	10.25 (1.78)	0.14 (0.05)	35.73 (5.88)	17.42 (1.44)
SOH	2.32 (0.67)	0.02 (0.01)	0.12 (0.04)	0.01 (0.01)	238.76 (27.43)	9.84 (1.26)	0.28 (0.09)	31.22 (4.24)	14.15 (1.14)

[a] Represent pre-harvest values.
[b] Represent fine roots calculated from allometric equations in Perala and Alban (1993) and shrub data.

Table 3
Post-harvest woody debris, forest floor, soil, and total ecosystem biomass in Mg ha^{-1}, C in Mg ha^{-1}, and N in kg ha^{-1} by ecosystem component and slash retention treatment (WTH – whole-tree harvest, 20SR – 20% slash retention, SOH – stem-only harvest). "Total" column contains the sum of all components from Table 2 and the current table and was the only variable examined for significant differences among treatments. Values in the same column with similar letters are not significantly different ($p > 0.05$) based on ANCOVA results. Table shows means and standard errors that have not been adjusted for the respective covariates.

Treatment	Woody debris			Mineral soil		Total	
Slash	FWD	CWD	Forest Floor	0–5 cm	5–20 cm	w/o Soil	w/Soil
Biomass							
Control	6.85 (1.60)	12.56 (2.58)	26.94 (2.48)	–	–	221.19 (8.53)	–
WTH	18.18 (1.46)	22.04 (2.06)	30.69 (1.45)	–	–	108.18 (5.04)[a]	–
20SR	24.42 (2.24)	26.13 (4.21)	33.34 (5.17)	–	–	123.84 (6.61)[ab]	–
SOH	27.93 (3.93)	31.84 (4.72)	32.54 (5.14)	–	–	131.20 (6.51)[b]	–
Carbon							
Control	3.50 (0.82)	6.07 (1.26)	10.97 (1.70)	25.51 (2.67)	31.37 (5.43)	105.75 (4.17)	162.64 (6.43)
WTH	9.29 (0.75)	10.72 (1.01)	12.14 (0.87)	23.91 (1.82)	32.10 (3.36)	49.20 (2.20)[a]	105.20 (6.18)[a]
20SR	12.48 (1.14)	12.72 (2.03)	13.95 (2.34)	26.93 (2.87)	33.04 (2.91)	57.36 (3.05)[ab]	117.34 (3.83)[ab]
SOH	14.27 (2.01)	15.55 (2.30)	13.24 (2.29)	25.41 (1.31)	30.55 (3.91)	60.75 (3.14)[b]	116.72 (2.41)[b]
Nitrogen							
Control	13.33 (3.12)	13.31 (2.59)	385.46 (74.58)	1730.61 (80.51)	2081.87 (156.52)	787.60 (62.04)	4600.08 (245.91)
WTH	35.41 (2.84)	17.53 (6.54)	373.08 (51.41)	1453.39 (101.34)	1955.48 (164.82)	711.02 (53.91)[a]	4119.89 (278.23)[a]
20SR	47.55 (4.36)	14.24 (3.08)	449.63 (117.67)	1810.47 (216.67)	2083.77 (209.99)	842.41 (95.73)[a]	4736.65 (404.82)[a]
SOH	54.38 (7.66)	10.34 (2.92)	431.96 (94.85)	1733.49 (179.67)	2167.21 (368.30)	793.41 (75.99)[a]	4694.11 (490.09)[a]

