Nutrient retention and leaching potential of coarse wood bolts collected from logged and burned upland boreal sites: a greenhouse misting experiment

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This 16-week, *ex situ* greenhouse misting trial was designed to isolate and compare the patterns of carbon and nutrient release from coarse woody debris (CWD). Comparisons included: hardwood (aspen) *versus* conifer (spruce); harvest- *versus* fire-origin; and among decay classes (DC1 to DC5). In terms of nutrient concentrations in the CWD bolts, with the exception of C and Mn, the aspen logs had significantly higher concentrations than the spruce logs and lower C:N ratios. The spruce logs did, however, contain six times higher levels of Mn as compared with those of aspen. In terms of origin, only Mn was altered (volatilized) as a result of being burned/charred, resulting in significantly lower concentrations levels. As decomposition progressed, there was a general increase in nutrient concentrations, and a reduction in C:N ratios. In all cases, the logs were a source of DOC for both species and decay class. In the case of decay class, DOC leachate was relatively low for the first three decay classes, peaked as a strong source for DC4, then a small, but significant reduction for the DC5 logs. The leachate pattern for N, however, differed in that both DC1 and DC2 logs had negative fluxes, indicating immobilization of N, but thereafter (DC3–5) the CWD leachate was an increasing source of N. For P, K, Ca, Mg, and Mn there was an overwhelming effect on the cumulative flux exerted by species, with significantly higher levels of P, K, Ca, and Mg from the aspen logs, but significantly lower levels of Mn. This pattern corresponds to the weighted concentrations in the logs, with aspen having three to four times higher concentrations of P, K, Ca, Mg, but six times lower levels of Mn. In light of initiatives calling for increased utilization of unmerchantable or low value wood within typical boreal harvesting systems, the current results suggest that careful consideration of the type and amount of CWD (species, decay class) that should be retained on site, as well as consideration for CWD "recruitment" (i.e., green tree retention) should be incorporated into biomass harvesting guidelines.

Introduction

In Canada, and elsewhere, the forest sector is undergoing a significant shift from primarily the production of traditional wood products (i.e., lumber, pulp and paper), to an ever-increasing broad array of bio-products, such as fuel for energy, specialty chemicals, and polymers (Puddister *et al*. 2011). In particular, the opportunity exists for forests to have a significant role in the development and use of bioenergy technologies (Janowiak and Webster 2010). In part, unmerchantable or low-value coarse wood, commonly by-passed during normal forest operations, is likely to be a targeted fibre source as this new bio-economy matures (Borjesson 2000, Rudolphi and Gustafsson 2005, Gan and Smith 2006, Perez-Verdin *et al*. 2009). These higher utilization levels, in turn, have the potential to further impact current and future coarse woody debris (CWD) loadings, which are already depleted in many managed forest systems (Spies *et al*. 1988, Harmon and Hua 1991).

CWD is known to be an important ecological component in forest ecosystems. Beyond its well-recognized value as habitat for forest-dwelling organisms (Berch *et al*. 2011), CWD has been shown to reduce soil erosion (Shakesby *et al*. 1996, Thomas *et al*. 2000), modify soil microclimate conditions (Castro *et al*. 2011, Marañón-Jiménez *et al*. 2013b), and contributes to carbon sequestration (Marañón-Jiménez and Castro 2012, Wiebe *et al*. 2014), nutrient cycling processes (Harmon *et al*. 1986, Krankina *et al*. 1999, Brais *et al*. 2006, Marañón-Jiménez *et al*. 2013a). The importance of CWD in nutrient cycling, however, is still debated in the literature, with some consensus that its nutrient contribution is minor as compared with that of other nutrient pools (Laiho and Prescott 2004). As compared with nutrient-rich leaves, small branches and roots that decompose quickly, CWD is thought to provide essential nutrition to the developing stand through slow and steady decomposition (Means *et al*. 1992, Alban and Pastor 1993). Following stand-replacing disturbance (e.g., wildfire, harvesting), this contribution can be important through to crown closure where stands become self-sufficient in terms of cycling nutrients (Brais *et al*. 2006, Wiebe *et al*. 2013, Marañón-Jiménez *et al*. 2013a).

Solutes leaching from CWD into the underlying soil may contribute to the plant-available nutrient pool in forest ecosystems, especially in plant-available forms of N and P (Marañón-Jiménez and Castro 2012). To date, however, few studies have focused on analyzing nutrients directly released from CWD (Harmon *et al*. 1986, Kuehne *et al*. 2008, Marañón-Jiménez *et al*. 2013a). Harmon *et al*. (1986) hypothesized that leaching would increase in importance as decay progressed, the result of microbial colonization and the subsequent breakdown of polymers into soluble substances. Results from *in situ* leachate studies have reported conflicting results. For example, Spears *et al*. (2003) found large differences between CWD *versus* soil (control) solutes in the middle decay classes. In contrast, Kuehne *et al*. (2008) found increasing solute nutrient concentrations as decay proceeded for most elements, however, some solute elements (i.e., P and K) remained constant throughout the decay process. In most cases, the complex mediation of nutrient cycling processes by a variety of biotic (e.g., wide range in nutrient concentrations in CWD in different tree species — Brais *et al*. 2006) and abiotic factors (e.g., soil microclimate conditions — Metzger *et al*. 2008, Castro *et al*. 2011) have made the patterns of nutrient release difficult to predict.

The current study (16-week, *ex situ* greenhouse misting trial) was designed specifically to eliminate/control the interacting effects of external biotic and abiotic factors influencing nutrient cycling processes to better isolate the patterns of nutrient release directly from CWD along the decomposition continuum (decay classes 1 to 5). In this way, the following questions could be explored: (1) What nutrients are more readily leached from CWD? (2) Does the relative magnitude of this nutrient release vary along the decomposition continuum? (3) Does the nutrient release differ significantly depending on tree species, i.e., conifer (*Picea mariana*) *versus* hardwood (*Populus tremuloides*) differ in nutrient? and (4) Does CWD originating from a harvest have a similar pattern of nutrient leaching compared with CWD originating from wildfire disturbances (i.e., charred wood)?

Material and methods

Sample collection

Stem (bole) samples of CWD (40 bolts), approximately 1 m long and 15 cm in diameter, were collected from harvested (1-yr-old harvest — 10 bolts; 15-yr-old harvest — 10 bolts) and wildfire-origin (1-yr-old burn — 10 bolts; 15-yr-old burn — 10 bolts) sites in northwestern Ontario, Canada (49°07´N, 89°41´W to 49°05´N, 88°W). The collection sites were situated in the boreal forest region on the eastern edge of Rowe's (1972) Upper English River forest section. The sites experience a cold, continental climate with a mean annual temperature of 2 °C, annual precipitation of 670 mm (60% during the growing season), 1310 Growing Degree-Days GDD), and 68 Frost-Free Days (FFD). Prior to disturbance, the stands ranged in age from 50 to 80 years, with two stands dominated by black spruce (*Picea mariana*) and two stands dominated by trembling aspen (*Populus tremuloides*).

At each of the four sites, five bolts of black spruce and five bolts of trembling aspen were collected. The intent during the collections was to collect the full range of decay conditions for each of the species and disturbance types using the standardized 1–5 decay class continuum, as described by 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. Care was taken to select harvest debris wood (i.e., evidence of cut) or tipped up charred stems (i.e., roots intact), thereby assuming these samples were sourced from the disturbance event.

