Impacts of Biomass Harvesting on Biomass, Carbon, and Nutrient Stocks in *Populus tremuloides* Forests of Northern Minnesota, U.S.A.

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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 biomass (i.e., trees down through to forest floor material) resulting in a greater loss of biomass, nutrients, and habitat from a site. 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 in *Populus tremuloides*-dominated forests of northern Minnesota. Treatments examined included 0%, 20%, and 100% slash retention with no, dispersed, and aggregate live-tree retention.

Slash retention was the primary factor affecting immediate post-harvest biomass and nutrient stocks within total ecosystem and woody debris pools. High levels of biomass and nutrients in harvest slash were observed in all treatments compared to the unharvested control. Typically, 100% slash retained treatments contained significantly greater biomass and nutrient stocks than no slash retained treatments. Stocks of biomass and nutrients within the 20% slash retained treatment, a slash retention level currently recommended by Minnesota's biomass harvesting guidelines, were generally similar to both no slash retained and 100% slash retained treatments.

Given the importance of fine woody debris as a source of nutrients following harvest, nutrient concentrations were measured across an array of woody debris size and decay classes within the *Populus tremuloides*-dominated forests examined. Results indicate that fine woody debris has significantly greater nutrient concentrations than coarse woody debris. In addition, nutrient concentrations generally increased within both coarse and fine woody debris as decay progressed. Collectively, the results of this study underscore the importance of deliberate retention of fine woody debris as a source of nutrients following harvests of biomass feedstocks.

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Chapter One: Introduction

This thesis examines the impacts of silvicultural strategies on post-harvest biomass and nutrient stocks within *Populus tremuloides*-dominated forests of northern Minnesota, U.S.A. Specifically, two silvicultural practices were examined including slash retention and green-tree retention. Both of these practices were aimed at mitigating the negative impacts of harvesting forest biomass as a bioenergy feedstock by analyzing a range of levels within each factor including levels recommended within Minnesota state biomass harvesting guidelines. In order to provide more detailed analyses of the effects of slash and green-tree retention on nutrient stocks, this thesis aims to quantify and characterize nutrient concentrations of multiple size classes of woody debris across a range of decay classes and species.

The second chapter of this thesis examines three levels of slash retention and three levels of green-tree retention on biomass and nutrient stocks within *Populus tremuloides*-dominated forests of northern Minnesota. The project was implemented with support from the Minnesota Forest Resources Council, a state council developed under the Sustainable Forest Resources Act (SFRA) of 1995 to promote long-term sustainable forest management within the state of Minnesota. The impacts of three levels of slash retention and three levels of green-tree retention were assessed on post-harvest stocks of biomass and nutrients within the total ecosystem and woody debris pools. Results indicated that only the factor of slash retention had a significant effect on post-harvest conditions. Specifically, harvest retained large quantities of smaller, fine woody debris on site regardless of slash retention treatment.

The third chapter of this thesis quantifies the dynamics of nutrient concentrations within woody debris of *Populus tremuloides*-dominated forests of northern Minnesota. Specifically, the effects of species, decay class, wood type, and size of woody debris were examined on concentrations of macro- and micronutrients. The results of this study indicated that nutrient concentrations generally increased with increasing decay. Smaller, fine woody debris had greater nutrient concentrations than did larger coarse woody debris. Finally, differences in nutrient concentrations between species as well as wood types tended to vary and no distinct patterns emerged.

The fourth and final chapter of this thesis presents conclusions related to results from all chapters of this document, with emphasis placed on results from Chapter 2. Specifically, management recommendations are given based on results indicating strong effects of slash retention on biomass and nutrient stocks following harvest. This final chapter also includes a section on future research recommendations intended to point out key observations that can be made by continued monitoring of the study sites.

Chapter Two: Impacts of post-harvest slash and live-tree retention on biomass and nutrient stocks in *Populus tremuloides*-dominated forests of northern Minnesota, U.S.A.

1. Introduction:

Globally, there is considerable interest in the use of forest-derived biomass as bioenergy feedstocks. The removal of bioenergy feedstocks (biomass harvesting) from forested ecosystems includes typically unmerchantable forest components (i.e., saplings, shrubs, deadwood, and forest floor material) (MFRC 2007) potentially resulting in a much greater impact on organisms and ecosystem functions (Janowiak & Webster 2010). Many plants and animals rely on standing trees and deadwood as a source of habitat and intensive removal of these components of forest structure can have detrimental effects on these organisms (Kruys & Jonsson 1999, Åstrom et al. 2005, Riffell et al. 2011). Moreover, removal of these 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. In light of these concerns, several regions have developed formal biomass harvesting guidelines specifying retention of post-harvest legacies, including fine and coarse woody debris and live trees (Vanha-Majamaa & Jalonen 2001, MFRC 2007, 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.

Components of logging slash, including branches and foliage, typically have higher concentrations of nutrients compared to other tree components, most notably the stem wood (Alban et al. 1978, Whittaker et al. 1979, Wang et al. 1995). Logging slash is typically unmerchantable in conventional harvest (stem-only) systems and is usually retained on site following harvest, providing inputs of nutrients and organic matter into the soil (Johnson & Todd 1998, Belleau et al. 2006). Whole-tree harvesting is a common practice for pulp, paper, and fiber production and results in a greater removal of biomass from a site, specifically the logging slash generally left behind after stem-only harvesting (Mann et al. 1988). A number of studies have measured the effects of stem-only and whole-tree harvesting on site nutrients and organic matter (Boyle et al. 1973, Hendrickson et al. 1987, Mann et al. 1988, Johnson & Todd 1998, Belleau et al. 2006, Smolander et al. 2008, Smolander et al. 2010, Wall & Hytönen 2011, Jones et al. 2011, Helmisaari et al. 2011, Tamminen et al. 2012). These studies indicate that stem-only harvest results in a much lower removal of site biomass and nutrients (i.e., roughly 1/3 less material removed) when compared with whole-tree harvest (Hendrickson et al. 1987, Mann et al. 1988). A few studies suggest the greater removals associated with whole-tree harvest do not strongly affect soil nutrient stocks over one or more decades following harvest (Alban & Perala 1992, Johnson & Todd 1998, Tamminen et al. 2012). Moreover, it has been suggested that some sites could support continued, whole-tree harvests assuming inputs from precipitation, mineralization, and soil weathering provide additional nutrients and rotation lengths are not too short (Boyle et al. 1973). While most studies consider slash levels a number of years following harvest or over subsequent rotations (Rudolphi & Gustaffsson 2005, Eräjää et al. 2010, Briedis et al. 2011, Peltola et al. 2011, Rittenhouse et al. 2012), little empirical evidence exists quantifying slash levels immediately following harvest, whether from incidental breakage during harvest operations or from prescribed levels of slash retention.

Variable live-tree retention harvest systems (green-tree retention) in which live mature trees are retained following regeneration fellings (Franklin et al. 1997) have become a common component of many forest management systems around the globe (Vanha-Majamaa & Jalonen 2001). These 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 & 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 & Sullivan 2001, Sullivan et al. 2001, Martikainen 2001, Deans et al. 2003, Macdonald & Fenniak 2007, Sullivan et al. 2008). These benefits can depend on the patterns of trees on site which commonly include dispersed and aggregate clumps under varying levels of retention (i.e., percentage of basal area) (Vanha-Majamaa & Jalonen 2001, Beese et al. 2003). Dispersed patterns of retention can provide microclimates for regenerating plants (Macdonald & Fenniak 2007) while aggregate clump retention patterns are intended to provide habitat similar to an undisturbed forest (Halpern et al. 1999).

Both patterns of green-tree retention provide immediate habitat on sites following harvest as well as future inputs of woody debris as the stands age and the retained trees fall and collapse (Franklin et al. 1997). In addition, the pattern of green-tree retention can have an effect on the distribution of slash and woody debris following a harvest (Halpern & McKenzie 2001). This accumulation of slash following harvest and subsequent inputs of litter 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 & Jalonen 2001), an understanding of the way in which 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 including slash retention levels of 0%, 20%, and 100% crossed with no, dispersed, and aggregate clump green-tree retention were applied at four *Populus tremuloides*-dominated sites in northern Minnesota. Slash retention of 20% and dispersed and aggregate clump green-tree retention were based on current biomass harvesting guidelines for the state of Minnesota (MFRC 2007). The objectives of this study were to determine the effects of slash retention and green-tree retention on biomass and nutrient stocks within these harvested sites by analyzing empirical data from pre-harvest and immediate post-harvest field measurements for the various biomass harvesting scenarios applied on site.

2. Methods

2.1 Study Sites:

Study sites were located in St. Louis County, Minnesota, U.S.A. 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. Elevations at these four sites ranged from 395 – 428 m with slopes between 0 – 8%. Soils generally consisted of loams derived from till. Soils at IND consisted of stony to very stony loams and sandy loams while soils at MEL, PL, and LR were silt loams and loams. The climate of the study area is continental with a mean temperature of -16°C in January and 26°C in July. Mean annual precipitation ranges between 660 – 710 mm, about 75% of which occurs between the months of May and October.

Stands were mesic and generally hardwood dominated, most notably by *Populus tremuloides*. Other prevalent hardwoods included *Betula papyrifera*, *Acer rubrum*, and *Fraxinus nigra*. In addition, commonly occurring softwoods included *Abies balsamea*, *Picea mariana*, and *Picea glauca* with occasional *Thuja occidentalis* and *Pinus strobus*. 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 *Populus 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). Treatments were designed to examine the effects of two factors, slash retention and green-tree retention, each comprised of three levels including 0%, 20%, and 100% slash retention and no, dispersed, and aggregate clump green-tree retention. Dispersed green-trees were prescribed with a density of approximately 15 – 30 trees/ha and 21 m spacing across designated stands. For aggregate clump green-tree retention, two roughly square or rectangular clumps with area approximately 0.1 ha each were located within designated stands. Dispersed and aggregate clump green-tree retention and 20% slash retention were all based on recommendations within the Minnesota biomass harvesting guidelines (MFRC 2007) and were included in this study to examine their impacts on post-harvest stand conditions. Each block was setup in a 3X3 fully factorial design plus an unharvested control resulting in ten stands per block, each approximately 4.1 ha in area. 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 *Populus tremuloides* was determined to be >40% by sighting stems through a wedge prism. In addition, plot centers were located >20 m from stand boundaries, aggregate clump boundaries, all other plots, and wetlands; >10m from any roads or trails; and with no man-made cuttings or large man-made debris within plot boundaries. For stands prescribed with aggregate clump green-tree retention, a single plot was setup roughly within the middle of each retained clump and plot boundaries were within clump boundaries. Harvests were implemented in February of 2010.

2.3 Field-Sampling Methods:

A number of forest components were measured and sampled in order to best capture the effects of each treatment on biomass and nutrient stocks within stands. These included large woody stems (trees), smaller woody stems (saplings and shrubs/advance regeneration), litterfall (for nutrient analyses), fine woody debris (FWD), coarse woody debris (CWD), herbaceous vegetation, forest floor material, mineral soil, fine roots, and coarse roots (for nutrient analyses). Each of these components was measured both pre-harvest and immediately post-harvest during the summers of 2009 and 2010.

2.3.1 Woody Vegetation (Trees, Saplings, Shrubs/Advance Regeneration)

Diameter at breast height (DBH) was measured and recorded for all large woody stems (trees) ≥10 cm DBH rooted within the full area of each main plot. In addition, species, condition (live or dead), and snag height were recorded for each tree. Smaller woody stems (saplings, 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. Subplots for saplings were 25 m^2 in area while subplots for shrubs/advance regeneration were 3.14 m^2 in area. Saplings included all woody stems ≥2.5 cm and <10 cm DBH. Measurements for saplings included DBH, species, living or dead status, and snag height. Shrubs/advance regeneration comprised all woody stems >15 cm height and <2.5 cm DBH. Measurements for shrubs/advance regeneration included species and stem diameter at 15 cm height. In addition, dead shrubs/advance regeneration were measured within the same sampling area as live stems except only at one subplot within each plot.

Diameter at 15 cm height was the only metric recorded for dead shrubs/advance regeneration.

2.3.2 Woody Debris (FWD & CWD)

Sampling for both downed FWD and CWD was based on the line-intercept method as described by 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, manipulations to the levels of woody debris on plots designated with no slash retention and not within aggregate clumps were conducted at all sites to better reflect the prescribed level of retention. Specifically, slash from trees felled during harvest that were >7.5 cm in diameter, as measured at the base of each branch, and within a 20 m radius of plot center were moved outside the 20 m radius and, therefore, were not tallied for analyses.

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, all located along the three larger CWD transects. Size classes were based on estimates of fuel burning times of 1-, 10-, and 100-hours 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 levels of variability in FWD in post-harvest stands, a fourth FWD sampling transect was added to the larger 20 m transect located along the 30° azimuth.

2.3.3 Herbaceous Vegetation, Forest Floor, Mineral Soil, & Roots

Samples of litterfall, herbaceous vegetation, forest floor, mineral soil, and fine and coarse roots were also collected for laboratory determinations of nutrient concentrations and for quantifying biomass and nutrient stocks within each of these pools. Litterfall was collected at each plot in 45 cm diameter circular littertraps 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. Samples of herbaceous vegetation, forest floor, and soil were taken from within nested subplots in the main plot and were centered 5.5 m from main plot center. Herbaceous vegetation was clipped at ground level and collected within a 15 cm diameter PVC ring at one nested subplot within each plot. 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 for further analyses (0 to 5 cm, 5 to 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:

Oven-dry biomass estimates of both 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, stem wood, stem bark, foliage, and branches) provided by Jenkins et al. (2003) were used to calculate biomass estimates of the specific components of each tree. Oven-dry biomass estimates of dead trees and saplings were calculated using the same equations from Jenkins et al. (2003). However, these dead stems were assumed to have no foliage and so this component was excluded from all biomass estimates of dead stems. In order to calculate stem biomass of snags, stems were assumed to be parabolic and volume was calculated using an equation from Duvall (1997) based on DBH and snag height. Estimates of snag bark biomass were not included in estimates of total snag biomass since snag biomass was derived from the volume of a paraboloid with no means of including bark. In order to derive mass of each dead tree and sapling, wood specific gravities from Harmon et al. (2008) were converted to density and multiplied by snag volume to determine mass of each dead stem. Coarse roots of dead stems were calculated from ratios derived in Jenkins et al. (2003) and were added to stem biomass estimates to create estimates of total snag biomass. Since no decay classes were recorded for dead stems, 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 snag biomass, as stems are not exactly paraboloids in volume and were likely further decayed than was assumed. To account for coarse roots following harvest despite the removal of stems during harvest, all pre-harvest coarse root stocks were assumed to exist post-harvest. Therefore, post-harvest coarse root stocks are equal to pre-harvest coarse root stocks.

Stocks of biomass within total post-harvest woody debris were split into five size classes for analysis within each size class. Specifically, FWD was divided into the three size classes as measured in the field (≤0.6 cm, >0.6 cm to ≤2.5 cm, and >2.5 cm to ≤7.5 cm) representing 1-, 10-, and 100-hr burning times, respectively. These size classes have been referred to as FWD-S, FWD-M, and FWD-L, for the small, medium, and large size classes of FWD, respectively. In addition, CWD was divided into two size classes, unmerchantable (CWD-U, >7.5 cm to <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.

Oven-dry biomass estimates for shrubs/advance regeneration were calculated using species-specific allometric biomass equations from Perala & 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 equations for volume 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. Estimations of mass for herbaceous vegetation, forest floor, mineral soil, and fine roots were calculated by dividing oven-dry mass measurements from the laboratory by sampling area as measured in the field and then scaled to the appropriate level (Mg/ha or kg/ha).