other countries have provided biomass harvesting guidelines related to slash retention (MFRC, 2007; Briedis et al., 2011) and green-tree retention levels (Vanha-Majamaa and Jalonen, 2001), few studies have assessed the effectiveness of these management strategies for mitigating site-level impacts. Correspondingly, this study provides important insight on the consequences of potential biomass-utilization management strategies for a suite of site resources, specifically nutrients and habitat (Abbas et al., 2011). The levels of slash retention examined here were intended to span a wide range of conditions, including the recommended slash retention level (20SR) for biomass harvesting within several countries and US states. Similarly, the experimental levels of green-tree retention examined are representative of existing harvest guidelines for many regions of the globe. Of these two factors, only slash retention significantly affected biomass or nutrient stocks immediately following harvest. Despite the demonstrated importance of green-tree retention for maintaining other ecosystem components following harvesting (Sullivan and Sullivan, 2001; Sullivan et al., 2001, 2008), neither green-tree retention nor the interaction between slash retention and green-tree retention significantly affected the biomass, C, and nutrients in total ecosystem components, total woody debris, or woody debris by size class immediately following harvest. This finding most likely reflects the low levels of retention in this study which, although meeting recommended guidelines, did not strongly influence post-harvest conditions. Consequently the results and following discussion focus mainly on slash retention effects with a brief discussion of green-tree retention issues.

4.1. Effects of slash retention on woody debris biomass & nutrient stocks

Slash retention impacted biomass and nutrients in woody debris. Within each treatment, biomass and all nutrients in woody debris were at least double the unharvested control, indicating high levels of slash following harvest regardless of prescribed