Subsamples (cookies, 5 cm wide) were taken both pre- and post-experiment, and oven-dried at 50 °C until they reached a stabilized dry weight. Each wood cookie was separated into bark, sound and unsound components. To determine the ratio of the three components within each log, and to account for airspaces, the end of each log was scanned and the average area of each component was delineated using SigmaScan Pro 5 (Systat SSI Products, USA). Samples were then ground into 2 g 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). Additional nutrients (Ca, K, Mg, Mn, and P) were determined on 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).

Misting experiment

The remaining sections were suspended above separate containers and placed in the greenhouse in a completely randomized design (Fig. 1). In addition, eight blank containers were randomly placed in the design to account for any particulates from the water source, tubing, etc. Each CWD section was suspended with nylon line above separate containers to ensure that the CWD had no contact with any surface and was sufficiently aerated. It was necessary to hold the bolts in the later decay classes (4 and 5) together using tie wraps. A water-misting apparatus with flat-nozzle spray tips (TeeJet TP800067) was placed 20 cm above the logs. The spray coverage was contained to the length of each log, collecting water from the top, sides and bottom of the log. A zero-tension lysimeter was connected to each container to drain log leachate into 20 litre collection containers. The containers were emptied once per week, the volume recorded to ensure equal distribution, and a 200 ml sample taken for chemical analysis. Containers were not treated with anti-bacterial/fungal chemicals, but were rinsed out weekly. Each log was immersed in water for 48 hours prior to start-up, after which a misting schedule of four minutes every 12 hours (i.e., 500 ml per cycle) was set to keep logs moist but not saturated.

We compared the water inputs and collected leachate to the control (no log) amounts to ensure that logs were not absorbing excess water, as Sexton and Harmon (2009) found actual

Fig. 1. Photograph of the greenhouse experiment setup showing the suspended logs, overhead misting nozzles, and collection containers.

absorption by CWD accounted for only 3%–11% of throughfall inputs. In addition, a clear plastic covering was put over the entire setup and two temperature/relative humidity probes were placed at opposite ends to monitor heat/moisture distribution. Temperature was regulated and averaged (± SD) 23.3 (± 4) °C, but some large temperature fluctuations from 15 to 35 °C were recorded due to the placement in the greenhouse, sunlight intensity, and daily cycle of heating. The experiment lasted for 16 weeks, after which the logs were dried at 50 °C and samples were taken and analyzed in a similar manner as the pre-experiment samples, as described above, to determine changes in CWD mass and nutrient content.

Leachate samples were immediately filtered (P5 filter paper, pore size: 0.05 mm), decanted into 15 ml centrifuge tubes and frozen until analysis. Dissolved organic carbon (DOC) and total soluble nitrogen (TSN) were measured with the Technicon Instruments AutoAnalyzer II (Pulse Instrumentation Ltd., Saskatoon, SK) using Industrial Method Nos. 455-76W/A and G-086-93 A, respectively (N detection limit = 0.009 mg). Calcium, K, Mg, Mn, P, and S were analyzed with a Varian Vista Pro inductively coupled argon plasma spectrometer (ICAP/ICP) AES (Varian Inc.) for trace elements in water (> 5 ppm). Quality control samples were included every 10 samples to ensure accuracy.

Calculations and statistical approach

The amount (flux in mg) of carbon and nutrients collected from under the logs was calculated by multiplying the weekly collected volume times the solute concentration. The cumulative flux was simply the addition of the 16-week-long collection periods. To isolate the solute (concentration and flux) originating from the logs, the mean weekly blank water values (controls) were subtracted from the individual log solute values. In this case, negative values indicate uptake by the logs (sink); whereas positive values represent a net source.

The average solute concentration, adjusted for the blanks (control), and the cumulative flux were analyzed using a 3-factor Completely Randomized Design (CRD) ANOVA using SPSS 16.0 (SPSS Chicago). The three main factors in the general linear model were disturbance type (harvest *versus* wildfire origin), species (spruce *versus* aspen), and decay class (1–5). Unfortunately, at the time of collection, not all combinations were equally represented resulting in an unbalanced design. For example, although decay classes 1–2 and 4–5 were well-represented across the treatment combinations, decay class 3 tended to have fewer replicates than the other classes. To examine the temporal patterns in the release of nutrients over the 16-week experiment, repeated measures ANOVA was performed on the models described above for flux. The initial week was only a partial week (volumes averaged 2670 ml compared to 9270 ml for all subsequent weeks), so the repeated measures only included week2 to week16.

The *post-hoc* Student-Newman-Keuls (SNK) multiple range test (significant differences between levels determined as $p < 0.05$) was used

to examine the leaching patterns associated with the significant main effects.

Results and discussion

CWD characteristics: physical and chemical properties

A summary of both the physical and chemical attributes of the CWD logs, comparing the differences between species (aspen *versus* spruce), origin (fire *versus* harvest) and decay class (DC1 through DC5) is given in Table 1. Overall, spruce wood density (0.3673 g cm^{-3}) was significantly higher than that of aspen (0.2785 g cm^{-3}), but there was no difference between the fire-origin *versus* harvest-origin logs. As would be expected, wood density decreased significantly from decay class 1 to 5, with no significant declines between DC1 to DC3 (ranged between 0.3869 and 0.4041 g cm^{-3}), but as decomposition proceeded, density declined to 0.1631 g cm^{-3} by DC5. These values, and changes in wood density as decomposition advances are comparable to the values reported by Yatskov *et al.* (2003) for a range of hardwood and conifer species in boreal Russia. These density changes were also reflected in the percent contributions to overall log weights by individual wood components (i.e., sound, unsound, bark). Sound wood represented approximately 90% during the early stages of decay, but this shifted to nearly 90% in fragmented, unsound wood by DC5 and < 1% of bark remaining beyond DC3.

In terms of nutrient concentrations, with the exception of C and Mn, the aspen logs had significantly higher concentrations than the spruce logs and lower C:N ratios. The spruce logs did, however, contain six times higher levels of Mn as compared with those of aspen. In terms of origin, only Mn, which is largely concentrated in bark tissue (Table 1), was altered (volatilized) as a result of having been burned/charred, resulting in significantly lower concentrations levels (47.5 compared with 102.8 mg kg^{-1} for the harvest origin logs). As decomposition progressed, there was a general increase in nutrient concentrations, and a reduction in C:N ratios (DC1: 574.8; DC5: 164.2) suggesting the potential for initial

immobilization followed by mineralization and subsequent release of nutrients during the later stages of decay. Although not specific to decay class, Brais *et al.* (2006) also reported increasing in N and P concentrations in logs along an age-since-disturbance chronosequence. In their case, N and P concentration changes in aspen and birch fit exponential functions; whereas changes in pine and spruce were linear and more gradual. These shifts in nutrient concentrations are clearly illustrated by comparing the low concentrations and high C:N ratios associated with sound wood compared to as much as a six-fold increase in concentrations in unsound (partially decomposed) wood, and greatly reduced C:N ratios (Table 1).

