Coarse Woody Debris Dynamics Following Biomass Harvesting: Tracking Carbon and Nitrogen Patterns During Early Stand Development in Upland Black Spruce Ecosystems

Scott Wiebe
Dave Morris
Nancy Luckai
Doug Reid

Abstract

Coarse woody debris (CWD) in the boreal ecosystem has been hypothesized to play an important nutritional role following stand-replacing disturbances such as fire or harvest. Sites with shallow soil over bedrock, or those with coarse-textured soils, can be especially susceptible to overstory removal because low carbon and nutrient pools may limit stand productivity in subsequent rotations. On these site types, CWD can provide essential nutrition to the developing second growth stand, prior to internal cycling processes stabilizing at crown closure (15 years to 20 years after stand initiation) through slow and steady decomposition. The current study sites were established in 1994 and in 2008 (14 years following harvesting) and were approaching crown closure. The experimental harvest areas were designed to document carbon loss and nutrient fluxes after the application of four levels of biomass removal from mature black spruce forested stands in northwestern Ontario, Canada. Two soil types (fresh, loamy : dry, sandy), with stand replicates (blocks), were selected to test whether residual CWD represents a source or sink for nutrients, and if the decay pattern varied depending on soil type. Measurement/sampling of CWD was done immediately after the harvest treatments were applied, and again in year 4 and year 14. The biomass removal treatment with the greatest carbon loss and fastest CWD decay rate had the highest initial mass of CWD, indicating possible synergistic decay dynamics. Nitrogen concentration in the CWD continued to increase from the initial measurements to year 14 (from 900 ppm to 2400 ppm), but was largely a function of increasing carbon loss. When converted to N content in CWD (kg ha^{-1}), however, nitrogen exhibited an initial upward trend (i.e., immobilization) through years 1to 4 (from 50 kg ha^{-1} up to 80 kg ha^{-1}) and a subsequent release in years 5 to 14 (from 80 kg ha^{-1}down to 27 kg ha^{-1}). This trend was more apparent on the dry, sandy sites where N content peaked at almost 100 kg ha^{-1} at year 4, but then reduced to 26 kg ha^{-1} by year 14. We compared the average loss of N from CWD in years 4 to 14 (5.3 kg ha^{-1} yr^{-1}) to the total soil inorganic N pool (based on a fresh K_2SO_4 extraction), and found that the N loss from CWD represented a substantive portion (80%) of the available N pool, particularly on the dry, sandy sites. After an initial peak in year 4, black spruce foliar N decreased significantly ($p<.0001$) through to year 10 but began to rebound by year 15. This increase, presumably, was in part the result of the documented release of N from CWD. These results suggest that CWD, although a small contributor to the total N pool, makes a substantial contribution to the relatively small available N pool, especially on dry, sandy soils. The trend of initial N immobilization and subsequent release shows CWD may also serve to buffer the initial leaching of nutrients from the site following harvesting and provide an available source of N to the regenerating stand prior to crown closure.

Keywords: coarse woody debris, black spruce, carbon and nitrogen dynamics.
Received 23 September 2010, Revised 11 December 2012, Accepted 13 December 2012.

Introduction

The use of forest biomass for energy/fuel may result in more intensive forest utilization, requiring a better understanding of the potential impacts of intensive harvest on forested sites. Coarse woody debris (CWD) has been shown to be a very important component of the forest ecosystem, especially for biological diversity of many types of flora and fauna (Samuelsson et al. 1994, Siitonen 2001, Lonsdale 2008). There is less clarity in the role CWD plays as a significant contributor to site nutrient pools, the temporal pattern of nutrient release, and the timing of this release compared to

Author information: Scott Wiebe (corresponding author) and Nancy Luckai, Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON CANADA P7B 5E1. Swiebe@lakeheadu.ca, nluckai@lakeheadu.ca. Dave Morris and Doug Reid, Ontario Ministry of Natural Resources, Centre for Forest Ecosystem Research, c/o Lakehead University, 955 Oliver Road, Thunder Bay, ON CANADA P7B 5E1. Dave.M.Morris@ontario.ca, doug.reid@ontario.ca .

International Journal of Forest Engineering
ISSN 1494-2119 (print) and 1913-2220 (online)

plant uptake demand. CWD has often been described as a "buffer" against nutrient losses following site disturbance (Graham and Cromack 1982, Lang 1984, Tenhagen et al. 1996, Krankina et al. 1999). Laiho and Prescott (2004) reported declining C/nutrient ratios and increased nutrient content of wood during early phases of decay, suggesting CWD plays an active role in maintaining site quality. Following the flush of more rapidly decomposing components (i.e., leaves, small branches, roots), commonly referred to as the assart effect (Romell 1957, Titus et al. 2006), CWD could provide essential nutrition to the emerging stand until crown closure when other cycling processes (e.g., litterfall, throughfall, stemflow) once again enable self-sufficiency.