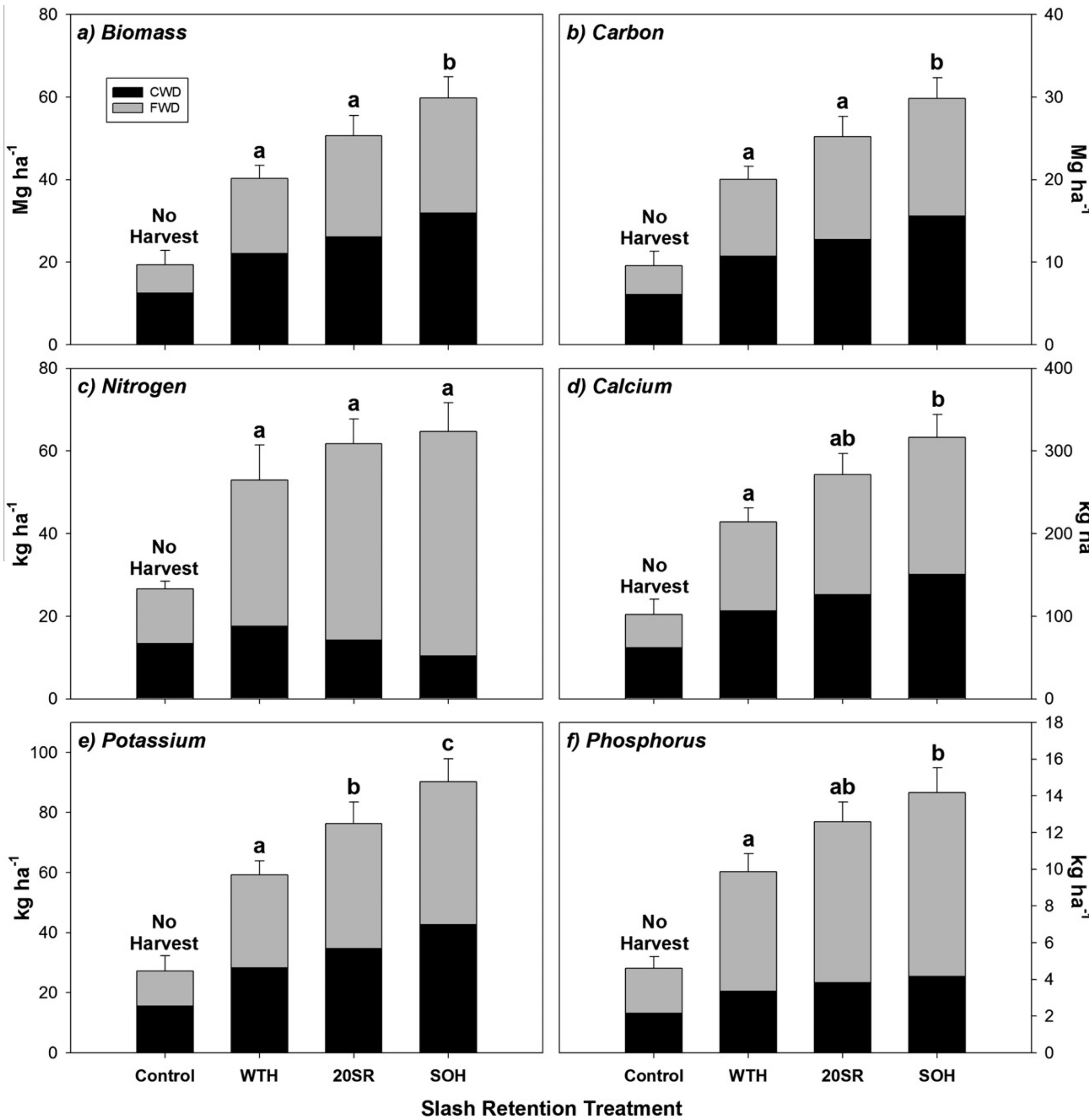

Fig. 1. Total post-harvest woody debris (a) biomass, (b) C, (c) N, (d) Ca, (e) K, and (f) P by FWD and CWD and slash retention treatment (WTH – whole-tree harvest, 20SR – 20% slash retention, SOH – stem-only harvest). Within each graph, bars with similar letters are not significantly different ($p > 0.05$) based on Tukey–Kramer comparisons from ANCOVA results. Figures show means and standard errors that have not been adjusted for the respective covariates however letters indicating statistical significance are based on adjusted values derived from ANCOVA results.

retention. The significant differences in biomass, C, Ca, K, and P between WTH and SOH treatments are consistent with trends observed elsewhere (Mann et al., 1988; Rittenhouse et al., 2012). *P. tremuloides* forests in Wisconsin had more retained slash biomass within SOH than WTH and both treatments had more slash biomass than an unharvested control (Rittenhouse et al., 2012). Similar woody debris trends with slash removal were also noted following clearcut operations in *Picea abies* systems in Finland (Eräjää et al., 2010) and intensively harvested sections of northern hardwood forests managed using selection systems in Ontario (Vanderwel et al., 2010).

Despite the common recommendation of 20% slash retention for mitigating the impacts of WTH, we found no difference in biomass, C, N, Ca, and P stocks between the 20SR treatment and the WTH treatment. Only N, Ca, and P stocks in 20SR were statistically similar to both WTH and SOH. Woody debris N concentrations in a companion study were found to be consistently low for the predominant species on site (Klockow, 2012). It is unclear as to what caused these low N levels. Additionally, Ca is an important element in *P. tremuloides* forests and exists in high concentrations (Hendrickson et al., 1987; Klockow, 2012). Potassium was the only element that differed significantly between all three slash retention levels and the only element to have significantly greater stocks in 20SR than in WTH. These results suggest that biomass and nutrients within 20SR are variable and that this level does not necessarily represent a distinct threshold of slash retention greater than WTH. Given this ambiguity, longer-term monitoring of these sites will determine if the levels of woody debris in WTH and 20SR