2.5 Nutrient Analyses & Calculations:

Nutrient analyses were conducted on a number of sampled components in order to better assess the impacts of each treatment on post-harvest carbon (C) and nitrogen (N) pools. Specifically, litterfall, herbaceous vegetation, forest floor material, coarse and fine roots, and mineral soil were all analyzed for percent total C and N. These values were then used to determine the total amount of C and N within each respective pool (i.e., foliage, herbaceous vegetation, forest floor material, coarse and fine roots, and mineral soil) by multiplying nutrient concentrations by biomass stocks or mass stocks in the case of mineral soil. In the case of litterfall, nutrient concentrations from this pool were used to calculate stocks of nutrients within foliage. All values utilized for calculating pre- and post-harvest C and N stocks were from samples collected pre-harvest. The exception to this was mineral soil which was from both pre-harvest and post-harvest samples and was used to calculate the corresponding pre-harvest or post-harvest nutrient total. All samples analyzed for nutrient concentrations were dried at a temperature of 65-75°C until a constant mass was reached and were then ground and homogenized in Wiley mills. Percent total C and N was determined by use of a LECO Truspec CHN Macro analyzer (LECO Corporation, St. Joseph, Michigan).

Nutrient stocks in all trees, saplings, and shrubs, and nutrient concentrations in FWD and CWD were based on values derived from intensive destructive sampling from a separate study conducted within the harvest sites and surrounding forests of this study (see Chapter 3 for details). In short, this work generated species-specific nutrient concentrations for woody debris for 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. More information on the nutrient concentrations in FWD and CWD can be found in Chapter 3.

A total of 240 litterfall samples were collected with one sample representing one plot. Nutrient values from each plot were used to calculate total nutrients in foliage from that plot. A total of 240 herbaceous vegetation samples were collected, one from each plot, and were homogenized by treatment to generate nutrient totals. A total of 720 forest floor samples were collected across all four sites. Three sub-samples were collected within a plot and homogenized into a single representative sample for analysis. A total of 720 mineral soil samples were collected and split by depth (0 to 5 cm, 5 to 20 cm) and homogenized in a similar fashion as forest floor samples for each depth. Finally, roots were removed from soil samples and divided by size to represent coarse roots (>5 mm diameter) and fine roots (2 to ≤5 mm diameter). As with soils, root samples were homogenized by plot (240 total homogenized root samples) within each size class and nutrient concentrations determined for calculating nutrient totals 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 of these factors indicated no significant effect from green-tree retention therefore 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. In all cases, the covariate was the pre-harvest value of the dependent variable (post-harvest values) and served as a control to further explain 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. In some cases, data still did not meet the necessary assumptions for these tests after applying these transformations and, thus, rank transformations were applied (Conover & 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, specifically, the Tukey-Kramer method.

Once initial diagnostics were complete, the effect of the covariate was tested in order to determine its relevance in explaining variation in the dependent variable. This testing included evaluating the estimates of the slopes for each treatment group in the model. Specifically, 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. When ANOVA was applied, diagnostics testing for normality of residuals and homogeneity of variances was conducted with appropriate mathematical or rank transformations (Conover & Iman 1981) applied as necessary. The Tukey-Kramer method was employed to find significant differences between the slash retention treatments for both ANCOVA and ANOVA. The unharvested control was not included in analyses but is presented alongside the analyzed data as a reference for visual comparison. All significance testing was at $\alpha = 0.05$ level and all 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, & Nitrogen:

3.1.1 Biomass & Carbon

Slash retention significantly affected total post-harvest biomass stocks ($F = 3.53$, $p = 0.0410$) and total post-harvest C stocks without soil pools included ($F = 4.19$, $p = 0.0241$). Slash retention had a marginally significant effect on C stocks with soil pools included ($F = 3.29$, $p = 0.0504$). Carbon stocks were roughly half the magnitude of biomass stocks (Table 1a, b). More specifically, for stocks of biomass, C with soil, and C without soil, ‘all-slash retained’ treatments were significantly higher than ‘no-slash retained’, whereas ‘20%-slash retained’ treatments were not significantly different from ‘no-slash retained’ and ‘all-slash retained’ treatments (Table 1b). The unharvested control was not statistically analyzed but is presented for visual comparison to individual treatments. When compared to the unharvested control, there were substantial reductions in stocks of biomass and C in overstory vegetation across all treatments, directly related to harvest removals (Table 1a). In addition, stocks of FWD and CWD biomass and C were substantially greater in all treatments than in the unharvested control reflecting influence from the prescribed slash retention levels (Table 1b). Stocks of C within the soil were far greater than any other pool of C within the forest ecosystem in all treatments and the unharvested control (Table 1b).

3.1.2 Nitrogen

Slash retention did not significantly affect stocks of N both with ($F = 1.10$, $p = 0.3451$) and without soil ($F = 0.89$, $p = 0.4187$) and the levels of slash retention did not differ significantly from each other. Stocks of N within the soil were by far the greatest in magnitude among all pools of N (Table 1b). In fact, N stocks within the soil pool alone were an order-of-magnitude greater than all other pools of N combined (Table 1b). Nitrogen in standing trees and saplings was very low (Table 1a) and the unharvested control was lower in total N than two of the three slash retention treatments both with and without soil (Table 1b). Specifically, '20% slash retained' and 'all slash retained' treatments were greater than the unharvested control (Table 1b) in total N stocks. Excluding soil, N stocks in pools of forest floor and coarse roots were dramatically greater than any other pool of N (Table 1b & Table 1a, respectively). For all slash retention treatments, stocks of N in forest floor were greater in magnitude than coarse roots. Other pools with relatively high levels of N included understory vegetation, particularly herbaceous material, and FWD.

Table 1a. Post-harvest ecosystem biomass in Mg/ha, C in Mg/ha, and N in kg/ha by ecosystem component and slash retention treatment. 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 (2009)	Live Shrubs	Dead Shrubs	Herbs	Fine Roots (to 20 cm)
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)
None Retained	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)
20% Retained	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)
All Retained	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)
None Retained	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)
20% Retained	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)
All Retained	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)
None Retained	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)
20% Retained	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)
All Retained	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)

Table 1b. Post-harvest ecosystem biomass in Mg/ha, C in Mg/ha, and N in kg/ha by ecosystem component and slash retention treatment. "Total" column contains the sum of all components from Table 1a and Table 1b. 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. However, letters indicating statistical significance are based on adjusted values derived from ANCOVA results.

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)	-
None Retained	18.18 (1.46)	22.04 (2.06)	30.69 (1.45)	-	-	108.18 (5.04)[a]	-
20% Retained	24.42 (2.24)	26.13 (4.21)	33.34 (5.17)	-	-	123.84 (6.61)[ab]	-
All Retained	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)
None Retained	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]
20% Retained	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]
All Retained	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)
None Retained	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]
20% Retained	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]
All Retained	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]

3.2 Woody Debris (FWD & CWD) Biomass & Nutrients:

3.2.1 Biomass and Carbon

Given the importance of FWD and CWD pools within the context of bioenergy harvesting, we conducted further analyses of total post-harvest woody debris (FWD & CWD) across slash retention treatments. Slash retention had a significant effect on both biomass ($F = 13.06$, $p < 0.0001$) and C ($F = 13.26$, $p < 0.0001$) of total post-harvest woody debris. Specifically, 'all slash retained' treatments were significantly greater than 'no slash retained' and '20% slash retained' treatments while 'no slash retained' and '20% slash retained' treatments were not significantly different from each other (Figure 1a, b). Analyses of both biomass and C stocks within total post-harvest woody debris followed the exact same patterns as total ecosystem components, with C being roughly half the magnitude of biomass. Biomass and C stocks in FWD and CWD pools were roughly similar in magnitude across all slash retention treatments (Figure 1a, b).

3.2.2 Other Nutrients (N, Ca, K, P)

Analyses of N stocks in total post-harvest woody debris indicated that slash retention did not have a significant effect on total post-harvest N stocks ($F = 0.28$, $p = 0.7580$) in woody debris and no significant differences existed between each level of slash retention (Figure 1c). When looking at the magnitude of N stocks in FWD and CWD within the total post-harvest woody debris pool, FWD was substantially greater than CWD across all slash retention treatments (Figure 1c).

In addition to the major elements contained within biomass (C and N), stocks of Ca, K, and P were also analyzed in total post-harvest woody debris. Results showed that slash retention had a significant effect ($F = 9.72$, $p = 0.0005$) on Ca stocks in total post-harvest woody debris. Comparisons of each slash retention level showed that 'all slash retained' treatments were significantly greater than 'no slash retained' treatments (Figure 1d). Also, the Ca stocks in '20% slash retained' treatments were similar to both 'no slash retained' and 'all slash retained' treatments (Figure 1d). Similar magnitudes of Ca stocks were evident in the FWD and CWD pools within each slash retention treatment post-harvest (Figure 1d).

As with Ca, slash retention had a significant effect on stocks of K ($F = 14.84$, $p < 0.0001$) in total post-harvest woody debris. Specifically, each slash retention treatment was significantly different than all other treatments (Figure 1e). Stocks of K in 'all slash retained' treatments were significantly greater than 'no slash retained' and '20% slash retained' treatments (Figure 1e). 'No slash retained' treatments had significantly lower stocks of K than '20% slash retained' and 'all slash retained' treatments (Figure 1e). Finally, '20% slash retained' treatments had significantly greater stocks of K than 'no slash retained' treatments but significantly lower stocks than 'all slash retained' treatments (Figure 1e). Also, stocks of K within FWD and CWD pools were relatively similar in magnitude (Figure 1e).

Slash retention had a significant effect on stocks of P in total post-harvest woody debris ($F = 6.88$, $p = 0.0033$). Specifically, 'all slash retained' treatments had significantly greater stocks of P than 'no slash retained' treatments while '20% slash retained' treatments were similar to both 'no slash retained' and 'all slash retained' treatments (Figure 1f). Similar to N in woody debris, stocks of P in FWD were substantially greater in magnitude than in CWD within slash retention treatments (Figure

1f). Within CWD, stocks of P generally appeared to be equivalent across each treatment if only slightly greater in treatments with higher slash retention levels (Figure 1f).

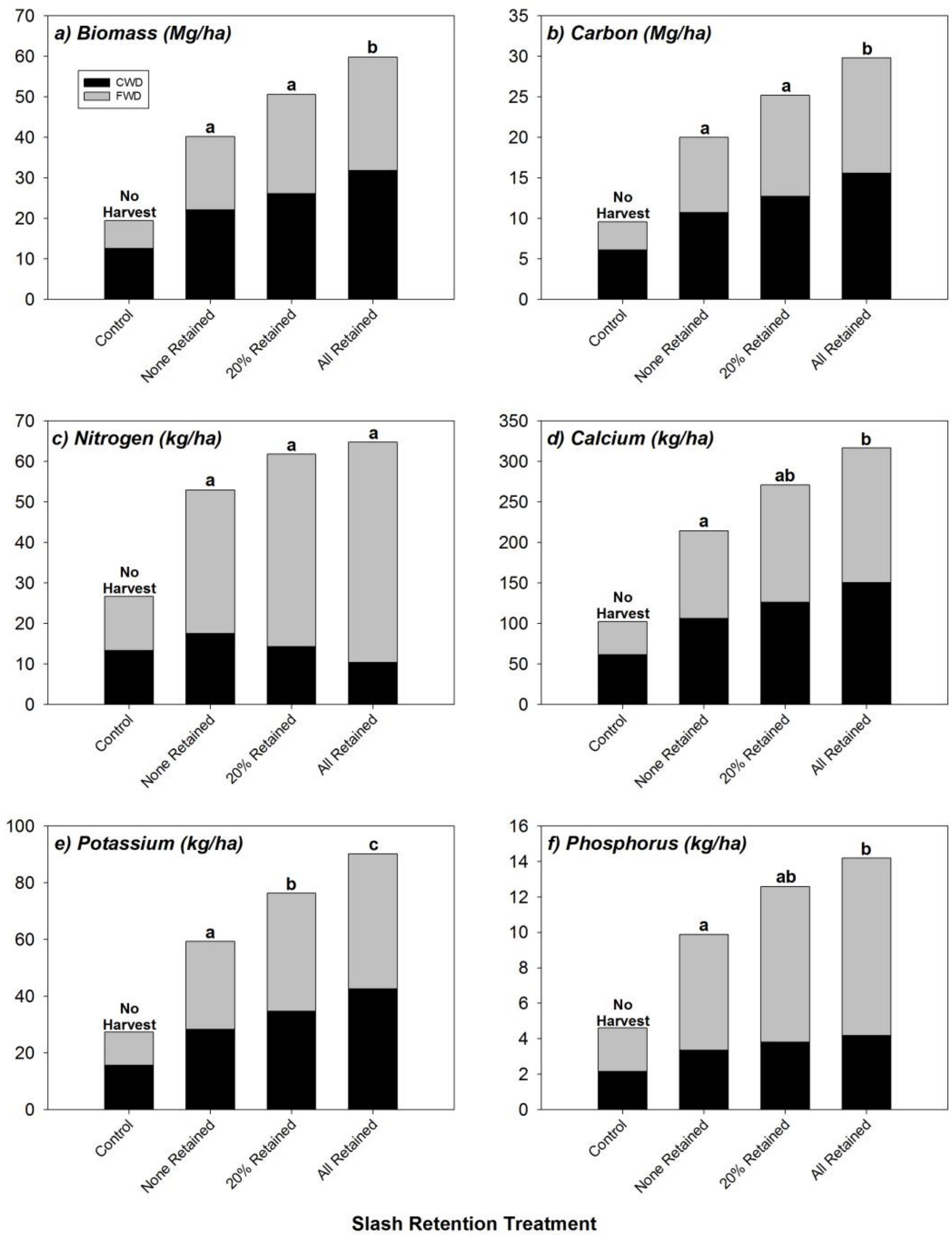

Figure 1a-f. Total post-harvest woody debris a) biomass in Mg/ha, b) C in Mg/ha, c) N in kg/ha, d) Ca in kg/ha, e) K in kg/ha, and f) P in kg/ha by FWD and CWD and slash retention treatment. Within each graph, bars with similar letters are not significantly different ($p > 0.05$) based on Tukey-Kramer 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.

3.3 Woody Debris Biomass by Size & Treatment:

Slash retention had a significant effect on most size classes of woody debris biomass, specifically FWD-M ($F = 3.75$, $p = 0.0341$), FWD-L ($F = 7.16$, $p = 0.0026$), and CWD-U ($F = 4.45$, $p = 0.0198$). Slash retention did not significantly affect biomass stocks in FWD-S ($F = 0.45$, $p = 0.6394$) and CWD-M ($F = 0.76$, $p = 0.4749$). More specifically, for FWD-M and CWD-U, 'all slash retained' treatments had significantly greater stocks of biomass than 'no slash retained' treatments while '20% slash retained' treatments were similar to both (Figure 2). For FWD-L, both '20% slash retained' and 'all slash retained' treatments were similar and had significantly greater stocks of biomass than 'no slash retained' treatments (Figure 2). The smallest and largest size class groupings, FWD-S and CWD-M, did not significantly differ between each level of slash retention (Figure 2). As with all other results, the unharvested control was not statistically analyzed but is presented for visual comparison to individual treatments. Within each size class, the magnitude of biomass stocks within slash retention treatments were substantially greater than stocks in the unharvested control, most notably for FWD-M, FWD-L, and CWD-U.

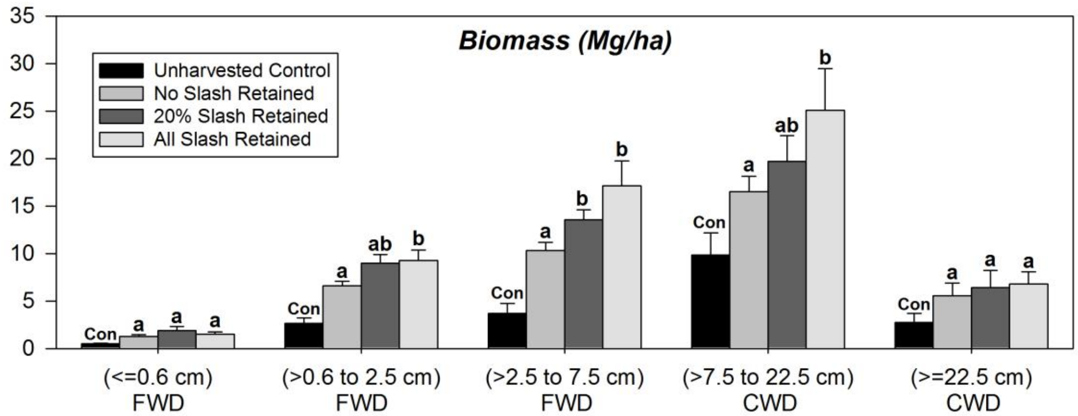

Figure 2. Total post-harvest woody debris biomass in Mg/ha by size class and slash retention treatment. Bars within the same size class with similar letters are not significantly different ($p > 0.05$) based on Tukey-Kramer comparisons from ANCOVA or ANOVA results, depending on which analysis was most 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.