Observed contributions of CWD are roughly 4% to 6% of plant uptake (Hart 1999) and less than 5% of total N released from aboveground litter (Arthur and Fahey 1989, Laiho and Prescott 1999). While CWD has been dismissed as a non-significant contributor to total N cycling (Laiho and Prescott 2004), the timing of N immobilization and subsequent release by CWD has not been related to forest stand requirements following stand disturbance and initiation. Krankina et al. (1999) and others (Hafner et al. 2005, Butler et al. 2007) point to the broad range of nutrient and carbon pool estimates in the literature as evidence that further research is required to fully understand nutrient dynamics. This will be particularly critical should forest biomass be increasingly utilized as a renewable energy source in the coming decades.

In a review, Laiho and Prescott (2004) pose two hypotheses with respect to the role of CWD in forest productivity. Specifically, that 1) on sites where nutrients, especially N or P, limit plant growth, CWD accumulation may reduce primary productivity through immobilization of those nutrients by decomposers, and 2) on dry sites, where lack of moisture limits plant and microbe growth, CWD may increase primary productivity and enhance element cycling by improving moisture retention. On such sites, CWD may also be important for the retention and accumulation of soil organic matter. The current study was designed to address the amount or form of nutrients sequestered within and provided by the CWD.

Using established experiments with a history of pertinent data supplemented by additional measurements, our goal is to clarify the role of CWD in these forest types and identify the potential effects of increased utilization for biofibre and bio-energy on these ecosystems. Another important aspect to consider is the timeframe when CWD might contribute to site nutrition in terms of the ecological rotation of forested stands. The stands examined in this project have been tracked for 14 years post-harvest and are now approaching the critical period of time between stand establishment and canopy closure. Because this monitoring effort includes repeated measures of CWD nutrient levels, it is possible to quantify the change in both biomass and nutrient retention throughout the timeframe.

Our specific research questions related to Laiho and Prescott's (2004) over-arching hypotheses were the following:

1. What is the temporal pattern of mass loss in CWD, and does this differ depending on soil type (loam versus sand)?

2. How do CWD-C pools compare to total soil C reserves, and does this vary depending on soil type and level of biomass removal?

3. How do nitrogen concentration and content change in CWD over time since disturbance, and how does this compare to inorganic N soil pools?

4. Does the pattern of CWD nitrogen retention/release correspond to the temporal patterns in planted black spruce foliar nutrition?

Materials and Methods

Study location

For this study, four sites were selected that represented two soil types and site quality classes (good—fresh, coarse loamy tills; poor—dry, sandy outwashes). The fresh, coarse loamy sites are situated approximately 60 km north of Thunder Bay, Ontario, Canada (latitude: 49°07'N, longitude: 89°41'W), and represent well-drained, fresh (moisture regime 2) sites dominated by black spruce (*Picea mariana* L.) and jack pine (*Pinus banksiana* Lamb.), with a scattered occurrence of trembling aspen (*Populus tremuloides* Michx.). These sites are shallow (<20 cm) morainal tills overtopping granitic bedrock (Dystric Brunisols—Can. Soil Classification Working Group 2006).

The two dry, sandy sites are located north of Geraldton, Ontario, Canada (latitude: 50°42'N, longitude: 86°24'W). Both sites are representative of sandy outwash soils dominated by black spruce and jack pine, and have well-developed Humo-ferric podzolic profiles (Can. Soil Classification Working Group 2006). One site is a deep, fine-to-medium sand that is rapidly drained and has a moderately dry moisture regime (MR: 1), while the second site is very rapidly drained and represents a slightly drier (MR: 0), medium-coarse sandy site.

Experimental design

The study was designed as a 2 x 4 Randomized Complete Block Design (RCBD), with two soil types, as described above, and four levels of biomass removal, with two site replicates (blocks) within each site type. These removal treatments were carried out during the winter of 1994 and included: stem only (SO) —delimbed at the stump; full-tree chipping (CH)—chipped debris returned to the harvest plot; full-tree (FT)—delimbed at the roadside; and full-tree + blading (FT+B) —complete removal of vegetation and forest floor. Each of the four sites included three plot replicates (30 × 30 m) of each of the four biomass removal treatments (12 plots per site, with 48 plots in total), each one separated by 20 m buffers. On each treatment plot, two 4 m^2 slash plots were established immediately after harvest (June 1994) in the center of two randomly selected plot quadrants. The slash on each sub-plot was sorted by component (bole, branches, bark, cones, twigs, needles), weighed and sub-samples collected for dry weight and nutrient analysis. Slash was then returned to the plot according to the original distribution. Sampling was conducted immediately after the biomass removal treatment (June 1994), at year 4 (June 1998), and year 14 (June 2008). Slash loadings and their associated nutrient pools were calculated for each biomass removal level × site combination for the period immediately following harvest, 4 and 14 years after harvest (summer 2008). At each sampling period, representative subsamples of CWD (i.e., collection of branches covering the range of diameters and discs cut from stems > 7 cm in diameter) remaining from slash plots was removed and analyzed for total carbon and nitrogen. In total, 96 slash plots were tracked through the 14-year period.