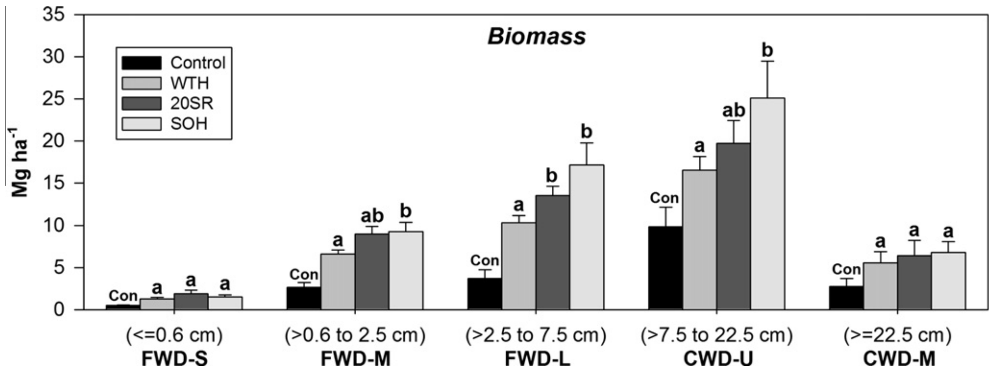

Fig. 2. Total post-harvest woody debris biomass by size class (FWD-S, M, L = small, medium, and large size classes, respectively; CWD-U, M = unmerchantable and merchantable size classes, respectively) and slash retention treatment (WTH – whole-tree harvest, 20SR – 20% slash retention, SOH – stem-only harvest). Bars within the same size class with similar letters are not significantly different ($p > 0.05$) based on Tukey–Kramer comparisons from ANCOVA or ANOVA results, depending on which analysis was most appropriate. The unharvested control (Con) was not included in statistical analyses. Where ANCOVA was applied, figures show means and standard errors that have not been adjusted for the respective covariates; however, letters indicating statistical significance are based on adjusted values derived from ANCOVA results.

represent a large enough pool of nutrients to maintain site quality following biomass harvesting, which has been suggested by other work for WTH (Alban and Perala, 1992; Johnson and Todd, 1998; Tamminen et al., 2012).

The 20SR treatment was examined in this study to facilitate evaluation of actual slash levels occurring on a site where operations are trying to achieve a targeted level of retention stipulated by biomass harvesting guidelines. Although specifying the deliberate retention of 20% of available slash, many guidelines recognized that 10–15% of available slash will be unintentionally retained on site due to breakage from harvest operations, resulting in approximately 33% of available slash retained on site (MFRC, 2007; Briedis et al., 2011). Similarly, studies from Finland and Sweden in coniferous forests indicated similar slash retention levels as prescribed in our study, achieving retention of approximately 30% and 35% of all residues (Rudolphi and Gustafsson, 2005; Peltola et al., 2011).

Quantifying percent slash retained within this study was difficult since total available slash was determined through allometric equations and not directly measured. We assumed that SOH contained 100% of available slash and that total available slash was represented by the difference between total woody debris in SOH and the unharvested control, thus excluding any influence from legacy woody debris. Using these assumptions, slash levels in WTH and 20SR corresponded to roughly 52% and 77%, respectively, of available slash following harvest. Remaining slash in the WTH and 20SR treatments was substantially greater than the expected retention levels of 10–15% and ~33% (accounting for incidental breakage) for these harvest types, respectively. Interestingly, 20SR showed 25% greater slash retention than WTH, the difference expected between the prescribed slash retention levels for these treatments. The high levels of residual slash in WTH and 20SR in our study indicate substantial slash contributions from incidental breakage following clearcut harvesting and underscore the operational nature of this study, which captured the degree of breakage of branches and stems during felling and skidding operations. This highlights the difficulty with prescribing and operationally attaining actual WTH within these systems. Smith et al. (1986) noted much less incidental breakage (10% of material retained) following summer WTH in conifer-dominated stands of *Picea rubens* Sarg.-*A. balsamea* in Maine essentially achieving the 10–15% incidental breakage expected at our sites. The degree of breakage and corresponding high levels of woody debris within WTH in our study were likely accentuated by the cold conditions during harvest (Lieffers et al., 2001; Rittenhouse et al., 2012), resulting in greater breakage of felled hardwood stems, most notably *P. tremuloides*.