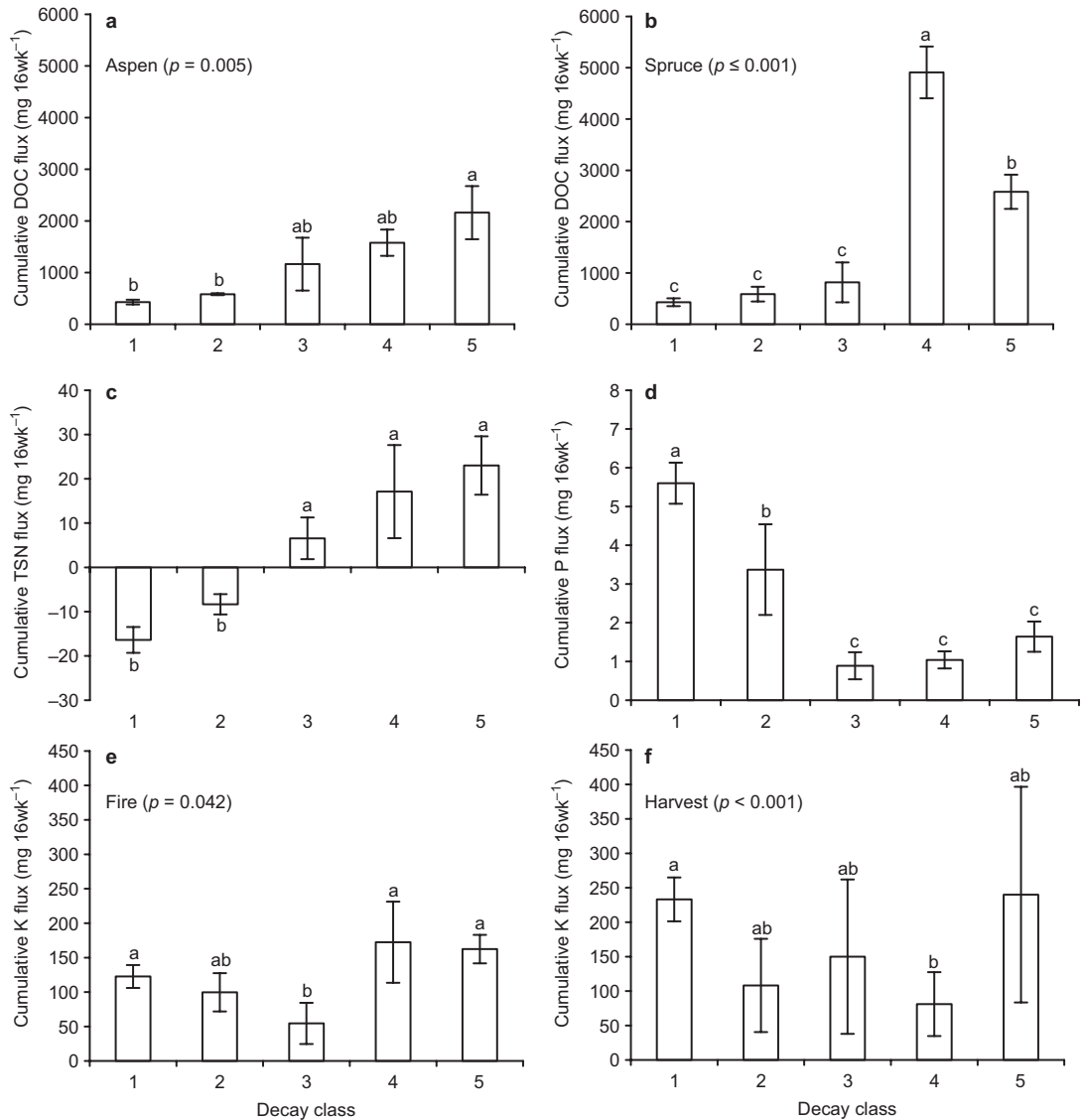### Nutrient leaching patterns from CWD

Carbon

After adjusting for the blank greenhouse water DOC flux, the DOC leaching directly from the CWD logs was largely driven by decay class (SNK: $F_{4,20} = 50.61$, $p < 0.001$) and species (SNK: $F_{1,20} = 7.24$, $p = 0.015$; Table 2). In all cases, the logs were a source of DOC for both species (aspen: 1007 mg 16wk^{-1}; spruce: 1414 mg 16wk^{-1}) and decay class. In the case of decay class, DOC leachate was relatively low for the first three decay class (429–956 mg 16wk^{-1}), peaked as a strong source for DC4 (3243 mg 16wk^{-1}), then a small, but significant reduction for the DC5 logs (2329 mg 16wk^{-1}). There was, however, a significant species × decay class interaction (*see* Fig. 2a and b). For the aspen logs, DOC leachate increased from DC1 (429 mg 16wk^{-1}) to DC5 (2160 mg 16wk^{-1}), corresponding to the more commonly reported exponential decay function (Harmon *et al.* 2000, Rock *et al.* 2008). DOC leachate trends for spruce, however, were similar to the polynomial carbon/mass loss curves reported for other *Picea* species (Shorohova and Shorohov 2001, Yatskov *et al.* 2003). For spruce, the DOC leachate pattern through the five decay classes mirrored the three-phase decay model (Yatskov *et al.* 2003, Zell *et al.* 2009) showing: (1) an initial slow phase (DC1–DC3: < 820 mg 16wk^{-1}), (2) a rapid

Table 1. Mean wood density and nutrient concentrations for CWD logs (with standard errors in parentheses), comparing log characteristics between species, origin, and decay class. Letters in superscript indicate significant differences at $p < 0.05$ (SNK multiple range test).