To determine if the original 4 m^2 slash plots were representative of the overall slash loadings for each biomass removal treatment × site combination, additional transects were measured in 2008 (48 in total). Transects were 10 m in length and 2 m wide and were situated diagonally within one quadrant that had an existing slash plot. Log diameters and lengths were recorded and converted to mass using density. Density was determined by classifying each log into decay classes similar to Maser et al. (1979), Sollins (1982) and Naesset (1999): 1] Recently dead tree, bark intact, 2] bark mostly intact, wood of outer layers (sapwood) of the log has started to soften due to rot, 3] bark sloughing or absent, soft outer layers of log and are easily removed with a knife, heartwood mostly sound, 4] bark detached, wood soft, no solid core, 5] Fragmented, no structural integrity. Average densities for each decay class were determined through volume displacement of subsampled logs. Overall, the plots did appear to be representative when compared to the transects, with a percentage difference of 2.6%. There was a tendency, however, for underestimates in the SO treatments due to the clumpy nature of the slash distribution.

Field sampling of soil for the determination of mineralizable N (anaerobic incubation) and inorganic N (fresh extraction) occurred in the summer of 2008 (year 14). One forest humus (O horizon) and one upper mineral soil sample (0 to 20 cm) were randomly taken from each treatment plot. Samples were air dried; organic samples were hand ground, removing cones and branch fragments > 2 cm in diameter; mineral samples were sieved (2 mm) to remove coarse fragments. Soil carbon and nitrogen pools, by horizon, were calculated as horizon depth (cm) × elemental concentrations ($mg \cdot kg^{-1}$) × fine fraction bulk density ($g \times cm^{-3}$), and then converted to a per-hectare basis. Bulk density measurements were done as part of the ongoing monitoring of these Long-Term Soil Productivity (LTSP) trials.

Foliar sampling was conducted repeatedly (years 4, 8, 10, 15) on nine randomly selected planted black spruce seedlings on each of the four study sites and 12 treatment plots per site (432 seedlings × 4 sampling periods). Current foliage was clipped from 10 branches (bulked into 1 sample per tree) located in the upper one-third of the crown at the end of August in each of the sampling years. Samples were processed/ analyzed in the lab following the procedures described below for the CWD samples. The initial samples were obtained from nine trees at the time of felling.

Analysis

Solid wood samples were dried at 50^0C until they reached a stabilized dry weight. Each wood cookie was separated into bark, sound and unsound components. Samples were then ground into 2g portions using a Thomas Scientific Wiley Mini-Mill (Model 3383-L10), with a 0.85 mm sieve (20 mesh). Total carbon, nitrogen and sulfur were analyzed using a combustion technique with a LECO CNS-2000 (LECO Corporation, St. Joseph, MI). Al, B, Ca, K, Mg, Mn, Na, P, S and Zn analysis was completed with a Varian Vista Pro inductively coupled argon plasma spectrometer (ICAP/ICP) AES (Varian Inc.) following a 10% HNO_3 acid digestion (adapted from Miller 1998).

Mineralizable nitrogen was determined using an anaerobic incubation procedure to measure the potential of the soil, collected in 2008, to provide available nitrogen. Ten grams of the air-dried mineral sample or 5 grams of the organic sample were added to 50 mL of deionized water and placed in an incubator for 14 days at 30^0C (following the procedures outlined by Powers (1980)). Following incubation, 4 M KCl solution was added to the samples, which, when combined with the deionized water, yielded a 2 M extraction solution (Binkley et al. 1990). Samples were then agitated for one hour at 180 rpm, filtered, and analyzed for ammonium using a Technicon Instruments AutoAnalyzer II (Pulse Instrumentation (1992) Ltd., Saskatoon, SK) (Kalra and Maynard 1991). In addition, inorganic nitrogen ($NH_4 + NO_3$) was measured to obtain a point-in-time ($Time_{14}$) reading of available N, and was similarly obtained using 2 M KCl extraction on fresh soil, following Kalra and Maynard (1991).

Data (nutrient concentrations and content) were analyzed as a repeated measures ANOVA, with site type and biomass removal treatment as main (fixed) factors, and sampling time was treated as a repeated measure in the GLM, using SPSS (ver. 17). Post hoc analysis was performed using the Student-Neuman-Kuels (SNK) multiple range test, with the critical level for significance set at 0.05.

Decay rate was calculated using a standard CWD exponential decay model (Harmon et al. 1986, Laiho and Prescott 2004, Tobin et al. 2007) and is expressed as:

$$Y_t = Y_0 e^{-kt} \qquad [1]$$

Where Y_0 is the initial quantity of the material (mass or density), Y_t is the quantity remaining at time t, and k is the decay constant. Linear transformation of the equation to express k from the equation is as follows:

$$k = \frac{(\ln Y_0 - \ln Y_t)}{t} \qquad [2]$$

Decay constants were then computed for the different sampling periods (years 0, 4, and 14, as well as an average constant).

Results

CWD mass and carbon loss

Initial CWD slash loadings for the SO, CH and FT treatments were in the range of 13-23 Mg ha^{-1}, with significantly higher values on the loam sites for the FT and FT+B treatments (Figure 1). After 14 years, the CW remaining was less than 4 Mg ha^{-1}, dropping on average nearly 10 Mg ha^{-1} across the treatments. There was no significant difference in the amount of material lost between the SO, CH and FT treatments at time 0 (p=0.952), year 4 (p=0.323) or year 14 (p=0.193). The FT+B treatment, as expected, had little to no CWD after the treatment was applied.