We observed several important differences in the relative magnitude of nutrient pools contained within FWD and CWD. While biomass, C, Ca, and K were approximately equivalent between FWD and CWD, FWD contained a substantially greater magnitude of N and P than CWD. It is important to note that if legacy woody debris were excluded from total woody debris stocks, the magnitude of FWD stocks post-harvest would generally exceed CWD stocks. As such, these results can be attributed to the high levels of smaller FWD, regardless of legacy woody debris, following harvest operations (Eräjää et al., 2010; Rittenhouse et al., 2012) and the higher concentrations of nutrients within this material relative to CWD, specifically for N and P (Whittaker et al., 1979; Miller, 1983; Klockow, 2012). These results highlight the importance of retaining FWD as a source of nutrient stocks following intensive biomass removals.

Woody debris size strongly affects habitat value and nutrient concentrations (Juutilainen et al., 2011; Klockow, 2012) and our results suggest that the distribution of biomass between different woody debris size classes was strongly affected by the type of slash retention treatment applied. As with the total woody debris pools, the greatest differences in piece sizes were between WTH and SOH and, in one case, within FWD-L, biomass stocks in 20SR were significantly greater than WTH. These collective differences reflect the increased prevalence of smaller woody debris in treatments where slash was deliberately retained relative to WTH in which slash was not deliberately retained yet still existed in large quantities.

The observed differences in abundance of woody debris in particular size classes can have different impacts on these ecosystems. Beyond its importance as a nutrient source, FWD serves as a source of habitat in natural and managed forests (Söderström, 1988; Kruys and Jonsson, 1999; Juutilainen et al., 2011; Brazee et al., 2012). For example, Kruys and Jonsson (1999) noted that species richness of cryptogams was greater on equivalent volumes of FWD relative to CWD and similar for both FWD and CWD when consistent surface areas were compared. In addition, work examining polyporoid fungal communities in *P. tremuloides* forests indicate that smaller woody debris (<5 cm diameter) represent a key substrate for enhancing species richness in these systems (Brazee et al., 2012). Our findings suggest that the 20% slash retention recommendation for biomass harvesting can, in practice, retain a significantly greater proportion of this important substrate type for fungal communities than WTH. However, given the substantial stocks of FWD in WTH, it is possible that this treatment may also maintain sufficient habitat for fungal communities in these forests following harvest.

4.2. Effects of slash and green-tree retention on total ecosystem biomass and nutrient stocks

Given that C concentrations in woody debris are relatively consistent across species and ecosystem components (roughly 50% of total biomass at these particular sites; Klockow, 2012), we found that stand-level biomass and C stocks displayed similar patterns among treatments. In contrast, stocks of N in harvested components were very low relative to the other ecosystem pools, mostly due to the low concentrations of N and other nutrients within stemwood of trees and saplings (Johnston and Bartos 1977; Whittaker et al., 1979; Lambert et al., 1980; Jokela et al., 1981; Lang et al., 1982; Miller, 1983; Wang et al., 1995). Total ecosystem N stocks for the unharvested control fell within the range of mean total ecosystem N stocks for all slash retention treatments, reflecting in part the low concentrations of N within the stemwood of trees and saplings and the higher concentrations of N in the branches and tops (Klockow, 2012). In 20SR, the majority of branches were retained on site and in SOH all branches were retained on site, essentially transferring N in branches of standing trees and saplings to the FWD pool. Moreover, branch biomass in the unharvested control was determined through allometric equations whereas inputs of slash were measured as FWD and CWD using the line-intercept measurement. These two means of quantifying slash resulted in different estimates of potential (branches) and actual (woody debris) harvest slash stocks. Understory vegetation showed increases in N stocks compared to the unharvested control following harvest, likely due to the high levels of regeneration in the newly open conditions during the growing season following harvest (Outcalt and White, 1981).