4. Discussion:

Given the growing interest in the use of forest-derived biomass as a source of bioenergy in north temperate regions 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 U.S. states and other countries have provided biomass harvesting guidelines related to slash retention (MFRC 2007, Briedis et al. 2011) and green-tree retention levels (Vanha-Majamaa & Jalonen 2001), there have been few empirical evaluations of the effectiveness of these management strategies at mitigating site-level impacts. As such, this study provides an important body of knowledge for informing management strategies to mitigate potential impacts of increased levels of biomass utilization on various site resources, specifically nutrients and habitat (Abbas et al. 2011). The levels of slash retention were meant to cover a wide range of conditions and specifically, to examine recommended slash retention levels (20% slash retained) for biomass harvesting within the state of Minnesota. Similarly, the experimental levels of green-tree retention examined were based on the harvest guidelines for Minnesota. Of these two factors, only slash retention had a strong, significant effect on biomass and nutrient stocks immediately following harvest. Despite the demonstrated importance of green-tree retention in supporting other ecosystem components following harvesting (Sullivan & Sullivan 2001, Sullivan et al. 2001, Sullivan et al. 2008), this factor and the interaction between slash retention and green-tree retention did not have a significant effect on the variables measured in this study, specifically, biomass, C, and N in total ecosystem components, total woody debris, and woody debris by size class immediately following harvest. Given this, the results and following discussion focus mainly on slash retention effects.

4.1 Effects of Slash Retention on Woody Debris Biomass & Nutrient Stocks:

The direct manipulation of woody debris through various levels of slash retention in this study had significant effects on total stocks of biomass and nutrients within this pool. Within each treatment, biomass and all nutrients in woody debris were at least twice the magnitude of the unharvested control indicating high levels of slash following harvest regardless of prescribed retention. Specifically, the stocks of woody debris biomass and nutrients in the 'no slash retained' treatment were more than twice the magnitude of those in the unharvested control. The significant differences within biomass, C, Ca, K, and P between 'no slash retained' and 'all slash retained' treatments are reasonable given that these levels represent the extreme range of slash retention levels for a harvest and have been observed elsewhere in comparisons of stem-only and whole-tree harvests (Mann et al. 1988, Rittenhouse et al. 2012). Specifically, Rittenhouse et al. (2012) conducted a study in *Populus tremuloides* stands of Wisconsin and noted higher volumes of retained slash biomass within stem-only harvests than whole-tree harvests with both treatments having higher volumes of retained slash biomass than an unharvested control. A study from Finland assessed the impacts of slash removal following clearcut operations and, similar to this study, noted higher volumes of slash than expected following the clearcut operations (Eräjää et al. 2010). In addition, a study from Canada noted higher volumes of slash in more intensively harvested sections of forests managed using selection systems (Vanderwel et al. 2010).

Within the '20% slash retained' treatment, stocks of biomass, C, N, Ca, and P were all statistically similar to the 'no slash retained' treatment. Only N, Ca, and P stocks in the '20% slash retained' treatment were statistically similar to both the 'no slash retained' and 'all slash retained' treatments. In addition, K was the only element analyzed that differed significantly between all three slash retention levels. More specifically, K in the '20% slash retained' treatment was the only element to have significantly greater stocks than in the 'no slash retained' treatment. These results generally indicate that stocks of biomass and nutrients within the '20% slash retained' treatment are variable and that this level does not necessarily represent a distinct threshold of slash retention greater than the ‘no slash retained’ treatment. In addition, longer-term monitoring of these sites will determine if the levels of woody debris in the ‘no slash retained’ treatments represent a large enough pool of nutrients to maintain site quality following biomass harvesting, which has been suggested by other work (Alban & Perala 1992, Johnson & Todd 1998, Tamminen et al. 2012).

The ‘20% slash retained’ treatment was chosen in this study to serve as an evaluation of the suggested level of retention from the Minnesota biomass harvesting guidelines for mitigating the negative impacts of biomass harvests on site nutrients, habitat, and biodiversity while still providing high yields of biomass feedstocks. These guidelines indicate that 20% slash is to be intentionally retained while 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). The 33% slash retention recommendation is consistent with other state guidelines within the U.S. that also suggest retention of approximately 1/3 of all slash material during biomass harvests (Briedis et al. 2011). Studies from Finland and Sweden indicated similar slash retention levels as in our study, achieving retention of approximately 30% and 35% of all residues (Rudolphi & 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 was not directly measured. In an effort to overcome this limitation and provide estimates of percent slash retained, we assumed that the ‘all slash retained’ treatment contained 100% of available slash and that total available slash was represented by the difference between total woody debris in the 'all slash retained' treatment and the unharvested control. Using these assumptions, rough estimates of percent slash retained were determined for 'no slash retained' and '20% slash retained' treatments. Specifically, 'no slash retained' and '20% slash retained' represented roughly 52% and 77% of available slash retained on site following harvest. These values are vastly greater than the expected retention levels of 10-15% and ~33% (accounting for incidental breakage) for 'no slash retained' and '20% slash retained', respectively. It was evident that incidental breakage following clearcut harvesting was reflected in the high levels of slash in both 'no slash retained' and '20% slash retained' treatments and underscores the operational nature of this study, which captured the degree of breakage of branches and stems during felling and skidding operations. In addition, the degree of breakage and corresponding high levels of woody debris within the 'no slash retained' treatment was likely accentuated by the cold conditions during harvest (Lieffers et al. 2001, Rittenhouse et al. 2012), which tend to result in greater breakage in felled stems, particularly hardwood species such as *Populus tremuloides*.

Notable trends appeared in the distribution of biomass and nutrients within woody debris particularly within FWD and CWD. Across all slash retention levels, biomass, C, Ca, and K were approximately equivalent in magnitude in FWD and CWD. For N and P, FWD contained a substantially greater magnitude of these nutrients than did CWD. These results can be attributed to the high levels of smaller FWD 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 (Chapter 3, Whittaker et al. 1979, Miller 1983). In addition, P stocks were roughly equivalent in

CWD across all three levels of slash retention. Calcium is a key nutrient within *Populus tremuloides* forests (Hendrickson et al. 1987) and our results indicate that, with the exception of C, this nutrient was highest in all three treatments and the unharvested control. These results highlight the importance of retaining FWD as a source for replenishment of site nutrient stocks following biomass harvesting.

Further analyses of FWD and CWD by splitting them into size classes provided a more detailed look at the impacts of biomass harvesting on the pool of woody debris biomass following harvest. Particularly, slash retention had a significant impact on most woody debris size classes, including both FWD and CWD. The range of woody debris impacted most by slash retention ranged in size from >0.6 cm to <22.5 cm and represented nearly the entire pool of wood below merchantable size or, roughly, the entire pool of FWD. The significant differences between ‘no slash retained’ and ‘all slash retained’ treatments in FWD-M, FWD-L, and CWD-U reflect the same differences observed in the total woody debris pool. In addition within FWD-L, biomass stocks in the ‘20% slash retained’ treatment were significantly greater than biomass stocks in the ‘no slash retained’ treatment. These differences in FWD-M, FWD-L, and CWD-U indicate the increased prevalence of smaller woody debris in slash retention treatments.

Prevalence of woody debris in particular size classes can have different impacts on aspects of the ecosystem. The importance of FWD as a nutrient source following intensive harvest events is continually being researched, specifically in studies of biomass harvesting (Hendrickson et al. 1987, Mann et al. 1988, Johnson & Todd 1998, Belleau et al. 2006, Smolander et al. 2008, Smolander et al. 2010, Helmisaari et al. 2011, Jones et al. 2011, Wall & Hytönen 2011, Tamminen et al. 2012). Until recently, however, the importance of FWD as a source of habitat has received little attention (Söderström 1988, Kruys & Jonsson 1999). Kruys & Jonsson (1999) noted that species richness of cryptogams was greater on FWD relative to CWD and similar for both FWD and CWD when similar volumes and surface areas were compared, respectively. In addition, smaller woody debris persists roughly one to nearly two decades following a harvest event (Johnson & Todd 1998, Moroni & Ryan 2010). Given the prevalence of FWD following clearcut harvesting as documented in this study and others (McCarthy & Bailey 1994, Rudolphi & Gustaffson 2005, Eräjää et al. 2010, Moroni & Ryan 2010), there is great potential for this smaller woody material to serve directly as habitat or substrate and provide microclimatic conditions creating habitat for many species following harvest operations.

Despite no significant differences in CWD-M between slash retention levels, stocks of CWD-M increased post-harvest compared to the unharvested control indicating an increase in larger logs available as habitat following harvest. CWD is an important component of temperate ecosystems (Harmon et al. 1986) and removal of fresh and old CWD logs, a common practice in biomass harvesting, would eliminate this range of decayed woody debris from young, developing stands leaving little or no substrate for deadwood-dependent species following harvest (Jacobs et al. 2007, Riffell et al. 2011). Further analyses of CWD would provide a more detailed understanding of the potential effects of slash retention on CWD as habitat.

4.2 Effects of Slash & Green-Tree Retention on Total Ecosystem Biomass & Nutrient Stocks:

Patterns in biomass and C stocks of all ecosystem components were similar given the general consistency in C concentrations across species and ecosystem components (roughly 50% of total biomass; Chapter 3). In contrast, N stocks within total ecosystem components of harvested stands followed a very different pattern than biomass and C. Specifically, stocks of N in harvested components were very low relative to the other ecosystem pools. This is mostly due to the low concentrations of N and other nutrients within stem wood of trees and saplings (Johnston & Bartos 1977, Whittaker et al. 1979, Lambert et al. 1980, Jokela et al. 1981, Lang et al. 1982, Miller 1983, Wang et al. 1995). In addition, mean total ecosystem N stocks for the unharvested control fell within the range of mean total ecosystem N stocks for all slash retention treatments. This, in part, reflects the low concentrations of N within the stem wood of trees and saplings and the relatively high concentrations of N in the branches and tops of this material (Chapter 3). In the '20% slash retained' treatment, the majority of branches were retained on site and in the 'all slash retained' treatment all branches were retained on site, essentially transferring the N stock in branches of standing trees and saplings to the woody debris pool, specifically FWD. Moreover, the pool of branches in the unharvested control was determined by allometric equations whereas inputs of slash were measured as FWD and CWD using different methodologies. These two means of quantifying slash resulted in very different estimates of potential (branches) and actual (woody debris) harvest slash stocks. Finally, understory vegetation showed increases in N stocks compared to the unharvested control following harvest. This is due to the high levels of regeneration in the newly open conditions during the growing season following harvest (Outcalt & White 1981).

There were no distinct differences between slash retention levels in the size of biomass and nutrient pools for the forest floor and fine and coarse roots. For the forest floor pool, no major changes 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). Since fine roots in this study were only sampled to a depth of 20 cm they are likely an underestimate of this pool. Coarse root material, the larger pool of biomass in the soil column, was derived from allometric equations using DBH from pre-harvest measurements and these derivations were used as the post-harvest coarse root pool as well. Given that biomass harvesting can include removal of forest floor and coarse roots (stumps), retention of this material represents an important pool of biomass and nutrient stocks for future site productivity.

The green-tree retention treatment did not significantly affect biomass or nutrient stocks as measured within this work. A study in the U.S. Pacific Northwest measured more specific metrics of slash and ground conditions and showed different patterns of green-tree retention significantly affected ground disturbance and the accumulation of fresh CWD immediately following harvest (Halpern & McKenzie 2001). In the same study from the Pacific Northwest, Halpern & McKenzie (2001) examined tree retention only as low as 15% for both aggregate and dispersed patterns of retention. The relatively low levels of retained trees on sites in our study could explain the lack of any significant effect from green-tree retention. Specifically, green-tree retention represented a level of only 5% retention for both the aggregate clumps and dispersed patterns of retention within this study, 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.

5. Conclusions:

Results of this study indicated 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. For slash retention levels, significant differences existed between 'no slash retained' and 'all slash retained' treatments. The level of '20% slash retained', as recommended in Minnesota biomass harvesting guidelines, was variable and did not represent a distinct level of slash retention different from 'no slash retained' and 'all slash retained' treatments. Regardless of slash retention level, large stocks of FWD biomass existed post-harvest and represented large pools of C, N, Ca, K, and P. Unsurprisingly, biomass and C showed nearly identical trends in amount and statistical significance across pools. No significant differences were observed in post-harvest total ecosystem N stocks between harvested stands.

Given the high levels of slash retained within all slash retention levels, it seems difficult to retain a specific amount of slash on site following harvest or to identify an ideal level for retention in these systems. Particularly, the high levels of incidental breakage during winter harvest in *Populus tremuloides*-dominated systems provide large inputs of nutrient-rich FWD regardless of prescribed slash retention levels. Therefore, retaining some level of FWD as well as forest floor and roots would possibly lessen negative impacts of intensive biomass harvesting on site nutrient stores and subsequently on future site productivity. Further research is necessary to understand the impacts of these high levels of slash on regenerating plants and their importance as a source of habitat. 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.

Chapter Three: Nutrient concentrations in coarse and fine woody debris in *Populus tremuloides*-dominated forests of northern Minnesota, U.S.A.

1. Introduction:

Woody debris is a critical component of forested ecosystems and its importance has been well documented (Sollins et al. 1982, Fahey 1983, Harmon et al. 1986, Laiho & Prescott 2004, Evans & Kelty 2010). Coarse woody debris (CWD: large logs typically >10 cm in diameter) provides habitat and protection for a plethora of organisms (Bunnell & Houde 2010, Riffell et al. 2011), notably deadwood-dependent insects and fungi (Kruys et al. 1999, Siitonen 2001, Jonsell et al. 2007). CWD provides growth substrate or 'nurse logs' for regenerating trees and other plants (Cornett et al. 2001, Marx & Walters 2008, Svoboda et al. 2010, Bolton & D'Amato 2011), microclimates for protection from extreme conditions (Harmon et al. 1986, Åström et al. 2005), inputs of organic matter into the forest floor and soil (Keenan et al. 1993, Krzyszowska-Waitkus et al. 2006), and is important for controlling soil erosion, hydrology, and geomorphology (Harmon et al. 1986, Sollins et al. 1987, Amaranthus et al. 1989). Although lesser studied, fine woody debris (FWD; smaller woody material <10 cm in diameter) has recently received more attention in the literature and its importance as a component of forested ecosystems is becoming better understood. FWD provides a growth substrate for lichens, mosses, hepatics, and fungi (Söderström 1988, Kruys & Jonsson 1999, Nordén et al. 2004); as well as microclimates for bryophytes (Dynesius et al. 2008); and habitat for deadwood-dependent insects (Jonsell et al. 2007).

The role of woody debris in nutrient cycling within forested ecosystems has been widely studied (Lambert et al. 1980, Quesnel & Lavkulich 1981, Fahey 1983, Pastor &

Bockheim 1984, Sollins et al. 1987, Arthur & Fahey 1990, Means et al. 1992, Alban & Pastor 1993, Spears et al. 2003, Laiho & Prescott 2004, Saunders et al. 2011). Across this work, the significance of woody debris in nutrient cycling has been variable and hard to predict in managed and unmanaged forests (Spears et al. 2003, Laiho & Prescott 2004, Hermann & Prescott 2008, Krankina et al. 1999, Holub et al. 2001). Nutrient concentrations in living bole wood vary based on site and species factors (i.e., soil fertility and nutrient-use efficiency) (Pallardy 2008, Perry et al. 2008) and concentrations in bole wood are low relative to other tree components (i.e., foliage, bark, twigs, and small branches) (Johnston & Bartos 1977, Whittaker et al. 1979, Lambert et al. 1980, Jokela et al. 1981, Lang et al. 1982, Miller 1983, Wang et al. 1995). Given this, CWD initially contains low nutrient concentrations and, over time, concentrations in the wood generally increase (Lambert et al. 1980, Harmon et al. 1986, Arthur & Fahey 1990, Means et al. 1992, Alban & Pastor 1993, Krankina et al. 1999, Saunders et al. 2011). As CWD decays it becomes fragmented, nutrients are leached, organic matter is broken down by various decomposers, and the original material eventually becomes incorporated into the forest floor and soil (Harmon et al. 1986, Chapin III et al. 2002). Subsequently, forest floor usually contains the highest concentrations of nutrients among forest ecosystem components (Means et al. 1992, Alban & Pastor 1993). These patterns vary within woody debris and depend largely on type of nutrient, initial nutrient concentrations, as well as other factors including climate, topography, soil and forest type, and decomposers present (Fogel & Cromack 1977, Maser & Trappe 1984, Alban & Pastor 1993, Busse 1994).