Average CWD mass decreased on both soil types over the 14-year time period, with CWD mass on the loamy sites decreasing from 15.0 to 4.7 Mg ha^{-1} and CWD mass on sandy sites decreasing from 13.1 to 3.0 Mg ha^{-1}, with the rate of decrease similar across treatments (Figure 1). We did not detect any difference in average CWD mass loss between soil types at year 0 (p=0.363), year 4 (p=0.950) or year 14 (p=0.258).

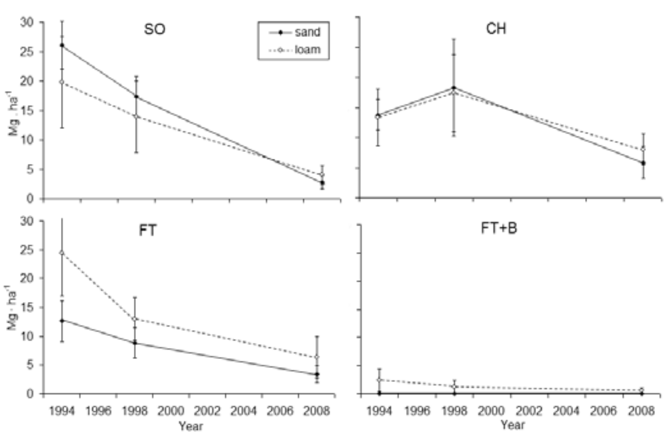

Figure 1. *Average CWD mass loss, by harvet treatment and soil type, for three measurement periods over a 14-year sampling period. Vertical bars represent standard errors.*

It is worth noting, however, that the CWD decay constants from year 0 to 4 were lower on sandy soils (k=0.05) than on the loamy sites (k=0.12) (Table 1). From years 4 to 14, the decay rate for CWD on loamy sites remained relatively constant (k=0.10), while CWD on sandy sites decayed at a much faster rate (k=0.13) during this phase of decomposition compared to the first four years, suggesting a "decompositional delay" on the dry, sandy sites.

Comparison of CWD-C pools to total soil C reserves

In both soil types and all harvest treatments, there was greater carbon content in the soil (mineral 0-20 cm and organic)

Table 1. *Decay constants (k) by soil type for the various sampling periods, derived from Equation 2.*

Decay period (year)	Sand (decay *k*)	Loam (*k*)
0 to 4	0.05	0.12
4 to 14	0.13	0.10
0 to 14	0.10	0.11

compared to CWD in year 14 (Figure 2). Total C reserves (CWD-C + soil C) averaged 56.8 (sand) and 83.6 Mg ha^{-1} (loam) 14 years after treatments were imposed. Total C in CWD at 14 years after harvest was <8% of total C reserves for both soil types, with the majority of C contained in the O horizon (nearly 70%), with the exception of the severe FT+B treatment.

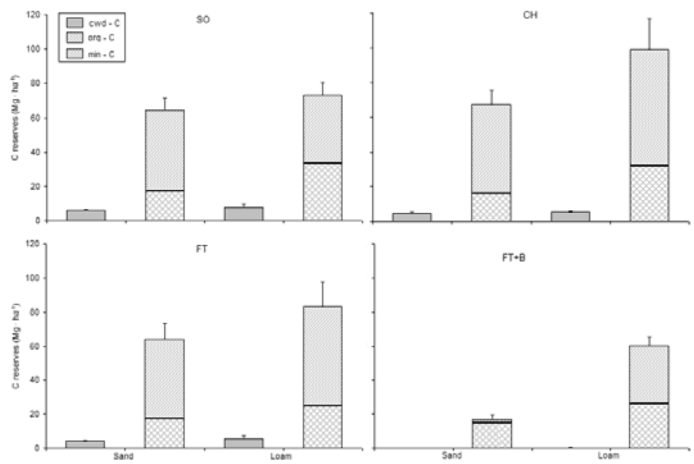

Figure 2. *Carbon content in CWD (CWD-C) and organic (ORG-C) and mineral (MIN-C) soil pools, by harvest treatment and soil type, 14 years after harvest. Vertical bars represent standard errors.*

Nitrogen concentration, content and pools

Overall, nitrogen concentration in CWD increased through time from 900 ppm to over 2400 ppm (nearly a threefold increase) regardless of removal treatment or soil type (Figure 3). Initial N concentrations in CWD were similar at year 0 for all treatments, with the exception of the FT+B, but were significantly higher (p<0.001) on the sandy sites (2091 ppm, ranging from 1814 (SO) to 2593 ppm (CH)) compared to CWD on the loam sites (850 ppm, ranging from 743 (FT+B) to 933 ppm (SO)) at year 4. Although the N concentration remained higher in year 14 on the sandy sites, (2728 *vs.* 2163 ppm) they were not significantly different from the loamy sites for any of the treatments, due to the high variability associated with the highly decomposed CWD (majority (65%) of CWD was at least decay class 4).