Log type	Density (g cm⁻³)	Wood components (%)			Weighted concentration*								C:N ratio
		Sound	Unsound	Bark	C (%)	N (%)	S (%)	P (mg kg⁻¹)	K (mg kg⁻¹)	Ca (mg kg⁻¹)	Mg (mg kg⁻¹)	Mn (mg kg⁻¹)	
Species													
Aspen	0.2785[b] (0.0262)	56.7 (8.59)	38.7 (9.40)	4.6 (0.92)	51.3[b] (0.220)	0.25[a] (0.043)	0.02[a] (0.004)	171.8[a] (28.16)	1252.2[a] (150.0)	3597.1[a] (550.7)	457.7[a] (60.61)	21.3[b] (5.47)	343.5[b] (45.6)
Spruce	0.3673[a] (0.0197)	72.7 (8.39)	23.3 (8.80)	4 (0.80)	52.2[a] (0.240)	0.09[b] (0.010)	0.01[b] (0.001)	49.6[b] (9.80)	325.4[b] (27.7)	1842.7[b] (199.2)	186.9[b] (28.2)	129[a] (17.1)	568.7[a] (35.3)
Origin													
Fire	0.3288 (0.0262)	64.7 (9.34)	30.9 (9.88)	4.4 (0.89)	51.9 (0.23)	0.16 (0.04)	0.02 (0.004)	112.5 (27.8)	829.1 (172.2)	2311.8 (397.9)	300.8 (50.4)	47.5[b] (9.80)	444.86 (51.4)
Harvest	0.317 (0.0244)	64.7 (7.98)	31.1 (8.63)	4.2 (0.83)	51.6 (0.27)	0.18 (0.03)	0.02 (0.003)	108.9 (22.6)	748.6 (126.7)	3128 (498.1)	343.8 (61.7)	102.8[a] (21.3)	448.7 (48.10)
Decay class													
1	0.3873[ab] (0.0074)	92.0[a] (0.187)	0[d] (0)	8.0[a] (0.187)	51.04[c] (0.134)	0.09[c] (0.002)	0.008[c] (0.001)	54.03[c] (4.59)	632.1[bc] (66.59)	1962.5[b] (74.53)	193.87[c] (16.28)	85.34 (25.63)	574.2[ab] (15.39)
2	0.4041[a] (0.0168)	92.1[a] (1.68)	2.0[d] (2.00)	5.9[a] (1.38)	51.48[bc] (0.152)	0.084[c] (0.011)	0.0085[c] (0.002)	45.78[c] (8.40)	470.2[c] (116.60)	1946.6[b] (180.95)	170.02[c] (17.99)	81.48 (31.08)	733.9[a] (167.33)
3	0.3497[b] (0.0623)	77.0[b] (12.08)	23.0[c] (12.04)	0.1[b] (0.10)	51.91[b] (0.512)	0.149[c] (0.054)	0.0141[c] (0.005)	110.29[bc] (56.04)	1182.9[a] (624.00)	2095.4[b] (727.95)	268.36[c] (85.79)	53.38 (21.60)	771.6[a] (326.65)
4	0.2195[c] (0.0261)	21.9[c] (6.88)	77.7[b] (6.95)	0.4[b] (0.17)	52.75[a] (0.501)	0.269[b] (0.082)	0.0258[b] (0.006)	155.01[b] (52.45)	858.1[ab] (248.45)	2694.9[b] (571.32)	437.63[b] (88.57)	70.52 (28.31)	382.8[bc] (109.68)
5	0.1599[d] (0.0152)	4.0[d] (2.62)	94.5[a] (2.40)	1.5[b] (0.59)	52.59[a] (0.524)	0.378[a] (0.073)	0.0363[a] (0.007)	276.78[a] (38.59)	1143.2[a] (311.39)	6065.1[a] (1320.99)	731.35[a] (110.78)	65.90 (20.53)	168.6[c] (33.53)
Component													
Sound					51.2 (0.16)	0.06 (0.003)	0.007 (0.001)	25.6 (4.70)	521.7 (81.7)	1108.4 (40.6)	165.9 (15.5)	61.1 (11.6)	917.8 (52.0)
Unsound					52.7 (0.38)	0.38 (0.06)	0.035 (0.002)	242.3 (39.8)	1240.11 (269.8)	4711.8 (821.3)	606.7 (78.6)	64.5 (15.9)	228.2 (52.3)
Bark					53.2 (0.28)	0.42 (0.02)	0.035 (0.002)	400.1 (20.4)	1680.2 (190.7)	12308.3 (584.6)	646 (37.8)	394.2 (108.9)	117.02 (4.23)

* The weighted concentration was based on the nutrient concentrations of the individual wood components (i.e. sound, unsound, bark, adjusted for the contribution (%) made of each component to total log weight.

Table 2. ANOVA results for average solute concentrations, adjusted for the blank water concentrations, and cumulative (16 week period) solute flux comparing the effects of species, origin, and decay class. *F* values set in boldface are considered significant.

Source	df	DOC		TSN		S		P		K		Ca		Mg		Mn	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Average solute concentration (mg l⁻¹)																	
Species (S)	1	**7.73**	0.010	**4.74**	0.043	**8.25**	0.010	**5.87**	0.026	**57.90**	<0.001	**32.33**	<0.001	**39.17**	<0.001	**84.06**	<0.001
Origin (O)	1	0.66	0.428	**6.33**	0.022	3.17	0.092	0.22	0.643	**7.05**	0.016	1.37	0.257	2.75	0.115	**36.96**	<0.001
Decay Class (D)	4	**46.40**	<0.001	**14.61**	<0.001	1.86	0.162	**11.51**	<0.001	**3.49**	0.028	**8.28**	0.001	**4.33**	0.013	2.01	0.136
S × O	1	1.16	0.296	1.57	0.226	0.83	0.374	1.36	0.260	**17.20**	0.001	0.02	0.885	1.15	0.298	**32.94**	<0.001
S × D	4	**15.59**	<0.001	0.09	0.983	0.35	0.838	1.85	0.164	1.63	0.211	**6.31**	0.002	1.81	0.171	2.09	0.124
O × D	4	1.44	0.262	2.79	0.058	0.37	0.828	1.45	0.260	**3.85**	0.020	**14.46**	<0.001	**4.21**	0.014	1.34	0.295
S × O × D	4	0.56	0.696	0.65	0.632	0.64	0.642	0.72	0.540	1.63	0.210	0.20	0.935	0.82	0.528	1.14	0.368
Error	20																
Cumulative flux (mg)																	
S	1	**7.24**	0.015	**4.60**	0.046	0.67	0.422	**4.58**	0.046	**46.00**	<0.001	**7.36**	0.014	**4.88**	0.040	**77.59**	<0.001
O	1	**5.48**	0.031	4.04	0.060	1.41	0.251	0.54	0.473	**10.68**	0.004	1.32	0.266	0.97	0.338	**35.32**	<0.001
D	4	**50.61**	<0.001	**15.96**	<0.001	0.47	0.756	**10.34**	0.001	**3.93**	0.018	1.31	0.304	0.50	0.738	2.06	0.129
S × O	1	4.17	0.056	0.89	0.357	0.13	0.726	0.97	0.339	**18.47**	0.001	0.63	0.438	0.13	0.723	**31.23**	<0.001
S × D	4	**15.54**	<0.001	0.17	0.951	1.27	0.319	1.16	0.363	0.90	0.487	2.42	0.086	1.36	0.286	2.09	0.125
O × D	4	1.58	0.222	**3.72**	0.022	0.98	0.441	1.05	0.410	**4.28**	0.013	**4.56**	0.010	0.98	0.441	1.45	0.258
S × O × D	4	0.19	0.943	1.48	0.249	1.75	0.183	0.54	0.710	1.95	0.145	1.58	0.223	1.86	0.162	1.26	0.321
Error	20																

Fig. 2. Changes in the cumulative leachate flux for carbon and nutrients along the decay class continuum. Vertical bars represent standard errors. Letters above or below the bars denote significant differences at $p < 0.05$ (SNK multiple range test).

phase (DC4: > 4900 mg 16wk⁻¹), followed by (3) a reduced, moderately slow phase (DC5: < 2600 mg 16wk⁻¹). As outlined by Laiho and Prescott (2004), a recently fallen log must first become adequately saturated with moisture to allow for microbial habitation and decay is very slow. The second stage is relatively short lived, as simple carbon compounds and cellulose are rapidly decomposed through microbial activity. The last stage involves complex compounds (mostly lignin) that decompose very slowly. Our

oldest, most highly decomposed logs were 15 years old, so it stands to reason that some were approaching the final, moderately slow stage of decomposition.