Contrary to CWD, the smaller branches that make up FWD contain a relatively high concentration of nutrients (Miller 1983) as branches contain higher nutrient concentrations than bole wood (Johnston & Bartos 1977, Whittaker et al. 1979, Lambert et al. 1980, Jokela et al. 1981, Lang et al. 1982, Miller 1983, Wang et al. 1995). The presence of FWD is most notable after a disturbance event, particularly following a harvest, when it is found in large quantities (Moroni & Ryan 2010, Gore & Patterson 1986, McCarthy & Bailey 1994). Given its ubiquitous presence following disturbance and relatively quick decomposition rates (Moroni & Ryan 2010), FWD can provide rapid return of high amounts of nutrients to the forest floor and mineral soil (Maser et al. 1988, Miller 1983).

Despite the large number of studies on CWD across a range of regions and forest types, and given the limited number on FWD, further information is necessary to better understand the significance of woody debris in nutrient cycling, particularly in FWD. Given the increased removal of woody debris from sites subjected to biomass harvesting, quantifying nutrient dynamics in FWD and CWD of biomass harvested sites will provide crucial information for understanding future stand regeneration and productivity. Within the upper Great Lakes, studies have mainly focused on CWD of a few important species including *Populus tremuloides*, *Picea glauca*, *Pinus resinosa*, and *Pinus banksiana* in limited stages of decay (Alban & Pastor 1993, Duvall & Grigal 1999) and few have looked at FWD of similar species (Miller 1983, Mladenoff et al. 2010). Our objective is to characterize nutrient concentrations within woody debris across the dominant tree species of *Populus tremuloides* forests of northern Minnesota and various stages of decay. Specifically, we will focus on four hardwoods, *Populus tremuloides*, *Acer* *rubrum, Betula papyrifera*, and *Fraxinus nigra* as well as one softwood, *Abies balsamea*. We will present and compare nutrient concentrations for these species across a range of decay stages for both CWD and FWD. To our knowledge, this is the only study that assesses the nutrient content of FWD across multiple species in various stages of decay within northern Minnesota.

2. Methods:

2.1 Study Sites:

Study sites were located in St. Louis County, Minnesota, U.S.A., near the towns of Independence, Minnesota (47° 0' N, -92° 24' W); Melrude, Minnesota (47° 15' N, -92° 19' W); and north of Orr, Minnesota (48° 9' N, -92° 59' W). Elevations at these three sites ranged from 395 – 428 m with slopes between 0 – 8%. Soils generally consisted of loams derived from till. The site near Independence contained stony to very stony loams and sandy loams while soils near Melrude and Orr were silt loams and loams. The climate of the study area is continental with a mean temperature of -16°C in January and 26°C in July. Mean annual precipitation ranges between 660 – 710 mm, about 75% of which occurs between the months of May and October.

Stands were mesic and generally hardwood dominated, most notably by *Populus tremuloides*. Other prevalent hardwoods on these sites included *Betula papyrifera*, *Acer rubrum*, and *Fraxinus nigra*. In addition, commonly occurring softwoods included *Abies balsamea, Picea mariana*, and *Picea glauca* with occasional *Thuja occidentalis* and *Pinus strobus*. Common disturbance events in these forests include light surface fires and patchy windthrow approximately every 160 years (Minnesota DNR, 2003) with insect outbreaks occurring more frequently (Reinikainen et al. 2012). Stand-replacing events, including catastrophic fire and windthrow, are believed to occur less frequently, every 430 and 960 years, respectively (Minnesota DNR, 2003).

2.2 Study Design & Sample Collection:

Over the winter of 2010, the study sites were subjected to a series of biomass harvests consisting of tree removal with varying levels of slash and green-tree retention. For a more detailed description of these harvests see Chapter 2. Forested areas surrounding these recent biomass harvests originated from clearcutting and ranged in age from 55 to 68 years. In addition, a few scattered trees were removed from the Melrude site in 1999 following a windthrow event. Sampling for this experiment took place during the summer of 2010 within both the harvested and unharvested areas of these sites.

Samples consisted of FWD (≤7.5 cm diameter) and CWD (>7.5 cm diameter) collected by cutting downed wood with a hand-held saw. These size classifications were based on those from Brown (1974) and were the same basis for classifying woody debris in Chapter 2. Depending on diameter, either a disk (CWD), small segment of branch (FWD), or small group of twigs (FWD) were removed. Each piece of downed wood was sampled only once. We selected samples both directly in contact with the ground and elevated above the ground in order to better sample the range of nutrient concentrations of woody debris in various positions. Measurements for both FWD and CWD included diameter, species or wood type (hardwood [HW] and softwood [SW]), and decay class.

Five species were sampled for both FWD and CWD including *Populus tremuloides*, *Abies balsamea*, *Acer rubrum*, *Betula papyrifera*, and *Fraxinus nigra*. These species were selected based on calculated importance values in the overstory of the pre-harvest stand. Decay was assigned based on two systems, one for CWD and another for FWD. For CWD, decay state was assigned based on a five-class system derived from Sollins (1982): Class 1 – bark was intact, structure was sound, and current-year twigs were present; Class 2 – bark was mostly intact, sapwood was somewhat decayed with sound heartwood, and entire branch system was intact with larger twigs still present; Class 3 – bark was sloughing or absent, log supported its own weight with heartwood mostly sound, and only larger branches were present; Class 4 – bark was detached or absent, heartwood was rotten, and branch stubs were still present but could be pulled out; Class 5 – bark was detached or absent with invading roots present, log had no structural integrity, and no branches were present. For FWD, decay state was assigned based on a two-class system defined as follows: Class 1 – bark was intact, twigs and smaller branches were pliable or easily bent without breaking, and foliage could still be present; Class 2 – bark was sloughing but generally still present, twigs and smaller branches were easily snapped when bent, and foliage was absent.

In all cases, an attempt to collect bark was made when present on the sample. For decay class 4 CWD, samples were identified to HW or SW only. For decay class 5 CWD, species and wood type were indistinguishable and were therefore not recorded. Samples in greater states of decay were wrapped in plastic wrap and duct tape to stabilize any sloughing bark and rotten sapwood or heartwood during cutting and removal. After removal, each sample was placed inside a labeled, re-sealable plastic storage bag, returned to the laboratory, and frozen until processing.

2.3 Sample Processing & Nutrient Analyses:

A total of 180 CWD samples were collected with 10 samples of each species in decay classes 1 – 3 (150 total samples), 10 samples of HW or SW in decay class 4 (20 total samples), and 10 samples in decay class 5. A total of 100 FWD samples were collected with 10 samples of each species in each decay class. FWD samples were selected such that at least 3 samples of each species in each decay class were within each of the following 3 size classes: ≤1 cm (at the largest end), >1 – 2.5 cm, and >2.5 – 7.5 cm.

Samples were placed in a drying oven at 65 – 75°C until a constant mass was reached. After drying, pie-shaped wedges were cut with a bandsaw from CWD and larger FWD samples in an attempt to obtain equal proportions of bark-to-pith for analyses. Cut samples and smaller FWD were then ground and homogenized twice in Wiley mills. Any moss or foliage observed on the samples was removed prior to grinding in order to reduce bias in nutrient concentrations. Fruiting bodies on samples were not removed but noted.

Percent total carbon (%TC) and nitrogen (N) were determined for each sample using a LECO Truspec CHN Macro analyzer (LECO Corporation, St. Joseph, Michigan). Micronutrient concentrations (phosphorus (P), potassium (K), calcium (Ca), sodium (Na), magnesium (Mg), manganese (Mn), aluminum (Al), boron (B), copper (Cu), iron (Fe), and zinc (Zn)) were determined by Inductively-Coupled Plasma Atomic Emission

Spectrometry (ICP-AES) analysis with a Perkin Elmer Optima 3000 ICP Spectrometer (Perkin Elmer, Inc., Waltham, Massachusetts).

2.4 Statistical Analyses:

Analysis of variance (ANOVA) was used to determine the effects of size, species, wood type (HW or SW), and decay class on nutrient concentrations using PROC GLM in SAS (SAS Institute, Inc). Most nutrient data were highly skewed with non-normal residuals and heterogeneous variances and therefore did not meet the assumptions of ANOVA. In order to account for these violations, data were transformed using mathematical functions commonly used for data transformations, including natural logarithm, square root, and inverse. When these transformed data still did not meet the necessary assumptions for these tests, rank transformations were applied (Conover & Iman, 1981). The rank transformed data met the assumptions of ANOVA and allowed for the testing of interactions as well as the use of common post-hoc pairwise comparisons on the ranked data. The Tukey-Kramer method was employed to find significant differences between species-decay class and wood type-decay class combinations as well as between sizes of woody debris material (CWD vs. FWD).

Ideal characterization of CWD nutrient concentrations would include analyses of each species across a complete range of decay, in our case five stages of decay. However, limitations with identification of species and wood type in greater states of decay made this extremely difficult. Therefore, we present nutrient concentrations of CWD analyzed in three separate scenarios such that species and, at least, wood type are accounted for into as late of a decay stage as possible. The specific tests conducted for

CWD included an analysis of the effects of each species in decay classes 1 through 3, the effects of wood type in decay classes 1 through 4, and the effects of decay classes 1 through 5 on nutrient concentrations. Tests for FWD included an analysis of the effects of each species in decay classes 1 and 2 on nutrient concentrations. In addition, we conducted a test comparing nutrient concentrations of decay class 1 CWD with decay class 1 FWD to determine if nutrient concentrations generally differed based on size of woody debris material. All significance testing was at $\alpha = 0.05$ level and all data is presented in non-transformed format.

3. Results:

Diameters of all FWD ranged from 0.5 cm (at the large end) to 7.0 cm with a mean diameter of 2.6 ± 0.2 cm. The diameters of all CWD ranged from 7.6 cm to 26.0 cm with a mean diameter of 12.9 ± 0.3 cm.

The effect of size (CWD vs. FWD) was highly significant for nearly all nutrient concentrations in decay class 1 material. Nutrient concentrations in FWD were significantly greater than those found in CWD for all nutrients in decay class 1 material with the exception of Na and Mn which showed no significant difference (Table 1).

3.1 FWD Nutrient Concentrations by Species & Decay Class:

Nutrient concentrations in FWD were significantly affected by species and decay class (Table 1). Species was a significant factor for all nutrient concentrations with most differences among species occurring with %TC, Mn, and Zn and few differences among species occurring with P and Fe (Table 2a, 2b). *Betula papyrifera* tended to have the highest nutrient concentrations and *Acer rubrum* tended to have the lowest (Table 1).

Decay class was a significant factor for some nutrients, particularly, %TC, P, K, Mn, Al, and Fe. Generally, nutrient concentrations tended to increase from decay class 1 to decay class 2 with the exception of P, K, and B which all decreased (Table 1). More specifically, concentrations of %TC, Mn, Al, and Fe increased significantly while P and K decreased significantly from decay class 1 to decay class 2 (Table 2a, 2b).

Significant species and decay class interactions were detected in FWD for P, K, Mg, and Mn (Table 2a, 2b). Specifically, within *Populus tremuloides*, P, K, and Mg decreased from decay class 1 to decay class 2 by 73%, 72%, and 45%, respectively; within *Fraxinus nigra*, K decreased by 63% from decay class 1 to decay class 2; within *Abies balsamea*, Mn increased by 158% from decay class 1 to decay class 2; and, within *Betula papyrifera*, Al increased by 443% from decay class 1 to decay class 2 (Table 1). The highest nutrient concentrations among all species and decay classes in FWD occurred within decay class 1 *Populus tremuloides* and decay class 2 *Betula papyerifera* and the lowest concentrations were found within decay class 1 *Acer rubrum* followed by decay class 1 *Fraxinus nigra* (Table 1).

Table 1. Mean decay class 1 FWD and CWD nutrient concentrations averaged across all species and FWD nutrient concentrations for each species by decay class. Standard errors are in parentheses. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. Sample sizes are n=50 for decay class 1 FWD and CWD nutrient concentrations within each group and n=10 for FWD nutrient concentrations within each species/decay class combination. Within each row for decay class 1 FWD and CWD nutrient concentrations averaged across all species and separately for FWD nutrient concentrations by species and decay class, values with similar letters are not significantly different ($p > 0.05$) based on results from comparisons using the Tukey-Kramer method on transformed data.

Nutrients	Size		Species									
	FWD	CWD	*Populus tremuloides*		*Acer rubrum*		*Betula papyrifera*		*Fraxinus nigra*		*Abies balsamea*	
	Decay Class		Decay Class		Decay Class		Decay Class		Decay Class		Decay Class	
	1		1	2	1	2	1	2	1	2	1	2
% TC	50.9 (0.2)[a]	48.6 (0.2)[b]	50.8 (0.4)[bc]	51.1 (0.1)[bc]	49.5 (0.2)[d]	49.7 (0.2)[d]	52.2 (0.4)[ab]	53.5 (0.6)[a]	49.7 (0.1)[d]	50.5 (0.2)[cd]	52.1 (0.5)[ab]	51.8 (0.4)[ab]
N	1821 (334)[a]	275 (73)[b]	3583 (447)[a]	1622 (321)[ab]	378 (317)[b]	976 (356)[ab]	2365 (921)[ab]	3711 (1053)[ab]	1790 (849)[ab]	2486 (782)[ab]	991 (696)[b]	1570 (800)[ab]
P	465 (41)[a]	125.9 (7.5)[b]	649 (90)[a]	172 (15)[d]	325 (41)[abcd]	198 (24)[cd]	539 (111)[ab]	351 (40)[abc]	409 (102)[abcd]	211 (29)[cd]	403 (80)[abc]	330 (83)[bcd]
K	2336 (180)[a]	1704 (143)[b]	2555 (306)[ab]	718 (135)[c]	1424 (115)[bc]	754 (248)[c]	1526 (235)[bc]	842 (136)[c]	3984 (353)[a]	1459 (312)[bc]	2191 (351)[ab]	1601 (369)[bc]
Ca	5539 (390)[a]	3185 (247)[b]	8628 (951)[a]	7699 (1181)[ab]	4346 (644)[bc]	5333 (858)[abc]	4840 (477)[abc]	7829 (894)[ab]	5766 (425)[abc]	5653 (489)[abc]	4115 (958)[c]	5206 (1004)[abc]
Na	30.1 (1.8)[a]	26.0 (1.7)[a]	35.6 (3.0)[ab]	35.5 (4.3)[ab]	30.9 (3.9)[ab]	27.4 (3.9)[ab]	37.9 (4.4)[a]	40.6 (5.4)[a]	21.0 (3.9)[b]	30.8 (3.2)[ab]	25.2 (3.3)[ab]	35.3 (5.2)[ab]
Mg	558 (37)[a]	338 (16)[b]	866 (98)[a]	474 (34)[b]	405 (51)[b]	412 (48)[b]	500 (56)[b]	561 (76)[ab]	605 (57)[ab]	593 (89)[ab]	416 (56)[b]	576 (70)[ab]
Mn	101 (14)[a]	69.2 (8.5)[a]	25.5 (3.2)[c]	20.8 (3.1)[c]	222.7 (18.6)[a]	237.9 (39.4)[a]	144.5 (20.7)[ab]	200.9 (26.6)[a]	11.3 (1.5)[c]	20.2 (2.5)[c]	99.5 (31.8)[b]	256.7 (42.1)[a]
Al	21.9 (5.7)[a]	7.0 (1.2)[b]	8.6 (2.5)[c]	26.7 (8.6)[bc]	19.9 (6.4)[bc]	21.7 (4.2)[abc]	6.8 (1.7)[c]	36.9 (6.5)[ab]	15.4 (3.3)[bc]	43.0 (8.5)[ab]	58.6 (25.0)[ab]	110.3 (36.9)[a]
B	7.7 (0.5)[a]	3.4 (0.2)[b]	9.4 (0.9)[abc]	6.2 (0.8)[bcd]	7.7 (1.1)[abcd]	6.0 (0.8)[bcd]	5.7 (0.7)[cd]	6.6 (0.8)[abcd]	10.6 (1.2)[ab]	13.0 (2.9)[a]	5.1 (0.9)[d]	4.4 (0.8)[d]
Cu	3.8 (0.4)[a]	1.6 (0.1)[b]	6.4 (1.4)[c]	5.1 (0.9)[bc]	2.4 (0.2)[a]	2.8 (0.3)[ab]	2.9 (0.4)[abc]	4.0 (0.6)[abc]	4.1 (0.9)[abc]	5.3 (1.1)[bc]	3.0 (0.2)[abc]	3.0 (0.5)[abc]
Fe	27.1 (4.7)[a]	18.4 (2.8)[b]	16.9 (3.4)[b]	39.3 (11.3)[ab]	35.7 (6.0)[ab]	34.9 (6.1)[ab]	13.5 (3.0)[b]	46.6 (8.2)[ab]	30.0 (6.4)[ab]	76.7 (14.2)[a]	39.1 (21.3)[ab]	104.0 (38.9)[a]
Zn	56.6 (8.0)[a]	28.2 (3.8)[b]	87.9 (8.3)[ab]	88.7 (10.9)[ab]	16.2 (2.3)[de]	19.4 (2.6)[cde]	130.9 (18.4)[a]	173.4 (26.9)[a]	10.2 (3.2)[e]	14.0 (3.6)[e]	37.6 (11.6)[cd]	56.3 (18.8)[bc]

Table 2a. Summary of Type III tests of fixed effects for all macronutrients (%TC, N, P, K, Ca, and Mg) in FWD by species and decay class including the source of variation, degrees of freedom for both the numerator and denominator, and F-values and probabilities for each nutrient analyzed. Comparisons among species and decay class are presented with significant differences highlighted in bold lettering. All significant differences are at the p < 0.05 level.