In terms of nitrogen content, the CWD on both soil types displayed immobilization for the first four years (sand: -12.7 kg ha^{-1} yr^{-1} ; loam: -2.4 kg ha^{-1} yr^{-1}), with subsequent release from years 4 to 14 (sand: 7.1 kg ha^{-1} yr^{-1} ; loam: 3.4 kg

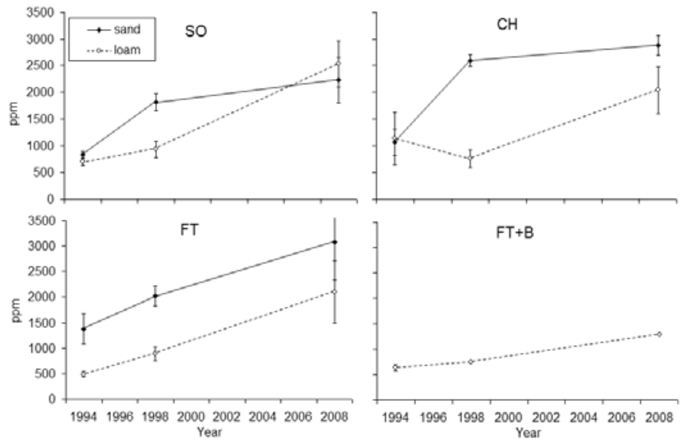

Figure 3. *Changes in nitrogen concentration in CWD by harvest treatment and soil type, for three sampling times, over a 14-year sampling period. Vertical bars represent the standard errors. Note: No samples were available for chemical analysis for the FT+B treatment on the sandy sites.*

ha^{-1} yr^{-1}) (Figure 4). Because plants take up inorganic N (NH_4 and NO_3), we also compared the CWD contribution [i.e. release of N (kg ha^{-1} yr^{-1})] to the plant-available N pools at year 14 (Figure 5). On sandy sites, annual CWD N release (7.6 kg ha^{-1} yr^{-1}) was comparable to the inorganic N pool, but both were significantly lower than the potentially available (mineralizable N) N pool. On the loamy sites, both the inorganic N and mineralizable N pools were significantly larger than the N released from CWD (3.6 kg ha^{-1} yr^{-1}).

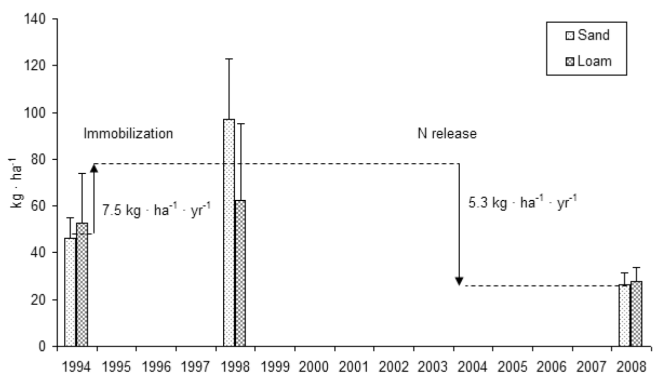

Figure 4. *Changes in N content in CWD, by soil type, over a 14-year period following harvest. Vertical bars represent the standard errors.*

Temporal patterns in foliar N

In terms of planted tree (*Picea mariana*—black spruce) response, Figure 6 illustrates the temporal pattern in foliar N concentration during the first 15 years following harvest. For both soil types, a significant peak in foliar N occurred at year 4, presumably resulting from a soil assart flush (i.e., increased soil mineralization following harvesting and rapid

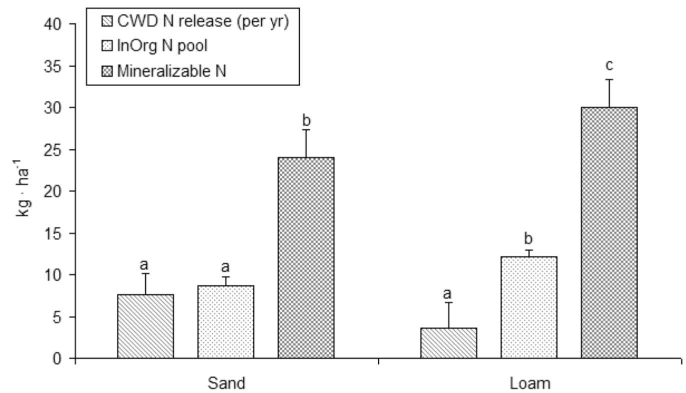

Figure 5. *Average annual CWD nitrogen release compared to plant-available N pools by soil type, 14 years after harvest. Vertical bars represent the standard errors. Lowercase letters denote significant (p<.05) differences between the N pool estimates based on the SNK post hoc test.*