Nitrogen

Similar to carbon, both species (SNK: $F_{1,20}$ = 4.60, $p = 0.046$) and decay class (SNK: $F_{4,20}$ = 15.96, $p < 0.001$) had significant influen-
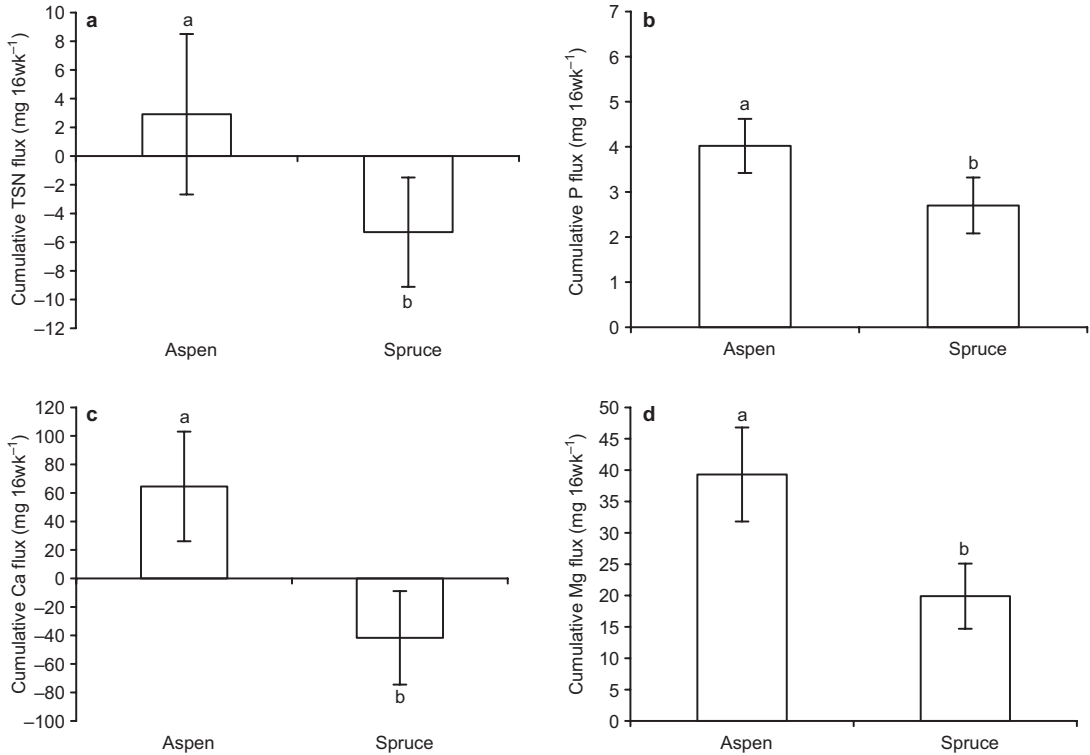
Fig. 3. Differences in the cumulative leachate flux of nutrients as influenced by species (aspen versus spruce). Vertical bars represent standard errors. Letters above or below the bars denote significant differences at $p < 0.05$ (SNK multiple range test).

ces on the cumulative flux of TSN (Table 2), however the patterns of TSN release from the logs were not the same as those illustrated for DOC. Opposite to DOC, the 16-week cumulative TSN flux was positive (a source) for aspen logs, but negative (a sink) for the spruce logs (Fig. 3a). This difference is likely due to a combination of higher N concentrations in the aspen logs (0.25%) as compared with that in spruce (0.09%), as well as the significantly lower C:N ratios (aspen: 343.5; spruce: 568.7) (Table 1).

In terms of the pattern in TSN flux associated with decay class, both DC1 (–16.4 mg 16wk^{-1}) and DC2 (–8.3 mg 16wk^{-1}) logs had negative fluxes (i.e., the collected solute levels were below the levels in the collected greenhouse water), indicating immobilization of N (Fig. 2c). For decay classes 3 through 5, however, CWD leachate was an increasing source of N (6.6, 17.1, 23.0 mg 16wk^{-1}, respectively) (Fig. 2c). Initial immobilization of N in early decay classes

has been well documented (Yavitt and Fahey 1985, Herrmann and Prescott 2008, Harmon *et al*. 1994, Moore *et al*. 2006) where C:N ratios are high (in our study, DC1: 574.8 and compared with DC5: 164.2; *see* Table 1), requiring decomposer microbes to access N from external sources to begin decomposition of cellular structures in the wood. This trend from sink to source is still debated, as Brais *et al*. (2006) found only white birch (*Betula papyrifera*) acted as a net sink for N, while trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) were all net sources of N, although the latter two were of little magnitude. Similar to our results, increases of N (and P) content in leachate were found in *Picea abies* between DC3 and DC5 (Butler *et al*. 2007) and in long-resident DWD (i.e., logs between 30 and 55 years following tree death) in *Pinus contorta* (Fahey 1983). Garrett *et al*. (2008) also found that nitrogen content of stumps and coarse roots

of *Pinus radiata* also increased substantially during decay. In our study, the weighted N concentrations (i.e., accounting for weight contributions by bark, sound, and unsound wood to total log weight) in the logs increased from DC1 (0.09%) through to DC5 (0.40%), with marked differences between sound (0.06%) and partly decomposed, unsound wood (0.38%) (Table 1). In contrast, Krankina *et al*. (1999) reported N losses from CWD of three boreal tree species in Russia, but do indicate that differences in methodology (e.g., accounting for bark loss), species, and environmental conditions as possible explanations for the reported differences.

Log origin was also a significant factor for average TSN concentrations (SNK: $F_{1,20}$ = 6.33, p = 0.022), with significantly lower concentrations in the fire-origin logs (0.007 mg l^{-1}) as compared with those in the harvest-origin logs (0.060 mg l^{-1}). Volatilization of N from the bark and/or outer stemwood layer during the wildfire event was likely the cause for these differences. Higher leaching volumes from the charred, fire-origin logs, however, negated the origin effect in the 16-week cumulative flux, and although not significant, resulted in a higher, positive (source: 2.4 mg 16wk^{-1}) flux of TSN in the fire-origin logs as compared with a negative (sink: –5.3 mg 16wk^{-1}) flux in the harvested logs. Higher N leaching from fire-origin logs could be due to decomposition of subcortical tissues *(*i.e., phloem) and higher insect activity, as was suggested by Boulanger and Sirois (2006) to explain their similar observation of an initial pulse of N from CWD following wildfire.

Phosphorus and sulphur

Similar to N, both species (SNK: $F_{1,20}$ = 4.58, p = 0.046) and decay class (SNK: $F_{4,20}$ = 10.34, p = 0.001) significantly influenced the cumulative P flux (Table 2). The P flux associated with the aspen logs (4.02 mg 16wk^{-1}) was nearly double that generated by the spruce logs (2.70 mg 16wk^{-1}) (Fig. 3b), which corresponds to the significantly higher (four times) weighted concentrations in the aspen logs (Table 1). The pattern of P release across the decay classes did differ from that of C and N, in that the first decay

class was the largest source of P (5.6 mg 16wk^{-1}), with a rapid decline by DC2 (3.37 mg 16wk^{-1}), then low values for DC3–5, although there appeared to be a small, albeit non-significant, rebound in DC5 (1.64 mg) (Fig. 2d). This slight increase in P solute in the latter stages of decay, most likely originated from the decomposing, unsound wood in the log, which had much higher P concentrations (242 mg kg^{-1}) then sound wood (26 mg kg^{-1}), and represented a significantly higher proportion of the log total weight (88.4%) by DC5 (Table 1). Harmon *et al*. (1986) found that older, more decayed logs accounted for the majority of P storage in *Pseudotsuga* dominated conifer stands, and they suggested that the increase of P in the decomposing wood could be from microbial activity or previous activity of the soil interface with the log.

Corresponding to the low S concentrations in the log components (0.007–0.04 mg kg^{-1}), the cumulative S fluxes were extremely low with no significant differences detected between species (SNK: $F_{1,20}$ = 0.67, p = 0.422), origin (SNK: $F_{1,20}$ = 1.41, p = 0.251), or decay class (SNK: $F_{4,20}$ = 0.47, p = 0.756). Although the adjusted concentrations in the leachate were significantly different between the two species (aspen: 0.04 mg l^{-1}; spruce: 0.06 mg l^{-1} , SNK: $F_{1,20}$ = 8.25, p = 0.010), these differences were negated by the lower volumes generated by the spruce logs.