Source of variation	d.f. (numerator)	d.f. (denominator)	Macronutrients %TC F	%TC p	N (mg/kg) F	N (mg/kg) p	P (mg/kg) F	P (mg/kg) p	K (mg/kg) F	K (mg/kg) p	Ca (mg/kg) F	Ca (mg/kg) p	Mg (mg/kg) F	Mg (mg/kg) p
Species	4	90	38.11	<.0001	5.26	0.0007	2.57	0.0431	7.70	<.0001	6.37	0.0001	5.18	0.0008
Decay Class	1	90	6.28	0.0140	1.03	0.3124	27.09	<.0001	61.64	<.0001	2.52	0.1160	0.32	0.5756
Species X Decay Class	4	90	0.99	0.4175	1.28	0.2840	3.03	0.0215	2.66	0.0377	1.59	0.1829	4.09	0.0043
Comparisons														
Black ash vs. Balsam fir				**<.0001**		0.2692		0.7768		0.5241		0.3495		0.3905
Black ash vs. Paper birch				**<.0001**		0.9912		**0.0490**		**0.0003**		0.9798		0.7836
Black ash vs. Red maple				0.2065		0.1898		1.0000		**<.0001**		0.6041		**0.0096**
Black ash vs. Aspen				**0.0028**		0.5318		0.6956		**0.0354**		0.0736		0.9350
Balsam fir vs. Paper birch				0.3886		0.1082		0.4782		**0.0451**		0.1197		0.9681
Balsam fir vs. Red maple				**<.0001**		0.9997		0.8194		**0.0202**		0.9937		0.5106
Balsam fir vs. Aspen				0.0519		**0.0052**		0.9999		0.6602		**0.0002**		0.0858
Paper birch vs. Red maple				**<.0001**		0.0697		0.0602		0.9984		0.2725		0.1800
Paper birch vs. Aspen				**0.0002**		0.8066		0.5667		0.5827		0.2448		0.3118
Red maple vs. Aspen				**<.0001**		**0.0028**		0.7438		0.3998		**0.0009**		**0.0007**
Decay1 vs. Decay2				**0.0140**		0.3124		**<.0001**		**<.0001**		0.1160		0.5756

Table 2b. Summary of Type III tests of fixed effects for all micronutrients (Na, Mn, Al, B, Cu, Fe, and Zn) in FWD by species and decay class including the source of variation, degrees of freedom for both the numerator and denominator, and F-values and probabilities for each nutrient analyzed. Comparisons among species and decay class are presented with significant differences highlighted in bold lettering. All significant differences are at the $p < 0.05$ level.

			Micronutrients													
Source of variation	**d.f. (numerator)**	**d.f. (denominator)**	**Na (mg/kg)**		**Mn (mg/kg)**		**Al (mg/kg)**		**B (mg/kg)**		**Cu (mg/kg)**		**Fe (mg/kg)**		**Zn (mg/kg)**	
			F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Species	4	90	4.03	0.0048	80.90	<.0001	8.11	<.0001	11.40	<.0001	6.52	0.0001	3.20	0.0167	59.31	<.0001
Decay Class	1	90	1.90	0.1718	11.14	0.0012	23.40	<.0001	2.01	0.1596	1.54	0.2185	20.86	<.0001	2.36	0.1279
Species X Decay Class	4	90	0.95	0.4385	4.44	0.0026	1.29	0.2804	1.41	0.2361	1.14	0.3431	1.69	0.1598	0.20	0.9357
Comparisons																
Black ash vs. Balsam fir				0.6208		**<.0001**		0.0590		**<.0001**		0.3195		0.9958		**<.0001**
Black ash vs. Paper birch				**0.0054**		**<.0001**		0.4525		**0.0002**		0.6378		0.0949		**<.0001**
Black ash vs. Red maple				0.7553		**<.0001**		0.8343		**0.0028**		**0.0306**		0.8520		0.2122
Black ash vs. Aspen				**0.0364**		0.2255		0.1037		**0.0485**		0.4463		**0.0470**		**<.0001**
Balsam fir vs. Paper birch				0.2125		0.9500		**0.0003**		0.2416		0.9847		0.2090		**<.0001**
Balsam fir vs. Red maple				0.9995		**0.0480**		**0.0027**		0.0522		0.8269		0.9693		**0.0026**
Balsam fir vs. Aspen				0.5707		**<.0001**		**<.0001**		**0.0031**		**0.0046**		0.1154		**0.0002**
Paper birch vs. Red maple				0.1360		0.2404		0.9690		0.9570		0.5124		0.5553		**<.0001**
Paper birch vs. Aspen				0.9665		**<.0001**		0.9286		0.4710		**0.0228**		0.9985		0.1046
Red maple vs. Aspen				0.4322		**<.0001**		0.6044		0.8752		**0.0001**		0.3788		**<.0001**
Decay1 vs. Decay2				0.1718		**0.0012**		**<.0001**		0.1596		0.2185		**<.0001**		0.1279

3.2 CWD Nutrient Concentrations by Species, Wood Type, & Decay Class:

As with FWD, variation in our CWD nutrient concentrations was related to species and decay class, specifically decay class 1 through decay class 3 (Table 3). Species effects were significant for all CWD nutrient concentrations (Table 4a, 4b). Zinc was the only nutrient to differ among all species closely followed by K, while Fe had the least differences among species (Table 4a, 4b). *Fraxinus nigra* tended to have the highest concentration of each nutrient whereas no particular species consistently had the lowest concentration of each nutrient (Table 3).

Decay class had a significant effect on most CWD nutrient concentrations (Table 4a, 4b). Most nutrients tended to increase from decay class 1 to decay class 3 with the exception of P and K, which decreased significantly and did not change, respectively, from decay class 1 to decay class 3 (Table 4a, 4b). No nutrient concentrations changed significantly from decay class 1 to decay class 2 yet, most changed significantly from decay class 1 to decay class 3 and/or decay class 2 to decay class 3 (Table 4a, 4b).

The interaction between species and decay class was significant for the majority of CWD nutrients with the exception of N, K, Na, Mn, and Cu (Table 4a, 4b). Other than %TC, Ca had the highest concentrations followed by K, while the lowest nutrient concentrations were typically Cu followed by B and Al (Table 4a, 4b). More specifically, within each nutrient, decay class 3 *Fraxinus nigra* tended to have the highest nutrient concentrations while decay class 1 *Acer rubrum* and decay class 1 *Betula papyrifera* tended to have the lowest concentration of each nutrient (Table 3). No N was detected below 24 mg/kg in decay class 1 and decay class 2 *Populus tremuloides* as well as decay class 1 *Acer rubrum* (Table 3) as this was the lowest detectable limit for N.

Table 3. Mean CWD nutrient concentrations for each species by decay class with standard errors in parentheses. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. Sample sizes within each species/decay class combination are n=10.

Nutrients	Species														
	Populus tremuloides Decay Class			*Acer rubrum* Decay Class			*Betula papyrifera* Decay Class			*Fraxinus nigra* Decay Class			*Abies balsamea* Decay Class		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
%TC	49.1 (0.1)	48.6 (0.3)	49.6 (0.1)	46.9 (0.3)	48.4 (0.2)	49.3 (0.4)	47.9 (0.3)	48.1 (0.2)	49.3 (0.7)	48.4 (0.1)	48.6 (0.1)	49.4 (0.2)	50.8 (0.1)	50.4 (0.3)	50.5 (0.1)
N	24.0 (0.0)	24.0 (0.0)	55.9 (31.9)	24.0 (0.0)	26.7 (2.7)	180.1 (156.1)	80.0 (56.0)	59.6 (35.6)	646.8 (290.0)	865.3 (221.8)	556.9 (148.8)	2231.0 (342.3)	380.2 (183.4)	329.8 (123.1)	437.3 (167.1)
P	163 (20)	118 (16)	75 (16)	131 (11)	137 (16)	141 (18)	141 (17)	98 (10)	125 (27)	81 (6)	84 (8)	88 (13)	113 (16)	105 (17)	75 (9)
K	1384 (102)	1357 (107)	1317 (576)	1292 (162)	1562 (489)	1701 (464)	695 (151)	783 (239)	723 (154)	3007 (304)	2849 (316)	3508 (886)	2144 (230)	2545 (447)	2005 (283)
Ca	5556 (581)	4691 (318)	4959 (1335)	2054 (205)	3045 (432)	4066 (473)	2082 (328)	3064 (633)	4400 (970)	3964 (304)	4086 (268)	6060 (984)	2268 (148)	2227 (270)	2977 (345)
Na	21.2 (2.2)	18.4 (2.3)	20.8 (3.8)	21.1 (1.7)	18.4 (0.9)	23.4 (1.9)	16.7 (2.5)	22.1 (4.6)	30.3 (5.4)	33.5 (4.0)	33.9 (4.0)	50.4 (7.8)	37.4 (3.5)	29.0 (4.5)	36.5 (4.2)
Mg	464 (40)	427 (35)	462 (94)	237 (25)	327 (43)	466 (50)	267 (19)	407 (85)	442 (57)	368 (20)	412 (26)	834 (183)	353 (28)	399 (53)	373 (21)
Mn	14.7 (2.5)	12.8 (1.5)	16.7 (2.9)	91.5 (10.3)	98.8 (11.1)	191.3 (44.3)	111.6 (17.3)	115.1 (24.6)	156.7 (26.2)	6.3 (0.8)	5.9 (0.8)	14.7 (2.1)	121.8 (14.9)	113.5 (30.0)	109.3 (26.6)
Al	6.2 (2.3)	3.3 (0.7)	10.7 (2.3)	4.2 (0.7)	3.3 (0.4)	6.1 (1.2)	3.1 (0.6)	2.2 (0.3)	5.4 (1.0)	4.4 (1.5)	4.1 (0.7)	20.6 (6.2)	17.2 (4.1)	11.3 (3.2)	11.5 (1.5)
B	4.0 (0.3)	3.4 (0.3)	3.8 (0.8)	2.7 (0.2)	3.5 (0.2)	5.1 (0.6)	2.3 (0.2)	3.4 (0.6)	5.8 (1.1)	5.5 (0.3)	6.3 (0.8)	12.5 (2.5)	2.3 (0.2)	2.5 (0.2)	2.7 (0.3)
Cu	2.2 (0.1)	2.4 (0.3)	2.9 (0.5)	1.4 (0.1)	2.1 (0.4)	2.7 (0.4)	1.6 (0.4)	1.3 (0.1)	2.0 (0.3)	1.4 (0.1)	1.5 (0.2)	2.3 (0.4)	1.6 (0.1)	1.5 (0.1)	1.7 (0.2)
Fe	28.0 (10.6)	14.3 (2.8)	24.8 (5.7)	17.5 (2.8)	21.4 (3.4)	14.1 (1.8)	9.2 (1.3)	9.2 (1.3)	14.0 (2.1)	14.4 (3.5)	15.6 (2.8)	45.7 (10.9)	22.9 (7.9)	11.3 (1.4)	16.6 (1.9)
Zn	55.9 (4.2)	46.2 (3.0)	49.1 (9.5)	7.7 (0.9)	10.8 (1.0)	19.9 (3.4)	58.9 (6.0)	90.0 (18.2)	122.7 (17.9)	2.4 (0.3)	2.5 (0.3)	4.7 (1.0)	16.1 (1.7)	17.9 (1.6)	19.1 (2.5)

Table 4a. Summary of Type III tests of fixed effects for all macronutrients (%TC, N, P, K, Ca, and Mg) in CWD by species and decay class including the source of variation, degrees of freedom for both the numerator and denominator, and F-values and probabilities for each nutrient analyzed. Comparisons among species and decay class are presented with significant differences highlighted in bold lettering. All significant differences are at the $p < 0.05$ level.

			Macronutrients											
Source of variation	**d.f. (numerator)**	**d.f. (denominator)**	**%TC**		**N (mg/kg)**		**P (mg/kg)**		**K (mg/kg)**		**Ca (mg/kg)**		**Mg (mg/kg)**	
			F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Species	4	135	45.67	<.0001	42.02	<.0001	6.54	<.0001	33.68	<.0001	18.11	<.0001	5.46	0.0004
Decay Class	2	135	23.02	<.0001	8.45	0.0003	5.99	0.0032	0.93	0.3954	5.41	0.0055	8.35	0.0004
Species X Decay Class	8	135	2.99	0.0040	1.13	0.3478	2.36	0.0209	0.47	0.8725	2.72	0.0081	2.37	0.0203
Comparisons														
Black ash vs. Balsam fir				**<.0001**		**<.0001**		0.8510		0.1379		**<.0001**		0.1915
Black ash vs. Paper birch				0.1174		**<.0001**		**0.0387**		**<.0001**		**<.0001**		**0.0106**
Black ash vs. Red maple				0.0545		**<.0001**		**<.0001**		**<.0001**		**0.0003**		**0.0049**
Black ash vs. Aspen				0.1136		**<.0001**		0.0879		**<.0001**		0.9782		0.9984
Balsam fir vs. Paper birch				**<.0001**		0.0550		0.3485		**<.0001**		0.7070		0.7968
Balsam fir vs. Red maple				**<.0001**		**<.0001**		**0.0029**		**0.0007**		0.3937		0.6577
Balsam fir vs. Aspen				**<.0001**		**<.0001**		0.5440		**0.0001**		**<.0001**		0.3269
Paper birch vs. Red maple				0.9978		0.1593		0.3522		**0.0009**		0.9874		0.9993
Paper birch vs. Aspen				**<.0001**		0.0654		0.9977		**0.0047**		**<.0001**		**0.0255**
Red maple vs. Aspen				**<.0001**		0.9953		0.1992		0.9897		**<.0001**		**0.0126**
Decay1 vs. Decay2				0.7801		0.9954		0.1504		0.9983		0.3895		0.1435
Decay1 vs. Decay3				**<.0001**		**0.0017**		**0.0021**		0.4487		**0.0039**		**0.0002**
Decay2 vs. Decay3				**<.0001**		**0.0013**		0.2563		0.4823		0.1276		0.0770

Table 4b. Summary of Type III tests of fixed effects for all micronutrients (Na, Mn, Al, B, Cu, Fe, and Zn) in CWD by species and decay class including the source of variation, degrees of freedom for both the numerator and denominator, and F-values and probabilities for each nutrient analyzed. Comparisons among species and decay class are presented with significant differences highlighted in bold lettering. All significant differences are at the $p < 0.05$ level.