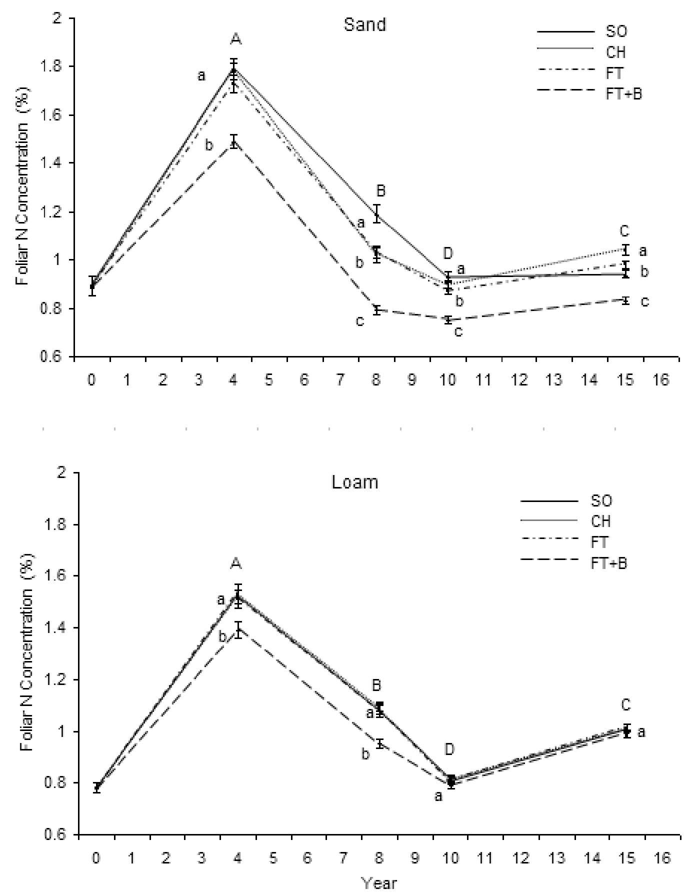

Figure 6. *Temporal patterns in planted black spruce foliar N (current foliage only) for the various harvest treatment and soil type combinations. Vertical bars represent the standard errors. Lowercase letters denote significant (p<.05) differences between treatments. Capital letters denote significant differences between sampling times.*

decompositiion of fine logging residues—foliage and twigs). At this point in time, the seedlings established on the FT+B treatments had significantly lower ($p<.0001$) foliar N concentration than the other 3 treatments on both soil types.

After this peak, foliar N decreased significantly ($p<.0001$) through to year 10, but began to rebound by year 15, particularly on the loam sites. This increase presumably was, in part, the result of the documented release of N from CWD from year 8 to 14 (Figure 4). On the sandy sites, foliar N on the FT+B treatment remained significantly lower ($p<.0001$) where little to no CWD had been retained.

Discussion

The exponential decay pattern of CWD among biomass removal treatments was similar to the patterns of CWD decay described by, for example, Harmon et al. (1986) and Tobin et al. (2007). When separated by soil type, however, the CWD on the sandy sites exhibited a distinct increase in decay rate after year 4, which more closely follows a three-stage decay function, described by Yatskov et al. (2003): 1) an initial slow phase, 2) a rapid phase, and 3) an extended period of moderately slow decay. This difference in decay rate pattern across soil types could be a reflection of moisture retention differences between the dry, freely draining sand versus the fresh loam soil types. CWD must achieve an adequate moisture content to promote microbial colonization (Harmon et al. 2000), and this may be delayed on the rapidly drained sandy soils compared to the moderately drained loamy soils.

Carbon pools in CWD have often been oversimplified in past assessments of carbon stores (Krankina et al. 2001), largely due to the significant variation of CWD inputs over forest succession. Many models simply apply a relative proportion to live biomass, but CWD does not parallel live biomass carbon storage patterns. The contribution of CWD in our study to total carbon reserves after 14 years (<8%) was comparable to other coniferous systems (Harmon et al. 1986), but relatively low compared with many other forest types (Shorohova and Shorohov 2001). Complete removal of all CWD, as in the FT+B treatment, may create a carbon deficit that could have a detrimental effect on long-term soil carbon stores and ecosystem energetics and therefore should be monitored over the longer term.

While patterns of CWD N retention, release and a combination of the two over time have been observed previously (Fahey 1983, Boulanger and Sirois 2006, Brais et al. 2006), studies showing these N patterns as related to substrate (i.e., soil type) are not available. We found N retention to be large on the nutrient-limited sandy site, consistent with Laiho and Prescott's (2004) hypothesis. However, after year 4, we found net N release from CWD at just slightly lower annual rates, meaning the initial N immobilization is countered by subsequent N release. Comparing the timing of this immobilization and release to the stages of stand development (Figure 7), the timing of N immobilization occurs at a period of low demand, while its release occurs during peak demand, as the stand nears crown closure. This pattern coincided with a rebound in planted black spruce foliar N concentrations between years 10 and 15.

Most studies, when comparing CWD to soil/aboveground N pools, use total N, and CWD contributions are 2% to 5% of this total (Sollins et al. 1980, Means et al. 1992, Laiho and Prescott 2004). Our study found similar percentages when CWD pools were compared to total N pools. However, when we compared them to the available N pools, the N release from CWD on the nutrient-poor, sandy sites was equivalent to the estimates of inorganic N pools (Figure 5). In contrast, the CWD contribution to the available N pool was negligible compared to the large inorganic N or mineralizable N soil pool on the loamy sites.