Cations

For the cations, there was an overwhelming effect on the cumulative flux exerted by species, with significantly higher levels of K (SNK: $F_{1,20}$ = 46.00, p < 0.001), Ca (SNK: $F_{1,20}$ = 7.36, p = 0.014), and Mg (SNK: $F_{1,20}$ = 4.88, p = 0.040) from the aspen logs, but significantly lower levels of Mn (SNK: $F_{1,20}$ = 77.59, p < 0.001). This pattern corresponds to the weighted concentrations in the logs, with aspen having three to four times higher concentrations of K, Ca, Mg, but six times lower levels of Mn (Table 1). In the case of K, both origin (SNK: $F_{1,20}$ = 10.68, p = 0.004) and decay class (SNK: $F_{4,20}$ = 3.93, p = 0.018) also influenced the K flux from the logs, but the patterns were influenced by other factors. For example, since overall K concentrations
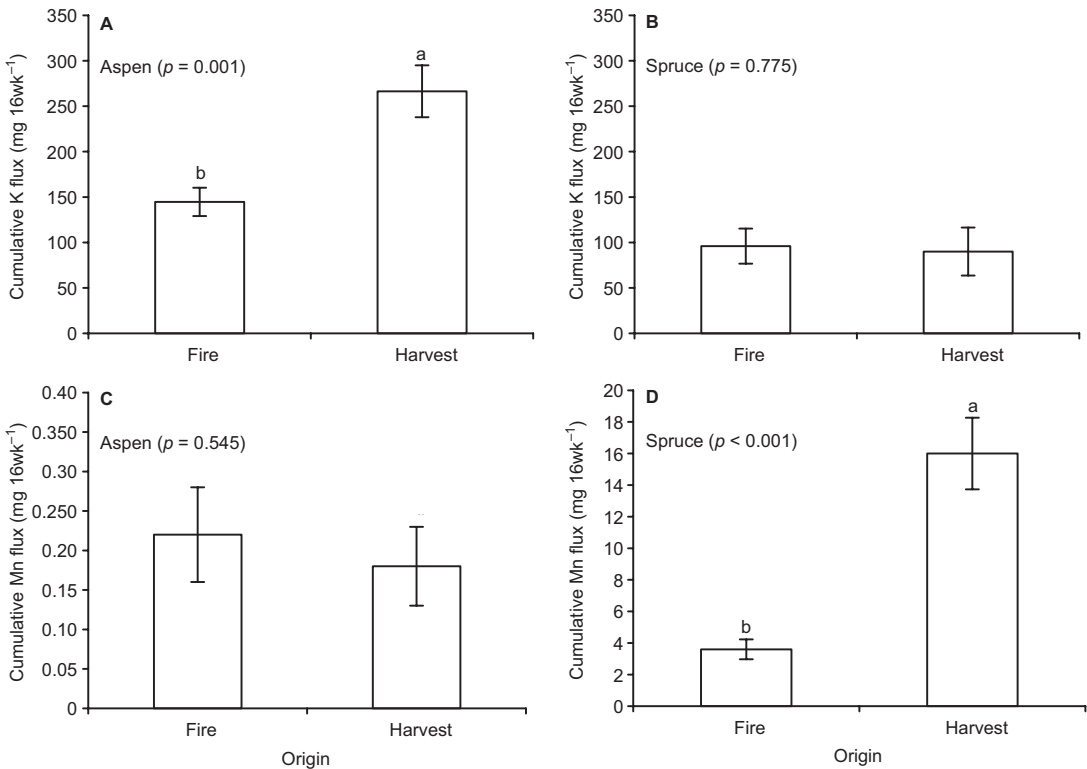
Fig. 4. Differences in the cumulative leachate flux of nutrients as influenced by origin (fire *versus* harvest). Vertical bars represent standard errors. Letters above the bars denote significant differences at $p < 0.05$ (SNK multiple range test).

were low in the spruce logs, fire had no effect (SNK: $F_{1,9} = 0.09$, $p = 0.775$) on the cumulative K flux (Fig. 4b); whereas in aspen, high volatilization during the wildfire resulted in relatively low levels of K leaching (Fig. 4a), albeit still higher than from the spruce logs. The fire event also reduced the K flux from the DC1 logs (fire: 123 mg 16wk^{-1}; harvest: 233 mg 16wk^{-1}), but the overall pattern was for an initial pulse of mobile K, followed by low flux levels, with high levels again in the final stages of decay (Fig. 2e and f).

Both Ca and Mg appear to be both recalcitrant (i.e., no decay class effect, SNK: $F_{4,20} = 1.31$, $p = 0.304$ and SNK: $F_{4,20} = 0.50$, $p = 0.738$, respectively) and resistant to volatilization during fire events, with only clear species differences in terms of cumulative flux (Fig. 3c and d, respectively). The extremely high levels of Ca in aspen bark (Table 1: 12 308 mg kg^{-1}) largely contributed to a strong positive Ca flux; whereas the overall spruce flux was negative (Fig. 3c).

Mg tends to be more evenly distributed between wood components (Table 1), resulting in positive fluxes for both aspen and spruce; however, the Mg flux associated with aspen was still two times greater than the spruce flux (Fig. 3d).

Similar to K, Mn was significantly influenced by both species and origin (both $p < 0.001$). The Mn flux from the aspen logs was nearly negligible (0.20 mg 16wk^{-1}) as compared with that from the spruce logs (10 mg 16wk^{-1}), corresponding to the substantial difference in Mn concentration in the logs (aspen: 21 mg kg^{-1}; spruce: 129 mg kg^{-1}, Table 1). As with K, the wildfire significantly reduced Mn concentrations in the logs (fire: 48 mg kg^{-1}; harvest: 103 mg kg^{-1}), resulting in a 4 fold decrease in the Mn flux. The significant species × origin interaction (SNK: $F_{1,20} = 31.23$, $p < 0.001$) was largely a function of little Mn in any of the aspen logs (Table 1). In their case, the wildfire event did not affect the Mn flux (SNK: $F_{1,9} = 0.40$, $p = 0.545$), with both

Table 3. Repeated measures ANOVA results for the cumulative flux to evaluate the effect of species, origin, and decay class on the temporal patterns (week 2 to week 16) of nutrient release from CWD. F values set in boldface are considered significant.