			Micronutrients													
Source of variation	**d.f. (numerator)**	**d.f. (denominator)**	**Na (mg/kg)**		**Mn (mg/kg)**		**Al (mg/kg)**		**B (mg/kg)**		**Cu (mg/kg)**		**Fe (mg/kg)**		**Zn (mg/kg)**	
			F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Species	4	135	17.52	<.0001	94.57	<.0001	16.15	<.0001	36.86	<.0001	9.24	<.0001	4.22	0.0030	300.54	<.0001
Decay Class	2	135	5.59	0.0047	4.94	0.0085	20.01	<.0001	12.06	<.0001	7.60	0.0007	6.26	0.0025	8.40	0.0004
Species X Decay Class	8	135	1.09	0.3763	1.27	0.2644	2.26	0.027	4.41	<.0001	1.73	0.0977	2.21	0.0305	4.05	0.0002
Comparisons																
Black ash vs. Balsam fir				0.9777		**<.0001**		**0.0003**		**<.0001**		1.0000		0.7122		**<.0001**
Black ash vs. Paper birch				**<.0001**		**<.0001**		**0.0102**		**<.0001**		0.9643		**0.0043**		**<.0001**
Black ash vs. Red maple				**<.0001**		**<.0001**		0.4594		**<.0001**		0.1501		1.0000		**<.0001**
Black ash vs. Aspen				**<.0001**		**0.0369**		0.9607		**<.0001**		**0.0001**		0.9124		**<.0001**
Balsam fir vs. Paper birch				**0.0004**		0.8168		**<.0001**		**0.0117**		0.9365		0.1472		**<.0001**
Balsam fir vs. Red maple				**<.0001**		0.9616		**<.0001**		**<.0001**		0.1912		0.7641		**<.0001**
Balsam fir vs. Aspen				**<.0001**		**<.0001**		**<.0001**		**<.0001**		**0.0002**		0.9940		**<.0001**
Paper birch vs. Red maple				0.9614		0.9943		0.4692		0.4829		**0.0290**		**0.0058**		**<.0001**
Paper birch vs. Aspen				0.5380		**<.0001**		0.0698		0.5462		**<.0001**		0.0557		**<.0001**
Red maple vs. Aspen				0.9090		**<.0001**		0.8613		1.0000		0.1704		0.9396		**<.0001**
Decay1 vs. Decay2				0.4091		0.7555		0.0937		0.1411		0.8338		1.0000		0.4971
Decay1 vs. Decay3				0.1079		0.0599		**0.0002**		**<.0001**		**0.0012**		**0.0073**		**0.0003**
Decay2 vs. Decay3				**0.0034**		**0.0087**		**<.0001**		**0.0099**		**0.0076**		**0.0075**		**0.0140**

After pooling nutrients by wood type (i.e., HW vs. SW) and including a fourth decay class, the main effects of both wood type and decay class were found to be significant. Effects of wood type were significant for all nutrients with the exception of N, Na, Mg, and Fe (Figure 1, Table A1). However, neither wood type had consistently higher or lower concentrations compared to the other. Softwoods had higher concentrations of %TC, K, Mg, Mn, Na, Al, and Fe (Figure 1, Table A1), while hardwoods had higher concentrations of N, P, Ca, Zn, B, and Cu (Figure 1, Table A1).

Decay class was a significant factor for all nutrients from decay class 1 to decay class 4 (Figure 1, Table A1). Concentrations tended to increase from decay class 1 to decay class 4 with the exception of K, which decreased (Figure 1, Table A1). Although most nutrients remained the same before increasing significantly in decay class 3 or 4, P, Al, and Fe decreased significantly from decay class 1 to decay class 3 before increasing significantly into decay class 4 (Figure 1, Table A1). Variability was usually highest in decay class 4 concentrations due to the smaller sample size for this class (Figure 1, Table A1).

The interaction of wood type and decay class was significant for %TC, N, Na, and Al (Figure 1, Table A1). In each case, %TC increased significantly in HW from decay class 2 to decay class 3 and N and Na increased in HW by 325% and 95%, respectively, from decay class 3 to decay class 4 while SW did not change for either N or Na (Figure 1, Table A1). In addition, Al increased in HW by 234% from decay class 2 to decay class 3 and by 868% from decay class 3 to decay class 4, while in SW Al increased by 452% from decay class 3 to decay class 4 (Table A1).

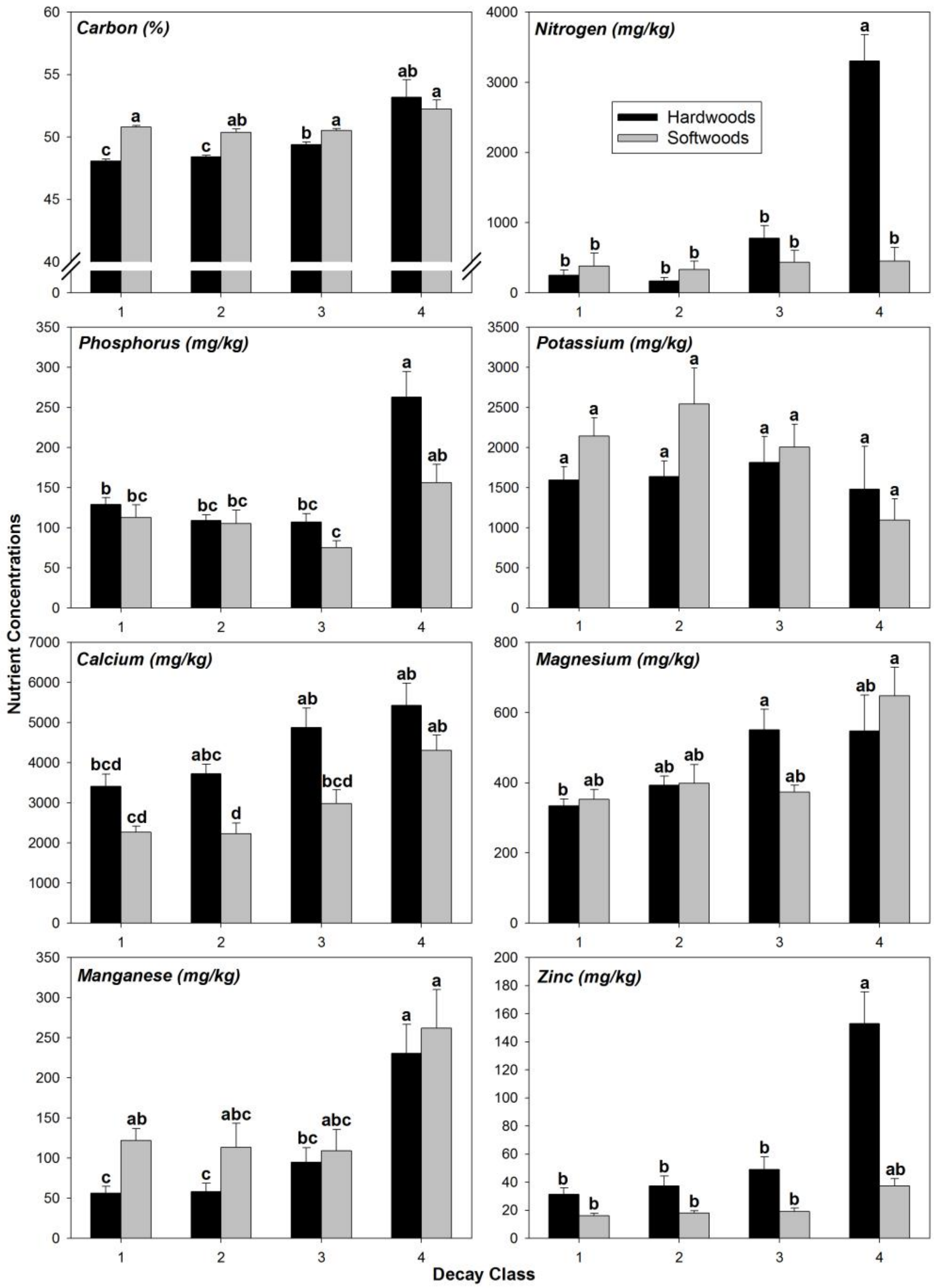

Figure 1. Mean CWD nutrient concentrations for each wood type (HW, SW) by decay class. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. Values with similar letters are not significantly different ($p > 0.05$) based on results from comparisons using the Tukey-Kramer method on transformed data. Sample sizes of SW

within each decay class and HW in decay class 4 are n=10. Samples sizes of HW within decay classes 1 – 3 are n=40.

3.3 CWD Nutrient Concentrations by Decay Class Only:

Decay class was highly significant for each nutrient analyzed from decay class 1 to decay class 5 (Figure 2, Table A1). Generally, nutrient concentrations increased from decay class 1 to decay class 5 with the exception of K which decreased (Figure 2, Table A1). A few nutrients worth noting included %TC which increased in concentration before decreasing by 23% from decay class 4 to decay class 5 and P which decreased in concentration before increasing by 409% from decay class 3 to decay class 5 (Figure 2, Table A1). For a number of nutrients, including N, K, Mn, Al, Fe, and Zn, concentrations changed by an order of magnitude or more from decay class 3 to decay class 4 and/or decay class 4 to decay class 5 (Figure 2, Table A1).

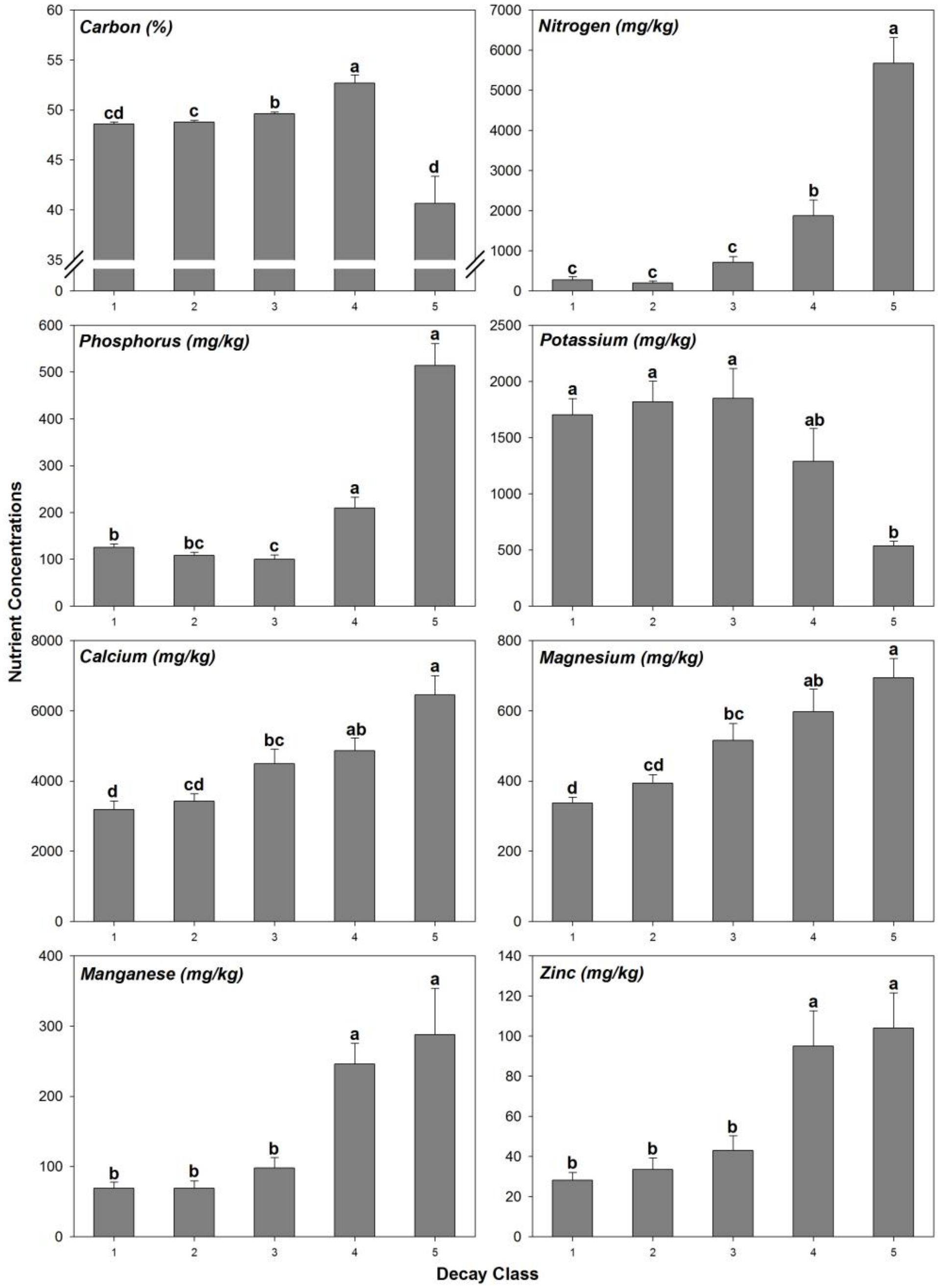

Figure 2. Mean CWD nutrient concentrations by decay class. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. Values with similar letters are not significantly different ($p > 0.05$) based on results from comparisons using the Tukey-Kramer method on transformed data. Sample sizes within decay classes 1 – 3 are n=50, decay class 4 are n=20, and decay class 5 are n=10.

4. Discussion:

The differences in nutrient concentrations among species and decay classes in this study suggest that the influence of CWD and FWD on ecosystem nutrient budgets can be complex and variable. This complexity and variability is frequently observed in other studies of woody debris and reinforces the importance of examining these factors in various regions and across different forest conditions. Increasing our knowledge of the role CWD and FWD play in forested ecosystems, particularly with regard to nutrient cycling, will be very informative for understanding future productivity of managed forests, especially within the context of assessing the impacts of increased utilization of these materials for biomass feedstocks.

4.1 FWD Nutrient Concentrations by Species & Decay Class:

Nutrient concentrations for FWD tended to be higher than those in CWD, which is consistent with many studies where smaller branches and twigs have greater nutrient concentrations than bole wood (Johnston & Bartos 1977, Whittaker et al. 1979, Miller 1983). These higher concentrations in branches are largely attributable to the high concentrations in branch bark (Lang et al. 1982) and the high bark-to-wood ratio (surface area) of FWD (Zavitkovski 1971).

FWD nutrient concentrations from our study were generally within the range or an order-of-magnitude of those from other studies (Sykes & Barr 1973, Johnston & Bartos 1977, Whittaker et al. 1979, Jokela et al. 1981, Lang et al. 1982, Miller 1983, Pastor & Bockheim 1984, Wang et al. 1995, Mladenoff et al. 2010). This was particularly true for decay class 1 samples, as nutrient content of more-decayed FWD has been less studied (Whittaker et al. 1979, Miller 1983, Mladenoff et al. 2010). Given the limited research on nutrients in FWD, many of the sources we used for comparison of our nutrient concentrations contained values for live branches while only a few were for downed wood. Despite the general similarities between our values and other studies, Ca and N tended to be low relative to other published values for most species while Fe and Mn were low for *Populus tremuloides* and *Acer rubrum*, respectively.

Calcium is a key nutrient in forested ecosystems, especially in forests dominated by *Populus tremuloides* (Hendrickson et al. 1987, Alban et al. 1978). Slightly higher Ca concentrations than ours were reported for FWD of *Populus tremuloides* in northern Minnesota (Miller 1983) and for multiple species of FWD in forests of northern Wisconsin (Mladenoff et al. 2010). This difference could be related to site quality as the *Populus tremuloides* in the former study were in fairly young (35-45 yr old) aspen stands on silty, clay loams while ours were in older (60 yr old) aspen stands and tended to be on stony, sandy loams. In addition, the forests studied by Mladenoff et al. (2010) were on silt loams in *Acer saccharum*-dominated forests, which tend to dominate richer sites than those we studied and may explain the higher Ca concentrations reported by Mladenoff et al. (2010).