Management of CWD is becoming increasingly integral to biomass harvesting operations, especially in Scandinavia (Siitonen 2001, Lilja-Rothsten et al. 2008). North American researchers have been following suit with long-term research projects (i.e., LTSP collaborators, etc.) as interest in "unutilized" forest biomass left after harvesting grows in the search for renewable and sustainable energy alternatives to traditional fossil fuel consumption. CWD has already been recognized as an important component of site structure for biodiversity of flora and fauna (Lonsdale et al. 2008), but comparisons of biomass harvesting intensity and CWD nutrient/site productivity impacts are few. Many of these long-term studies are now approaching or are past the crown closure stage of stand development, and it is imperative that impacts to long-term site productivity are thoroughly examined. While CWD nitrogen pools are small com-

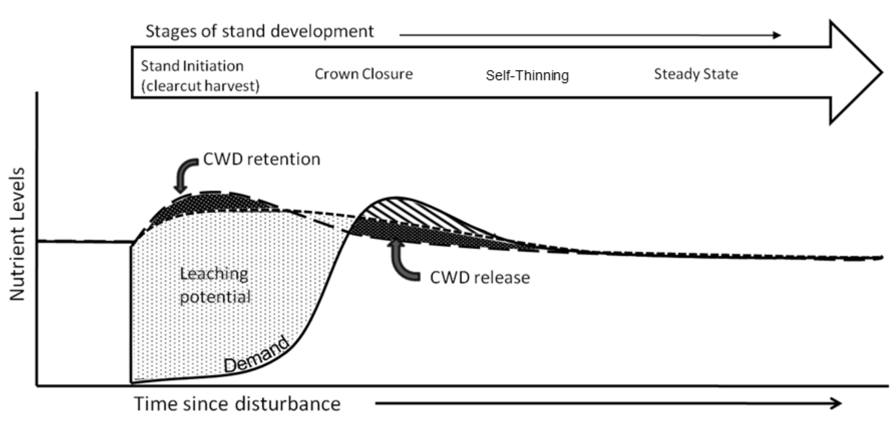

Figure 7. *Conceptual diagram illustrating the temporal pattern in nutrient demand (solid line), potential nutrient supply in the absence of CWD (long-dashed line) and the adjusted nutrient supply (short-dashed line) incorporating CWD retention and subsequent release during the stages of stand development.*

pared to underlying soils, there are two reasons why these small amounts may be important to plant nutrition: 1) The timing of retention and release of N in CWD coincides with stages of nutrient excess and deficit (respectively) and 2) N released from CWD is in plant-available form (Kuehne et al. 2008), which should have a positive impact on growth in N limited boreal ecosystems. CWD may also indirectly play an important role as a storage pool for base cations, as well as stabilized soil organic matter (Arthur and Fahey 1990).

The limited scope of this study in terms of study sites (i.e., 2 site replicates for each of the soil types) and CWD subplots (2) per replicated (3) treatment plot does need to be recognized, and is reflected in the large standard errors across treatments and sampling periods. These results, however, do suggest that on nutrient and/or moisture-limiting sites, the importance of CWD may be magnified and become a critical factor to maintaining long-term productivity. Research focusing on these less-productive sites may show more conclusively the unique role of CWD and better inform policy directives for biomass harvesting operations to ensure continued sustainability.

Conclusions

1. Soil type is a significant factor in determining the dynamics of CWD decay and nutrient release. The sandy sites, which are poorer quality than loamy sites, had a more pronounced response in terms of CWD decay rates and N dynamics. Forest management should include monitoring of CWD abundance based on soil type. Biomass removals beyond that of harvests for traditional wood products could have detrimental effects on soil C and N pools, particularly on nutrient-poor, sandy sites.

2. Studying active (available) pools of nutrients may provide a more accurate assessment of the role of CWD in nutrient retention and cycling compared to examining the total pools. In this study, N release from CWD was only 5% of total N stores, but up to 80% of available N during the critical growth phase prior to crown closure.

3. The contribution of CWD to site N reserves changes over time, particularly evident on sandy sites, with an initial immobilization of N followed by a period of release during phase 3 (extended period of moderately slow decay). This release appears to result, in part, in a rebound in tree foliar N concentrations by year 15.

4. In a managed forest scenario, nutrient retention by CWD occurs during a period of minimal demand and actually serves to minimize leaching potential from the site. Conversely, nutrient release by CWD release occurs as the stand approaches crown closure, which is a critical period of maximal demand.

Acknowledgments

This paper was originally presented during one of the technical sessions of the International Workshop “Sustainability Across the Supply Chain of Land-Based Biomass,” which was hosted jointly by IEA Bioenergy Task 43 Biomass Feedstocks for Energy Markets and the Long-Term Soil Productivity study (LTSP) in Kamloops, BC, Canada on 1-4 June 2010.