Source	df	DOC		TSN		S		P		K		Ca		Mg		Mn	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Week (W)	14	**17.20**	<0.001	**14.98**	<0.001	**5.04**	<0.001	**20.23**	<0.001	**15.15**	<0.001	**5.89**	<0.001	**6.05**	<0.001	**7.90**	<0.001
W × Species (S)	14	**8.27**	<0.001	**2.23**	0.007	0.46	0.952	1.28	0.220	0.36	0.985	0.53	0.916	0.61	0.852	**7.12**	<0.001
W × Origin (O)	14	0.41	0.971	**3.23**	0.001	0.40	0.974	0.88	0.579	0.55	0.890	0.39	0.978	0.35	0.986	**3.29**	<0.001
W × Decay Class (D)	56	**3.93**	<0.001	**4.68**	<0.001	0.54	0.997	**8.60**	0.007	**1.62**	0.007	0.53	0.997	0.55	0.996	**1.52**	0.017
W × S × O	14	1.84	0.034	**4.90**	<0.001	0.29	0.994	1.00	0.455	1.66	0.065	0.42	0.969	0.37	0.983	**3.22**	<0.001
W × S × D	56	**4.09**	<0.001	**3.21**	<0.001	0.52	0.998	0.54	0.997	1.15	0.236	0.53	0.997	0.49	0.999	**1.49**	0.022
W × O × D	56	1.74	0.002	**4.10**	<0.001	0.55	0.996	0.66	0.967	0.97	0.539	0.55	0.996	0.63	0.980	1.28	0.102
W × S × O × D	56	**2.43**	<0.001	**4.83**	<0.001	0.56	0.995	1.00	0.939	**1.41**	0.041	0.63	0.980	0.72	0.926	1.25	0.126
Error	252																

having low flux values (0.22–0.18 mg 16wk^{-1}) (Fig. 4c), but the fire did significantly reduce the Mn flux in the burned spruce logs (Fig. 4d).

Temporal patterns in leachate flux

Based on the repeated measures ANOVA results (Table 3), sampling week was a highly-significant factor (SNK: $F_{14,252} = 5.89$–20.23, $p < 0.001$) for all nutrients included in this study; however, notable differences in the temporal patterns in nutrient fluxes did occur (Figs. 5 and 6). Although there were a number of significant higher-order interactions identified in the analysis, these were largely the result of slightly different ordering of the 16 individual weeks when comparing between species, origin, and decay class, but were not strongly affecting the overall temporal trends, with the exception of P (Fig. 5c) and Mn (Fig. 6d).

For the DOC flux (Fig. 5a), after a brief peak at week 3 (117 mg wk^{-1}) there was declining outputs up to week 7, followed by stable, positive fluxes for the remainder of the experiment (60–80 mg wk^{-1}). In contrast, TSN release from the logs (Fig. 5b) had a strong initial positive flux (peaking at nearly 1.5 mg wk^{-1} in week 3 and 4); however, became negative (i.e., immobilized from the greenhouse water misted over the logs) for weeks 7–16 resulting in an overall net immobilization in the cumulative TSN flux (–1.4 mg 16wk^{-1}). As illustrated in Fig. 2d, the bulk of the P flux came from the fresh DC1 logs, but the initially high levels of P leachate dropped rapidly and converged with the other DC classes from week 7 onwards, being only slightly above baseline (i.e., greenhouse water P levels without being misted over CWD logs) (Fig. 5c). Although the flux associated with the DC2 logs was approximately half of that from the DC1 logs, the pattern and convergence was the same. The P flux from the DC3–5 logs was constant across all sampling weeks and only marginally above baseline levels. This rapid loss of P following tree mortality may help explain the variable patterns of P in the literature, which report CWD as both a P sink and source (Moore *et al.* 2006). As most of the P in fresh logs was accounted for in the bark (> 15 times higher in
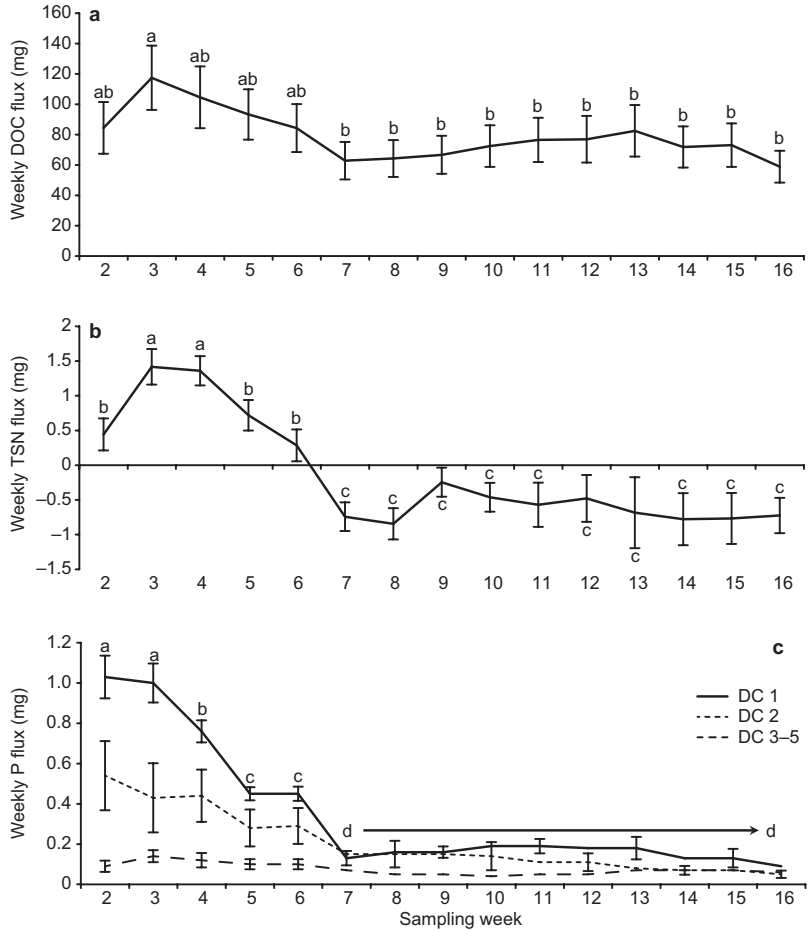
Fig. 5. Temporal patterns in leachate flux for (**a**) DOC, (**b**) TSN and (**c**) P. Letters above or below the error bars denote significant differences at $p < 0.05$ (SNK multiple range test).

bark than sound wood, Table 1), this "pulse" loss of P in fresh logs is likely driven by bark tissue decomposition (Krankina *et al*. 1999) and can be easily missed if bark is not included or if there is a delay in CWD nutrient assessments following tree mortality.

Different temporal patterns also emerged for the cations (Fig. 6). For K, there was a relatively large and extended initial period of K leaching (> 14 mg wk^{-1}), then a decline to low levels for weeks 7–9, but rebounded to a moderate high and steady flux of approximately 10 mg wk^{-1} for weeks 10–16 (Fig. 6a). After a brief (week 2 only) pulse in Ca release, the weekly fluxes rapidly became negative, then stabilized at nearly zero levels for weeks 10–16 (Fig. 6b). A similar pattern was observed in the Mg flux, although its release remained positive at approximately 1–2 mg wk^{-1} from week 3 to 16 (Fig. 6c). The tem-

poral pattern for Mn (Fig. 6c) was strongly influenced by origin (fire *versus* harvest) with no difference across all sampling weeks for the burned logs with levels barely above baseline (0.4–0.2 mg wk^{-1}), as might be expected based on the low Mn concentrations in burned logs (Table 1), and the low cumulative flux (Fig. 4c and d). In contrast, the harvest-origin logs had an initial pulse of Mn release (2.2 mg wk^{-1}), but then experienced an extended gradual decline towards to the end of the experiment (< 0.3 mg wk^{-1}).