A particularly interesting result of our analysis was the low N values observed in FWD. Nitrogen values were generally low for all species, most notably for *Acer rubrum* in decay classes 1 and 2 and *Abies balsamea* in decay class 1. It is possible that these low N concentrations are a product of nutrient retranslocation out of branches since most of our FWD samples came from winter-harvested material. *Acer saccharum*, a species similar to *Acer rubrum*, has been noted as having high rates of nitrate leaching on sites in which it is the dominant species (Lovett & Mitchell 2004). High rates of nitrate leaching are also associated with loss of base cations, including Ca (Chapin III et al. 2002). Given that *Acer rubrum* was a notable species on our sites based on importance value, this species could function similarly to *Acer saccharum* and contribute to the low concentrations of N and Ca through nitrate and base cation leaching.

Generally, it is unclear why FWD N concentrations from our study were low compared to other studies. There are a number of factors that could contribute to low concentrations of N in an ecosystem including types of N-fixers present; lack of organic matter; and increased volatilization, nitrification, denitrification, or leaching (Chapin III et al. 2002). These factors may have affected nutrient availability and, if so, may have affected nutrients in woody debris. Further comments on low N concentrations are discussed in the following section on CWD.

FWD nutrient concentrations differed significantly among species. The high concentrations of nutrients found in *Betula papyrifera* can likely be attributed to its recalcitrant, persistent bark, which contains higher concentrations of nutrients than bole or branch wood (Jokela et al. 1981, Lang et al. 1982). *Acer rubrum* tended to have the lowest nutrient concentrations among species sampled in our study. Given the limited studies of nutrient concentrations in *Acer rubrum*, Pastor & Bockheim (1984) noted relatively low concentrations of nutrients in *Acer saccharum* when compared with *Populus tremuloides* which may corroborate the low nutrient concentrations in *Acer rubrum* on our sites. *Acer rubrum* has a wide geographic range and has been noted as occurring on sites with highly variable degrees of quality (Burns & Honkala 1990). The low nutrient-use efficiency of *Acer saccharum* (Pastor & Bockheim 1984) and its wide-ranging site tolerance in conjunction with the potentially low site quality of our study could explain the low nutrient concentrations in *Acer rubrum*.

As previously reported, most nutrient concentrations in CWD increase with decay (Alban & Pastor 1993, Mladenoff et al. 2010, Saunders et al. 2011). However, few studies have examined the patterns of nutrient change in various decay stages in FWD, particularly in the Great Lakes states (Miller 1983, Mladenoff et al. 2010). Our results of the major tree species in this region indicated that most nutrients in FWD increased from decay class 1 to decay class 2. One criterion for defining our decay class 2 FWD samples was that bark was observed to be sloughing but still mostly present. For *Populus tremuloides*, half of the nutrient-rich branch bark has been observed to slough off within 4 years and macronutrient concentrations have been observed to decrease by half between 2 – 5 years (Miller 1983). This would indicate that, despite the loss of some bark, the sampled material had not been on the ground long and was still in the early stages of decay. In addition, the increase in nutrient concentrations were likely due to colonizing decomposers, including deadwood-dependent insects (Jonsell et al. 2007), microbes, or nutrient-rich basidiomycetes (Harmon et al. 1986), translocating nutrients to the material. It is likely that throughfall, and perhaps litterfall, could contribute to increases in nutrient concentrations as well (Grier 1978, Foster & Lang 1982, Arthur & Fahey 1990).

Despite a general increase in most nutrients from decay class 1 to decay class 2, we observed decreases in K and P, which is consistent with patterns observed for these nutrients in other studies of FWD and CWD (Grier 1978, Miller 1983, Mladenoff et al. 2010). Potassium concentrations decrease by half within approximately one year of decay in *Populus tremuloides* FWD in northern Minnesota (Miller 1983). In our study, K concentrations decreased between 27 – 72% from decay class 1 to decay class 2 within all species. This suggests that our decay class 2 FWD had been dead and on the ground for close to 2 years, which seems plausible given the presence of bark and the slightly longer rate of bark sloughing observed by Miller (1983). In addition, K is known to be highly mobile and concentrations tend to decrease before mass loss or fragmentation occurs (Arthur & Fahey 1990, Krankina et al. 1999, Holub et al. 2001). Phosphorus tends not to be a limiting nutrient in temperate, terrestrial ecosystems and has been known to move out of CWD over time (Harmon et al. 1986). Therefore, microbial decomposers are likely not starved for P and any excess leaches out of the CWD (Holub et al. 2001). This pattern of leaching from CWD due to unneeded microbial P could explain the loss of this nutrient observed in our FWD.

4.2 CWD Nutrient Concentrations by Species, Wood Type, & Decay Class:

4.2.1 Species & Decay Class

Nutrient concentrations for CWD in decay classes 1 – 3 were generally consistent with other studies for most nutrients (Sykes & Barr 1973, Lambert et al. 1980, Miller 1983, Alban & Pastor 1993, Krankina et al. 1999, Mladenoff et al. 2010, Saunders et al. 2011). As with FWD, Ca concentrations were highest among all nutrients, excluding %TC, for any given species in our study and have been commonly observed as such elsewhere (Lambert et al. 1980, Miller 1983, Alban & Pastor 1993, Saunders et al. 2011). The only comparable *Fraxinus nigra* values were with live stems of *Fraxinus nigra* in northern Wisconsin (Mladenoff et al. 2010) and *Fraxinus excelsior* in northern England

(Sykes & Barr 1973). A notable difference in these comparisons was that our *Fraxinus nigra* nutrient concentrations were slightly higher than those found in northern Wisconsin. However, this discrepancy can be attributed to our samples including both bark and bole wood whereas the samples from Wisconsin were split into bole wood and bark, separately.

There were some discrepancies between our nutrient concentrations and those of other studies. Our values for P, K, B, and Fe tended to be higher than Saunders et al. (2011) by at least an order-of-magnitude. Since soils in both studies were similar, ranging from sandy loams to silt loams with glacial till as the parent material, site quality was likely not a major factor in these differences. One possible reason for the discrepancy between our values was that Saunders et al. (2011) used a 4-class system of decay and we used a 5-class system. Therefore, the samples in similarly labeled stages of decay between our two studies are not likely at similar points in the decay process. Another reason for the differences between our values could be that the samples in Saunders et al. (2011) came from softwood-dominated forests while ours came from hardwood-dominated forests. More specifically, the litter layer in the softwood-dominated forest contains greater amounts of needles, which are more recalcitrant and decay less rapidly than deciduous leaves (MacLean & Wein 1978). Therefore, especially within temperate forests, nutrients are less available in the litter layer of a softwood-dominated site, while the high rate-of-decay of deciduous leaves from a hardwood-dominated site provides rapid turnover of nutrients (MacLean & Wein 1978, Jerabkova et al. 2006).

Another discrepancy between our CWD nutrient concentrations and values of other studies was the very low N we observed for all species and decay classes despite increasing with further decay. Generally, N concentrations increased by an order of magnitude from decay class 2 to decay class 3 indicating the presence of colonizing decomposers. In addition, it is likely that these nutrient increases could be due to throughfall and litterfall (Grier 1978, Foster & Lang 1982, Arthur & Fahey 1990). Nitrogen concentrations in all three decay classes of *Fraxinus nigra* were higher than any other species in similar decay classes yet these values still were lower than typical N concentrations for this region (Alban & Pastor 1993). As with FWD, the presence of *Acer rubrum*, which could have similar characteristics as *Acer saccharum*, could be causing a higher rate of nitrate leaching on our sites (Lovett & Mitchell 2004) resulting in low N concentrations in live wood and, therefore, woody debris.

One interesting result in our study was that *Populus tremuloides* and *Acer rubrum* showed no measurable N in decay classes 1 and 2 and decay class 1, respectively. Since woody debris samples were taken from both unharvested forest and clearcuts, many of the decay class 1 samples came from freshly harvested wood in the clearcut areas which were harvested over the winter (February 2010). Prior to senescence, deciduous trees retranslocate N to perennial tissues, such as stem wood and roots, to preserve nutrients over the winter and then move these nutrients back to meristematic tissues and leaves in the spring for new growth (Pallardy 2008). It seems unlikely that N would vacate these storage areas in perennial tissues as early as February in northern Minnesota and, therefore, N would be at relatively higher concentrations in these tissues during this time. Given this, our decay class 1 N concentrations should show some measurable concentration since most of our samples were from trees harvested over the winter and N likely was not mobilized to meristemic tissues for spring growth.

A potential explanation of the low N values observed in this study, particularly in *Populus tremuloides* and *Acer rubrum,* could be related to laboratory analyses using combustion analytical methods of organic nutrients. While care was taken to provide a homogeneous, representative sample, it can be difficult to carry this through to analysis when procedures require samples only on the order of milligrams. A comparison of the micro-Kjeldahl and CHN combustion methods for N concentrations in low N soils suggested that the greatest potential error in N results was due to particle-size bias in small subsamples (Wang et al. 1993).

Fraxinus nigra generally stood out as the species with the highest CWD nutrient concentrations. The low nutrient concentrations in decay class 1 *Acer rubrum* are corroborated by those of Pastor & Bockheim (1984) who observed that *Acer saccharum* had lower nutrient concentrations compared with *Populus tremuloides*. The low nutrient concentrations observed in *Betula papyrifera* seem counterintuitive to what we observed in our FWD. However, it is common for bole wood to contain lower nutrient concentrations than branchwood in *Betula papyrifera* (Jokela et al. 1981, Lang et al. 1982). In addition, the recalcitrant bark of *Betula papyrifera* may provide a barrier in the early stages of decay to colonizing organisms, throughfall, and stemflow, thus, resisting any possible increase or decrease in nutrient concentrations. High nutrient concentrations in *Populus tremuloides* have been observed in other studies (Perala & Alban 1982, Hendrickson et al. 1987, Alban & Pastor 1993). *Populus tremuloides* has been observed to have higher concentrations of K than other species in the Great Lakes states

(Hendrickson et al. 1987). The high concentrations of K we observed in our CWD could result from the high concentrations of this nutrient in the leaves of *Populus tremuloides*, the high mobility of K (Holub et al. 2001), and the rapid decay rate of these leaves (Jerabkova et al. 2006), thus, making it highly available for uptake by other species on our sites.

The lack of significant change in any nutrient concentration from decay class 1 to decay class 2 could be due to the length of time it takes for a large piece of wood to be colonized by decomposers (Harmon et al. 1986). This depends on the diameter of the CWD, as fungal colonization takes longer on larger logs (Buchanan & Englerth 1940). Position of CWD in relation to the ground can affect decomposer colonization and decay rate. Fresh CWD still contains the majority of its branches and, in some cases, is elevated off the forest floor allowing it to dry out and remain dry longer than material directly in contact with the ground (Söderström 1988). In addition, elevation of CWD keeps it out of contact with any ground-based flora (Söderström 1988). Since a number of our decay class 1 samples were selected in clearcut areas, it is possible that the open conditions of the clearcut allowed for rapid drying of CWD regardless of its proximity to the ground resulting in slow decomposer colonization and metabolism. Likewise, it is known that low N concentrations tend to impede rate of decay of wood (Merrill & Cowling 1965). The low concentrations of N evident in our CWD may result in few decomposers present initially, ultimately resulting in a slower overall decay and greater lag time before noticeable changes in nutrient concentrations could occur.

Significant differences between nutrient concentrations in decay class 1 and decay class 3 as well as decay class 2 and decay class 3 were expected as CWD spent more time on the ground and was further along in the decay process likely having experienced throughfall, stemflow, and colonization by decomposers (Harmon et al. 1986).

4.2.2 Wood Type & Decay Class

Nutrient concentrations of hardwoods and softwoods within our study generally were within the range of those found by Saunders et al. (2011). Unlike Saunders et al. (2011), we did not find a distinct difference between wood types in our study although inclusion of more than one species of softwood could provide more conclusive differences. Within decay class 4, where sample sizes were equal, most nutrient concentrations were statistically similar between the two wood types. However, significant differences existed for N and B; in both cases hardwoods were greater than softwoods. When looking at overall trends within decay class 4, hardwoods were greater than softwoods for every nutrient except Mg and Mn. This greater nutrient concentration in hardwoods over softwoods was observed by Saunders et al. (2011) and they attributed this result to the radially oriented rays and larger diameter vessels within hardwoods allowing them to be colonized faster than softwoods (Harmon et al. 1986).

The increases in nutrient concentration we observed from decay class 3 to decay class 4 are well documented in the literature (Lambert et al. 1980, Arthur & Fahey 1990, Means et al. 1992, Krankina et al. 1999, Holub et al. 2001, Saunders et al. 2011). As CWD reaches decay class 4, it has become extensively invaded by decomposers (Jonsell et al. 2007, Harmon et al. 1986). A key distinction between decay class 3 and decay class 4 material in our study was that branch stubs pulled out easily from decay class 4 material. This observation was noted by Sollins (1982) and indicates that decay has reached the heartwood. In addition, many studies have documented CWD as a key substrate for forest vegetation and tree regeneration as the log becomes further decayed (Cornett et al. 2001, Marx & Walters 2008, Svoboda et al. 2010, Bolton & D'Amato 2011). By the fourth stage of decay in our study, CWD was starting to experience this invasion by other plants as roots began to penetrate the material and translocate nutrients into the wood (Harmon et al. 1986).

4.3 CWD Nutrient Concentrations by Decay Class Only:

As logs reached decay class 5, material was typically indistinguishable by species or wood type, although we did observe in one instance that bark from *Betula papyrifera* was still present on decay class 5 CWD. All logs were essentially humps on the forest floor, highly colonized by decomposers and vegetation. Moss and seedlings were extensively evident on the surfaces of these logs and their roots were well dispersed through the woody material.

Trends in nutrient concentrations for CWD through decay class 5 from our study generally matched that of other studies using a five-class decay system (Arthur & Fahey 1990, Means et al. 1992, Krankina et al. 1999). Large increases in nutrient content and, in some cases, variability were observed, typically in decay class 5. While %TC generally increased from decay class 1 to decay class 4, the significant decline in %TC concentration from decay class 4 to decay class 5 in our study resembled that found by Krankina et al. (1999) who observed a decrease in %TC concentration from decay class 3 to decay class 4. Carbon concentrations have been observed to remain fairly constant through decay, generally reflecting mass loss (Lambert et al. 1980, Keenan et al. 1993).

The decrease in %TC observed in our study could be caused by increased respiration as N was translocated to the CWD and %TC was subsequently converted to carbon dioxide (CO_2). Potassium is a highly mobile ion and its loss from woody debris prior to fragmentation has been well documented (Lambert et al. 1980, Harmon et al. 1986, Arthur & Fahey 1990, Krankina et al. 1999, Holub et al. 2001). Loss of K has been observed in other sections of this study as well. Boron initially increased in concentration before declining slightly from decay class 3 to decay class 5, being the only other element besides K to exhibit some loss with decay. This slight decline in B concentration was not a significant decrease and was similar to trends in B found by Krankina et al. (1999).

As noted above, there are a number of factors contributing to trends in nutrient concentrations across decay classes. Since CWD can be present for long periods of time, it is possible that each of these factors contributes in some way to the nutrient concentrations found within each decay class. Deadwood-dependent insects contribute to the nutrient cycling of CWD by breaking down material and creating galleries for other organisms to invade (Harmon et al. 1986). Nutrient input via litterfall and throughfall has been observed to be a significant source of nutrients, particularly in the moist, coastal forests of the Pacific Northwest (Grier 1978). Nitrogen-fixation by microbes can be a key source of N input into CWD, particularly in slightly decayed and moist material (Roskoski 1980), and can vary with type of microbe and wood species (Hendrickson et al. 1991). Fungi also play a complex role in CWD nutrient cycling. Basidiomycetes are important in the cycling of some key macronutrients (Ca, K, P) as well as some micronutrients (Cu, Zn) in decomposing hardwood and softwood litter (Cromack et al.