We observed no distinct differences among slash retention levels in the size of forest floor or root biomass and nutrient pools. No major changes in forest floor were expected since this pool was not directly manipulated. Harvesting occurred during the winter, which typically results in minimal soil disturbance (Berger et al., 2004), however, disturbance to the forest floor from harvest operations can occur in late fall and winter (Mroz et al., 1985; Johnson et al., 1991). Below the forest floor, fine root stocks often extend into deep portions of the soil column (Finér et al., 2011). Despite the 20 cm sampling depth for fine roots in this study, our biomass estimates for this pool are likely a minimal underestimate given the shallow depth and stony nature of the soils at each site. Coarse root material, the larger pool of live biomass in the soil column, was derived from allometric equations using DBH from pre-harvest measurements and was assumed not to change immediately after harvest. Given that they can represent important pools of biomass and nutrient stocks for future site productivity, disturbance to forest floor and coarse roots should be minimized during biomass harvest operations.

The green-tree retention factors, as implemented in this study, did not significantly affect biomass or nutrient stocks in any of the variables analyzed and, therefore, were not included in our analyses. This result contrasts with work in *Pseudotsuga menziesii* forests within the U.S. Pacific Northwest in which different patterns of green-tree retention significantly affected ground disturbance and the accumulation of fresh CWD immediately following harvest (Halpern and McKenzie, 2001). These differences in findings could be due to the low levels of retained trees on the sites we examined relative to those in the Pacific Northwest (Halpern and McKenzie, 2001). In particular, the lowest level of tree retention examined by Halpern and McKenzie (2001) was 15% for both aggregate and dispersed patterns of retention, whereas our levels followed Minnesota guidelines and were only 5% retention for both AGR and DISP, essentially representing clearcut conditions. More detailed quantifications of slash and ground conditions following harvest, such as depth of slash and spatial distribution, and greater prescribed retention levels could result in significant effects of green-tree retention in our study sites. In addition, surveys of animal populations and regenerating plants within the various green-tree treatments would provide important information on the effectiveness of retained trees as immediate sources of habitat and at providing favorable conditions for growth, particularly with such low levels of retention.

5. Conclusions

Our results indicate that slash retention had a significant effect on post-harvest biomass and nutrient stocks, whereas there was no effect from green-tree retention immediately post-harvest. We found that the WTH treatment retained approximately half of available slash, much more than the expected 10–15% retention. Slash prevalence in 20SR was roughly 25% greater than stocks in WTH, closely matching the prescribed difference between these treatments. However, 20SR still did not result in slash conditions generally distinguishable from WTH and SOH. Large stocks of FWD biomass existed post-harvest representing large pools of C, N, Ca, K, and P regardless of slash retention level. Contrary to all other nutrients, no significant differences were observed in post-harvest N stocks across slash retention treatments.

Given the high levels of slash retained within all slash retention treatments and substantial variability in slash retained within treatments, it appears difficult to retain a precise amount of slash following harvest or to identify an ideal level for retention in these systems. In particular, the high levels of incidental breakage during winter harvest in *P. tremuloides*-dominated forests provide large inputs of nutrient-rich FWD regardless of prescribed slash retention levels. Therefore, retention of some amount of FWD should be relatively easy to achieve under typical operating conditions. It is likely that, within these systems, WTH along with minimal disturbance to forest floor and roots could represent a scenario which mitigates or at least minimizes any negative impacts of intensive biomass harvesting on site nutrient stores and subsequently on future site productivity in the short term. Following this, the slash retention level can be increased as necessary depending on concerns over specific site nutrient limitations.

These findings underscore the importance of accounting for the compositional and seasonal differences in slash levels that may occur due to incidental breakage. Most guidelines for slash retention apply a single value to all forest types and seasons of harvest, yet this and other work highlights the need for more refined guidelines that account for the range in variability in incidental breakage that may occur within a given region. Further research is necessary to understand the importance of the high levels of slash we documented as a source of habitat and their impacts on regeneration. In addition, more detailed analyses of larger CWD material will provide key information on the effects of slash retention level on CWD as a source of habitat within freshly harvested stands. Finally, continued monitoring of the harvested sites will provide crucial information on future site productivity as well as the prevalence and persistence of current and future woody debris inputs, specifically from retained green-trees.

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