The authors would also like to thank the Natural Sciences and Engineering Research Council, Ontario Ministry of Natural Resources and Agriculture Research Institute for Ontario for their generous financial support of this study. The help from field assistants Neil Hilis and Christine Hague was also greatly appreciated.

Literature Cited

Arthur, M.A., and Fahey, T.J. 1990. Mass and nutrient content of decaying boles in an Engelmann spruce-subalpine fir forest, Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 20:730-737.

Boulanger, Y., and Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. *Canadian Journal of Forest Research* 36:1770-1780.

Brais, S., Pare, D., and Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. *Canadian Journal of Forest Research* 36:2331-2340.

Canada Soil Classification Working Group. 2006. The Canadian system of soil classification. Research Branch, Agriculture and Agri-Food Canada. Ed 3. NRC Research Press, Pub No. 1646.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (pinus contorta ssp. Latifolia) ecosystems, southern Wyoming. *Ecological Monographs* 53:51-72.

Graham, R.L., and Cromack Jr., K. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Canadian Journal of Forest Research* 12:511-521.

Hafner, S.D., Groffman, P.M., and Mitchell, M.J. 2005. Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. *Biogeochemistry* 74:257-282.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., and Cummins., K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:33-302.

Harmon, M.E., Krankina, O.N., and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research* 30:76-84.

Hart, S.C. 1999. Nitrogen transformations in fallen tree boles and mineral soil of an old-growth forest. *Ecology* 80:1385-1394.

Kalra, Y.P., and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. Forestry Canada, Northern Forestry Center, Edmonton, Alberta, Information Report NOR-X-319.

Krankina, O.N., Harmon, M.E., and Griazkin, A.V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Canadian Journal of Forest Research* 29:20-32.

Kuehne, C., Donath, C., Muller-Using, S.I., and Bartsch, N. 2008. Nutrient fluxes via leaching from coarse woody debris in a *Fagus sylvatica* forest in the Solling Mountains, Germany. *Canadian Journal of Forest Research* 38**:**2405-2413.

Laiho, R., and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research* 29:1592-1603.

Laiho, R., and Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research* 34:763-777.

Lang, G.E. 1984. Forest turnover and the dynamics of bole wood litter in subalpine balsam fir forest. *Canadian Journal of Forest Research* 15:262-268.

Lilja-Rothsten, S., de Chantal, M., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I., and Puttonen, P. 2008. Microsites before and after restoration in managed *Picea abies* stands in southern Finland: effects of fire and partial cutting with dead wood creation. *Silva Fennica* 42:165-176.

Lonsdale, D., Pautasso, M., and Holdenrieder, O. 2008. Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research* 127:1-22.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., and Martin, R.E. 1979. Dead and down woody material. pp. 79-95 in J.W. Thomas, ed. Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook. No. 553.

Means, J.E., MacMillan, P.C., and Cromack Jr., K. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon. *Canadian Journal of Forest Research* 22: 1536-1546.

Naesset, E. 1999. Relationship between relative wood density of *Picea abies* logs and simple classification systems of decayed coarse woody debris. *Scandinavian Journal of Forest Research* 14:454-461.

Powers, R.F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. *Soil Science Society of America Journal* 44:1314-1320.

Romell, L.G. 1957. Man-made ‘nature’ of northern lands. pp. 51-53 in Proceedings and papers of the sixth technical meeting of the International Union for Conservation of Nature and Natural Resources, Edinburgh, June 1956. Society for the Promotion of Nature Reserves, London.

Rowe, J.S. 1972. Forest regions of Canada. Department of the Environment, Canadian Forest Service, Pub. No. 1300.

Samuelsson, J., Gustafsson, L., and Ingelög, T. 1994. Dying and dead trees—a review of their importance for biodiversity. Uppsala: Swedish Threatened Species Unit, Swedish University of Agricultural Sciences. ISBN 91-88506-03-7.

Shorohova, E.V., and Shorohov, A.A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. *Ecological Bulletin* 49:129-135.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletin* 49:11-41.

Sollins, P., Grier, C.C., McCorison, F.M., Cromack Jr., K., and Fogel, R. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecological Monographs* 50:261-285.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research* 12:18-28.

Tenhagen, M.D., Jeglum, J.K., Ran, S., and Foster, N.W. 1996. Effects of a range of biomass removals on long-term productivity of jack pine ecosystems: establishment report. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre Information Report O-X-454.

Titus, B.D., Prescott, C.E., Maynard, D.G., Mitchell, A.K., Bradley, R.L., Feller, M.C., Beese, W.J., Seely, B.A., Benton, R.A., Senyk, J.P., Hawkins, B.J., and Koppenaal, R. 2006. Post-harvest nitrogen cycling in clearcut and alternative silvicultural systems in a montane forest in coastal British Columbia. *Forestry Chronicle* 82:844-859.

Tobin, B., Black, K., McGurdy, L., and Nieuwenhuis, M. 2007. Estimates of decay rates of components of coarse woody debris in thinned Sitka spruce forests. *Forestry* 80:455-469.

Yatskov, M., Harmon, M.E., and Krankina, O.N. A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research* 33:1211-1226.