1975). In CWD, nutrients are sequestered by fungi, generally basidiomycetes, and translocated to fruiting bodies or distributed throughout a complex network of foraging mycelia that can stretch between multiple, separate pieces of CWD (Boddy & Watkinson 1995). We did not explicitly examine for any of these factors and cannot comment on the extent of their role in our nutrient concentrations. It is unclear how these factors may have interacted amongst each other in our samples to ultimately effect nutrient concentrations in each stage of decay.

5. Conclusions:

Generally, the trends in nutrient concentrations across sizes, species, decay classes, and wood types within this study were comparable to those reported from similar regions. Nutrient concentrations in FWD were significantly greater than in CWD, increased with decay, and differed among species, patterns seen in many studies of CWD. CWD also showed differences within species, wood type, decay class, and interactions between these factors. In addition, CWD showed general trends demonstrating an increase in nutrient concentration with increasing decay. Both FWD and CWD showed low levels of N in early decay classes yet no clear explanation for these low concentrations was determined. In addition, the high levels of Ca reported in all material underscore the importance of this element in *Populus tremuloides*-dominated forests.

The results of this study demonstrate that the roles of CWD and FWD in forest nutrient cycling are highly complex and difficult to define. Despite this complexity, understanding the nutrient dynamics of these materials is important for assessing site quality and productivity following disturbances, which typically leave high stocks of woody debris on a site, particularly FWD. Harvests, specifically biomass harvests, represent a disturbance which directly manipulates the pools of CWD and FWD through removal or retention. Knowledge of nutrient dynamics in FWD is of particular importance as retention of this nutrient-rich material following biomass harvesting could play a key role in future stand productivity and site quality by providing nutrient inputs immediately following harvest events. In addition, CWD of certain nutrient-rich species, such as *Populus tremuloides*, may be more crucial for maintaining long-term nutrient pools. Information from this and future studies of the roles FWD and CWD play in nutrient cycling will contribute key information for managers to refine harvest guidelines such that site quality and productivity are not compromised.

Chapter Four: Conclusions

The results presented in this thesis indicate that harvest operations have a dramatic effect on the level of FWD retained on a site following harvest. Direct manipulation of harvest slash significantly increased stocks of biomass and most nutrients within the ecosystem, most notably in nutrient-rich FWD. Generally, treatments prescribed with retaining all slash were significantly higher than those prescribed with retaining no slash within these systems. However, the prescribed level of no slash retention still provided substantial increases in woody debris following harvest compared to the unharvested control. The slash retention level of 20%, recommended in the Minnesota state biomass harvesting guidelines, was ambiguous in terms of providing an absolute threshold of material greater than no slash retention. Green-tree retention did not significantly affect the stocks of biomass and nutrients within the total ecosystem or woody debris pools.

These results underscore the importance of slash retention, particularly in terms of FWD stocks, immediately following harvest operations in *Populus tremuloides*-dominated systems. Important information can be gleaned from this study in terms of informing and improving the biomass harvesting guidelines within the state of Minnesota and potentially elsewhere. In addition, results from this study provide clues as to where future research and analyses of biomass harvests should focus. The following sections synthesize the results from this study and provide recommendations and suggestions for future biomass harvest operations and research.

Management Recommendations:

The 20% slash retention treatment was intended to leave approximately 1/3 of all available slash on site following harvest operations. This guideline was recommended in an effort to provide increased nutrient inputs for future productivity as well as provide habitat while still allowing for increased biomass removal. In other words, the intent behind providing a recommended threshold of slash retention was to make the impacts of removal on the ecosystem less harsh than the extreme of retaining no slash. Although 20% slash retention resulted in greater levels of biomass and nutrients than no slash retention, this level was generally not statistically distinguishable from the 'no slash retained' treatment. However, based on the assumption that the 'all slash retained' treatment contained roughly all available slash we determined that the 'no slash retained' treatment resulted in 52% of available slash retained on site and not the expected 10-15%. When looking at magnitudes of biomass and nutrient stocks, the 'no slash retained' treatment was typically twice the magnitude of the unharvested control. Given these results, it seems reasonable to suggest that within winter-harvested *Populus tremuloides*-dominated systems under typical harvest operations, prescribing no retention of slash (whole-tree harvest) will retain more than 1/3 of available slash as recommended in the biomass harvesting guidelines for Minnesota. Studies have indicated that whole-tree harvest and removal of available slash generally do not affect soil nutrient stocks for many years following harvest (Alban & Perala 1992, Johnson & Todd 1998, Tamminen et al. 2012). Given the evidence from these studies, retaining no slash (removing whole trees) likely would not significantly affect nutrient availability up to a few decades post-harvest. While this recommendation seems reasonable based on our estimates, more accurate measurements of available slash would provide a better assessment of % slash retained on these sites than our estimates and continued monitoring of site nutrient stocks would reveal any potential changes in these pools as a result of harvest operations.

The pools of forest floor and coarse roots represented the largest stocks of nitrogen within all measured biomass material. Since nitrogen is a limiting nutrient in terrestrial ecosystems, maintaining these stocks of nitrogen is important for future site productivity. Forest floor material provides nutrient inputs to the surface layers of the soil. In addition, the decomposition of roots below the ground surface can provide direct contribution of nutrients to deeper portions of the mineral soil column. Stumps can provide similar characteristics as CWD and when CWD is scarce stumps could provide a key substrate for deadwood-dependent organisms (Rudolphi et al. 2011). Stumps and roots are sometimes removed in biomass harvests eliminating this pool from the ecosystem altogether. In addition, removal of this material can result in a much greater disturbance to the forest floor and soil (Rabinowitsch-Jokinen & Vanha-Majamaa 2010) through mixing of forest floor and mineral soil, removal of soil material stuck to roots, and compaction of forest floor and mineral soil due to increased time of operations on site. Loggers conducting future biomass harvests should be strongly encouraged to leave stumps and forest floor material on site as a source of nutrients and habitat. In addition, special emphasis should be placed on minimizing the impact of skidding operations since dragging harvest materials to and from the landing can increase disturbance to the forest floor (Mroz et al. 1985, Johnson et al. 1991). In cases where delimbing trees in place is not possible, tree skidding should be limited to a restricted area of the harvest site to reduce negative impacts of operations.

Future Research Recommendations:

A unique aspect of this study was the operational nature of the harvests (i.e., commercial harvests). Specifically, harvesting was conducted by independent, commercial loggers working only under the guidelines of the particular levels of slash retention and green-tree retention designated in the study. Loggers utilized their own equipment and techniques during operations the same way they would any routine harvest operation. This facet of the project is particularly important for informing biomass harvesting guidelines since biomass harvests will be conducted similarly as commercial harvests and not experimental harvests conducted by researchers with different equipment, methods, and objectives. Tamminen et al. (2012) noted that experimental harvests, as conducted in their study, could result in differing levels of disturbance compared to typical commercial harvests. Specifically, harvest methods can vary in that commercial harvests might be motivated more by efficiency and financial gains with less regard for precision and accuracy in meeting harvest guidelines whereas experimental harvests might be motivated more by achieving particular guidelines and site characteristics (i.e., a particular level of slash retention) with less regard for time or effort. Future studies of biomass harvests should focus on collecting data from commercial harvests whenever possible in order to best characterize post-harvest conditions on these sites. Where time and funding allow, biomass harvests should be setup with statistical analyses in mind such that data collected from biomass harvests can provide strong clues as to the impacts of operations.

The variables measured in this study (i.e., biomass and nutrient stocks) provided important information for understanding the effects of slash retention and green-tree retention on post-harvest stand conditions. Many other variables remain to be tested in order to further understand the post-harvest impacts of biomass harvests. Specifically, detailed measurements of total available slash and slash removed or slash retained will provide more accurate estimates of the percentage slash retained on a site. Future measurements should also focus on more detailed metrics of the post-harvest ground conditions including depth and percent cover of slash and percent cover of forest floor as green-tree retention has been shown to significantly impact these variables (Halpern & McKenzie 2001). Data collected from such measurements will provide important information on the level of disturbance and spatial arrangement of slash, woody debris, and forest floor material following biomass harvesting. Finally, more specific measurements and analyses of CWD following biomass harvests is crucial given the importance of this material as a source of habitat for deadwood-dependent organisms, substrate for regeneration, and its role in nutrient cycling (Harmon et al. 1986).

Examination of the effects of slash retention and green-tree retention in biomass harvests should not be restricted to only immediate post-harvest effects. Continued monitoring of harvest sites is important for understanding trends in the persistence of woody debris, soil quality and productivity, and regenerating plants. FWD is known to decay rapidly in comparison to CWD and continued monitoring of slash levels on site would provide information on decay dynamics and nutrient cycling. Also, studies have noted that increased levels of woody debris following harvest can affect regenerating plants and animal populations (Outcalt & White 1981, Olsson & Staaf 1995, Egnell & Leijon 1999, Åström et al. 2005, Sullivan & Sullivan 2012). Monitoring the dynamics of plant and animal communities will elucidate the impacts of slash retention on these ecosystem components and will provide information on potential mitigating effects from green-tree retention. Continued monitoring of green-trees will provide information on their effectiveness as standing habitat for animals and as future inputs of CWD as the stands age and the trees succumb to windthrow, mortality, and other agents of disturbance. Finally, monitoring of stumps following harvests will provide evidence on their importance as a source of nutrients within the deeper soil horizons and as a source of habitat for deadwood-dependent organisms.

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Appendix A

Table A1. Mean CWD nutrient concentrations for each wood type and decay class with standard errors in parentheses. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. Sample sizes within each group are as follows: for HW, decay classes 1 – 3, n=40; decay class 4, n=10; for SW, decay classes 1 – 4, n=10. Within each row, values with similar letters are not significantly different ($p > 0.05$) based on results from comparisons using the Tukey-Kramer method on transformed data.

Nutrients	**Hardwoods Decay Class**				**Softwoods Decay Class**			
	1	**2**	**3**	**4**	**1**	**2**	**3**	**4**
%TC	48.1 (0.2)^{c}	48.4 (0.1)^{c}	49.4 (0.2)^{b}	53.2 (1.4)^{ab}	50.8 (0.1)^{a}	50.4 (0.3)^{ab}	50.5 (0.1)^{a}	52.2 (0.7)^{a}
N	248 (79)^{b}	167 (52)^{b}	778 (180)^{b}	3304 (377)^{a}	380 (183)^{b}	330 (123)^{b}	437 (167)^{b}	450 (197)^{b}
P	129 (9)^{b}	109 (7)^{bc}	107 (10)^{bc}	263 (32)^{a}	113 (16)^{bc}	105 (17)^{bc}	75 (9)^{c}	156 (23)^{ab}
K	1594 (166)^{a}	1638 (195)^{a}	1812 (325)^{a}	1481 (531)^{a}	2144 (230)^{a}	2545 (447)^{a}	2005 (283)^{a}	1094 (266)^{a}
Ca	3414 (297)^{bcd}	3721 (238)^{abc}	4871 (491)^{ab}	5428 (554)^{a}	2268 (148)^{cd}	2227 (270)^{d}	2977 (345)^{bcd}	4303 (384)^{ab}
Na	23.1 (1.6)^{c}	23.2 (1.9)^{c}	31.2 (3.1)^{bc}	60.7 (7.0)^{a}	37.4 (3.5)^{ab}	29.0 (4.5)^{bc}	36.5 (4.2)^{ab}	33.5 (3.8)^{abc}
Mg	334 (19)^{b}	393 (26)^{ab}	551 (59)^{a}	547 (103)^{ab}	353 (28)^{ab}	399 (53)^{ab}	373 (21)^{ab}	648 (82)^{a}
Mn	56 (9)^{c}	58 (10)^{c}	95 (18)^{bc}	230 (36)^{a}	122 (15)^{ab}	113 (30)^{abc}	109 (27)^{abc}	262 (48)^{a}
Al	4.5 (0.7)^{d}	3.2 (0.3)^{d}	10.7 (1.9)^{c}	103.6 (50.4)^{ab}	17.2 (4.1)^{abc}	11.3 (3.2)^{bc}	11.5 (1.5)^{abc}	63.5 (11.8)^{a}
B	3.6 (0.2)^{cd}	4.2 (0.3)^{bc}	6.8 (0.9)^{ab}	7.4 (0.9)^{a}	2.3 (0.2)^{d}	2.5 (0.2)^{d}	2.7 (0.3)^{cd}	3.0 (0.4)^{cd}
Cu	1.6 (0.1)^{d}	1.8 (0.1)^{cd}	2.5 (0.2)^{bc}	4.5 (0.4)^{a}	1.6 (0.1)^{bcd}	1.5 (0.1)^{d}	1.7 (0.2)^{cd}	3.4 (0.5)^{ab}
Fe	17.3 (3.0)^{c}	15.1 (1.5)^{c}	24.6 (3.7)^{bc}	113.7 (55.1)^{ab}	22.9 (7.9)^{bc}	11.3 (1.4)^{c}	16.6 (1.9)^{abc}	89.6 (24.9)^{a}
Zn	31.2 (4.6)^{b}	37.4 (7.1)^{b}	49.1 (8.8)^{b}	152.9 (22.8)^{a}	16.1 (1.7)^{b}	17.9 (1.6)^{b}	19.1 (2.5)^{b}	37.4 (5.0)^{ab}

Table A2. Mean CWD nutrient concentrations for each decay class with standard errors in parentheses. Carbon is presented in percent total (%TC) while all other nutrients are in mg/kg. F-values and p-values for each model are presented as well. Sample sizes within each decay class are as follows: decay classes 1 – 3, n=50; decay class 4, n=20; decay class 5, n=10. Within each row, values with similar letters are not significantly different ($p > 0.05$) based on results from comparisons using the Tukey-Kramer method on transformed data.

Nutrients	Decay Class					F-value	p-value
	1	2	3	4	5		
%TC	48.6 (0.2)^{cd}	48.8 (0.1)^{c}	49.6 (0.2)^{b}	52.7 (0.8)^{a}	40.7 (2.7)^{d}	15.06	<.0001
N	275 (73)^{a}	199 (48)^{a}	710 (148)^{a}	1877 (387)^{b}	5678 (632)^{c}	19.69	<.0001
P	126 (8)^{b}	108 (6)^{bc}	101 (9)^{c}	209 (23)^{a}	514 (46)^{a}	17.96	<.0001
K	1704 (143)^{a}	1819 (185)^{a}	1851 (266)^{a}	1288 (293)^{ab}	536 (42)^{b}	5.34	0.0004
Ca	3185 (247)^{d}	3423 (214)^{cd}	4493 (412)^{bc}	4865 (353)^{ab}	6457 (547)^{a}	9.11	<.0001
Na	26.0 (1.7)^{bc}	24.4 (1.8)^{c}	32.3 (2.6)^{b}	47.1 (5.0)^{a}	67.3 (5.5)^{a}	14.91	<.0001
Mg	338 (16)^{d}	394 (23)^{cd}	515 (48)^{bc}	597 (65)^{ab}	694 (55)^{a}	11.36	<.0001
Mn	69 (8)^{b}	69 (10)^{b}	98 (15)^{b}	246 (29)^{a}	288 (66)^{a}	15.67	<.0001
Al	7.0 (1.2)^{c}	4.8 (0.8)^{c}	10.8 (1.5)^{b}	83.6 (25.6)^{a}	1074.1 (236.6)^{a}	36.17	<.0001
B	3.4 (0.2)^{a}	3.8 (0.3)^{ab}	6.0 (0.7)^{b}	5.2 (0.7)^{ab}	5.4 (0.5)^{ab}	3.99	0.0040
Cu	1.6 (0.1)^{a}	1.8 (0.1)^{a}	2.3 (0.2)^{b}	3.9 (0.3)^{c}	6.3 (0.7)^{c}	28.94	<.0001
Fe	18.4 (2.8)^{c}	14.3 (1.2)^{c}	23.0 (3.0)^{b}	101.6 (29.5)^{a}	1344.6 (348.3)^{a}	24.02	<.0001
Zn	28.2 (3.8)^{b}	33.5 (5.8)^{b}	43.1 (7.2)^{b}	95.1 (17.4)^{a}	104.0 (17.5)^{a}	9.76	<.0001