Management implications

The results of this study support the hypothesis that CWD can play an important role in nutrient retention and cycling following disturbance. For example, the logs were a source of DOC for both
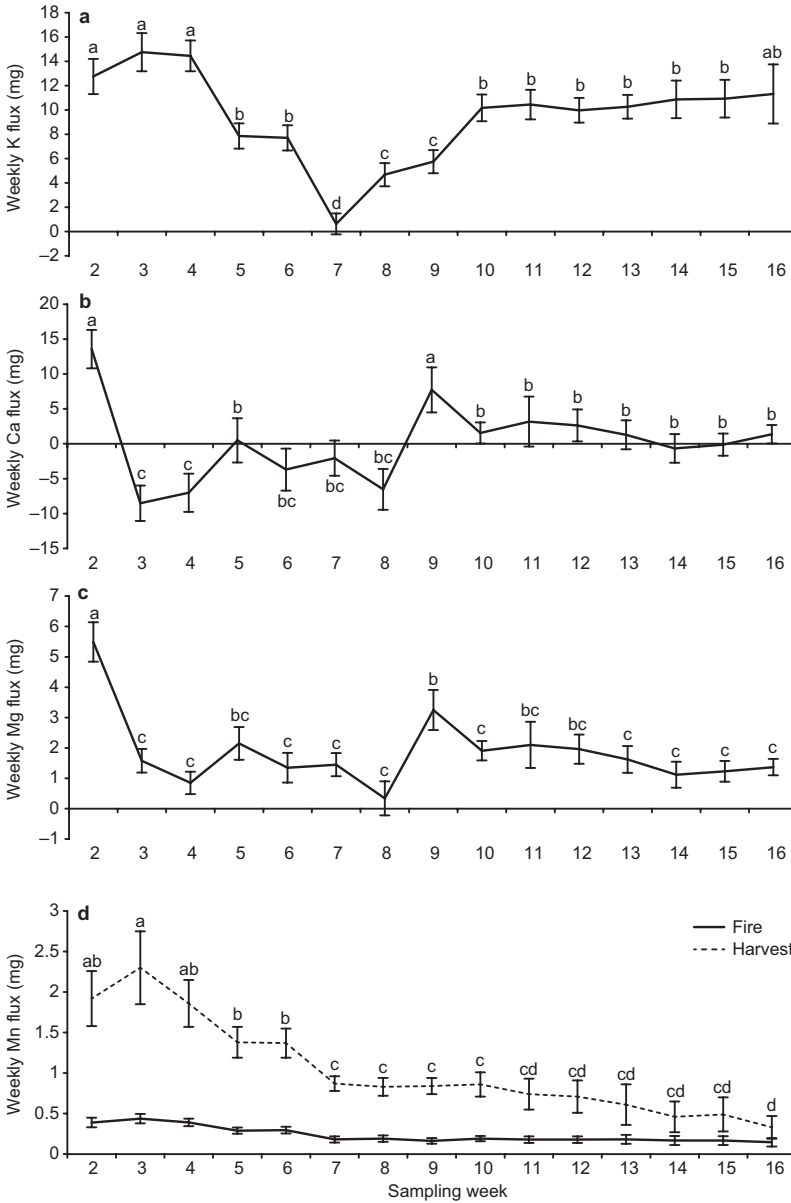
Fig. 6. Temporal patterns in leachate flux for (**a**) K, (**b**) Ca, (**c**) Mg and (**d**) Mn. Letters above or below the error bars denote significant differences at $p < 0.05$ (SNK multiple range test).

species and all decay classes with increasing DOC flux as decomposition proceeded (Fig. 2a and b). In addition, P and cation fluxes were strongly influenced by species with elevated levels of P, K, Ca, and Mg from aspen logs, but significantly lower levels of Mn (Fig. 3). In contrast, harvest-origin log leachate levels were similar, or sometimes higher (K and Mn), than that from logs originating from wildfire (Fig. 4). It does need to be recognized that at the site-level, CWD biomass is considerably higher

after wildfire (e.g., > 40 Mg ha^{-1}: Castro *et al*. 2010) versus clearcut harvest (e.g., < 20 Mg ha^{-1}: Morris *et al*. 2014), so its demonstrated positive influence on soil fertility and nutrient availability following wildfire (Marañón-Jiménez and Castro 2012) would not be expected to be as pronounced after clearcut harvesting operations (Wiebe *et al*. 2014).

Although this study was an *ex situ*, greenhouse misting trial, the results are relevant to boreal forest management, and, in particular, the

development of forest biomass harvesting guidelines. Intensification of biomass removal (i.e., harvesting of unmerchantable and/or undesirable species) would result in removal levels beyond harvesting systems that only target traditional wood products (i.e., pulp and paper). For example, boreal full-tree harvesting, where the entire aboveground portion of the tree is removed and processed at roadside, retains 8–10 T ha^{-1} of CWD (e.g., broken tops, undersized or damaged trees), approximately half the amount retained in stem-only removals (Morris *et al*. 2014). However, in a recent biomass harvesting trial, that removed a combination of traditional sawlog material and chipped biomass from undersized material, post-harvest surveys reported < 5 T ha^{-1} of CWD (Kwiaton *et al*. 2014). In response to this growing demand for forest biomass for energy and other alternative uses (Puddister *et al*. 2011), many jurisdictions have, or are developing mandatory or voluntary guidelines for biomass harvesting, aimed at conserving biodiversity and maintaining site productivity (Stupak *et al*. 2008, Berch *et al*. 2011). In terms of CWD management, these guidelines have largely focused on CWD retention levels (Minnesota Forest Resource Council 2007) and/or piece size (Densmore 2010). Results from our current study would suggest that careful consideration also be given to both the type (i.e., species, decay class), as well as the amount of CWD that should be retained on site. An additional consideration aimed at future CWD recruitment, would be through green-tree retention guidelines that provide for a mix in species (e.g., hardwoods and conifers), which have different nutrient signatures, leaching patterns, and decay rates.

Conclusions

Misting CWD in the absence of soil media exhibited similar source/sink trends from *in-situ* studies, indicating that (1) microbial and fungal processes occur on CWD without soil, (2) that these processes act quickly after tree death, and (3) beyond its physical presence and resulting modification to soil microclimate conditions (i.e., soil temperature and moisture profiles),

CWD plays an active role in nutrient cycling in forested systems. Of particular relevance, the *ex-situ*, soil-less environment of this study made it possible to identify clear source/sink dynamics of carbon and nutrients of two commonly occurring boreal species as decay progressed.

In all cases, the logs were a source of DOC for both species and decay classes, with increasing DOC flux from DC1 to DC5 for aspen logs (exponential response), and increasing DOC flux from DC1 to DC4 but declining by DC5 for spruce logs (polynomial response). The TSN leachate flux was positive (net release) for aspen logs, but negative (immobilization) in spruce. In terms of decay class, the logs were sinks for N in DC1 and DC2, but an increasing source in the later decay classes. The P flux was nearly double in aspen logs as compared with that in spruce logs, with the majority of P release coming from the DC1 logs during the first few weeks of the experiment. For the cations, there was an overwhelming species effect on the leachate flux, with elevated levels of K, Ca, and Mg from aspen logs, but significantly lower levels of Mn. For the most part, harvested log leachate levels were similar to those of fire origin, with the exception of K and Mn, suggesting considerable volatilization of these two nutrients during wildfire events.

In light of initiatives calling for increased utilization of unmerchantable or low value wood within typical boreal harvesting systems, careful consideration of the type and amount of CWD (species, decay class) that should be retained on site, as well as consideration for CWD "recruitment" (i.e., green tree retention) should be incorporated into biomass harvesting guidelines.

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