

A reanalysis of nutrient dynamics in coniferous coarse woody debris

Scott M. Holub, Julie D.H. Spears, and Kate Lajtha

Abstract: We analyzed net N, P, K, Ca, and Mg fluxes from decaying coarse woody debris (CWD) by developing a “volume-adjusted method” and applying it to existing chronosequence studies of CWD in temperate coniferous forests. Unadjusted nutrient concentrations may overestimate the amount of a given nutrient remaining or accumulating in CWD, because mass loss, primarily as microbially respired CO₂, occurs during decomposition. This overall mass loss tends to increase nutrient concentrations (e.g., µg N/g CWD) by decreasing the denominator and, therefore, can be misleading as an indicator of nutrient flux. Our volume-adjusted method corrects for mass loss, by assuming a constant volume as CWD decays. Using this method we determined that (i) Ca and K were lost from CWD as decay progressed; (ii) N and P increased or had no net change in amount; and (iii) Mg results were mixed. Several studies showed net gains of Mg and several showed net losses. We discuss the applicability and limitations of the volume adjusted method and propose the use of isotopic and conservative tracers as more accurate, but more difficult, methods of investigating CWD nutrient fluxes. We also discuss possible nutrient flux pathways into and out of CWD.

Résumé : Nous avons analysé les flux nets de N, P, K, Ca et Mg dans les débris ligneux grossiers (DLG) en développant une méthode qui pondère sur la base du volume et en l’appliquant à des études existantes de chronoséquences de DLG dans des forêts tempérées de conifères. La concentration non ajustée de nutriments peut surestimer la quantité d’un nutriment donné qui reste ou s’accumulent dans les DLG, en raison de la perte de masse via la respiration microbienne, principalement sous forme de CO₂, qui survient pendant la décomposition. Cette perte de masse globale tend à faire augmenter la concentration des nutriments (e.g., µg N/g DLG) en diminuant le dénominateur et peut par conséquent être trompeuse comme indicateur de flux des nutriments. Notre méthode qui pondère sur la base du volume corrige pour la perte de masse en assumant un volume constant à mesure que les DLG se décomposent. À l’aide de cette méthode, nous avons déterminé que : (i) Ca et K sont perdus à mesure que la décomposition des DLG progresse; (ii) la quantité nette de N et P augmente ou ne change pas et (iii) les résultats sont mixtes dans le cas de Mg. Plusieurs études rapportent un gain net et plusieurs autres une perte nette de Mg. Nous discutons de l’applicabilité et des limites de la méthode qui pondère sur la base du volume et nous proposons l’utilisation de traceurs isotopiques persistants, une méthode plus précise quoique plus laborieuse, pour étudier le flux de nutriments dans les DLG. Nous discutons également du cheminement des flux de nutriments dans et hors des DLG.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD) is a conspicuous and multifunctional component of many forest ecosystems (Harmon et al. 1986). The removal of trees during timber harvest removes the primary source of CWD and could potentially reduce the nutrient capital of a given site, eventually leading to a decline in site productivity. Many studies have observed the changes in nutrient concentrations through a chronosequence of coniferous CWD decay (Hungate 1940; Grier 1978; Lambert et al. 1980; Graham and Cromack 1982; Yavitt and Fahey 1982; Sollins et al. 1987; Arthur and Fahey 1990; Means et al. 1992; Busse 1994; Krankina et al. 1999; Laiho and Prescott 1999). These studies have frequently found increases in the unadjusted

concentrations of N, P, Ca, and Mg as the age of the CWD increases. However, unadjusted nutrient concentrations may overestimate the actual amount of a given nutrient remaining or accumulating in CWD, because mass loss occurs during decomposition, primarily as microbially respired CO₂ but also through organic matter leaching (Harmon et al. 1994). This overall mass loss tends to increase nutrient concentrations (e.g., µg N/g CWD) by decreasing the denominator and can therefore be misleading as an indicator of nutrient gain or loss.

Since nutrient concentrations alone are not an accurate measure of nutrient dynamics, other methods must be used to correct for the lost mass. Several authors have addressed this problem by expressing concentrations as mass of nutrient per volume of CWD (Grier 1978; Lambert et al. 1980; Graham and Cromack 1982; Sollins et al. 1987; Means et al. 1992) or other methods (Krankina et al. 1999; Harmon et al. 1999, 2000). Our main objectives were (i) to develop and explore standard methods for examining nutrient dynamics in decomposing CWD while correcting for mass loss during decomposition and (ii) to reanalyze previous CWD chronosequence studies to synthesize existing data on the nutrient dynamics in CWD as it decays.

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S.M. Holub,¹ J.D.H. Spears, and K. Lajtha. Department of Botany and Plant Pathology, Oregon State University, Cordley Hall 2082, Corvallis, OR 97331-2902, U.S.A.

¹Corresponding author (e-mail: holubs@bcc.orst.edu).

Table 1. Description of studies examined.

Source*	Species	No. of boles	Location
(1) Arthur and Fahey 1989	Engelmann spruce (<i>Picea engelmannii</i> Parry) – subalpine fir (<i>Abies lasiocarpa</i> (Hook.) Nutt.)	52 [†]	Rocky Mountains (Colorado)
(2) Busse 1994	Lodgepole pine (<i>Pinus contorta</i> var. <i>murayana</i> (Grev. & Balf))	30	Central Oregon
(3) Graham and Cromack 1982	Sitka spruce (<i>Picea sitchensis</i> (Bong.) Carrière)	35	Olympic National Park (Washington)
(4) Grier 1978	Western hemlock (<i>Tsuga heterophylla</i> (Raf.) Sarg.)	29	Cascade Head (coastal Oregon)
(5) Lambert et al. 1980	Balsam fir (<i>Abies balsamea</i> (L.) Mill.)	38	Mount Moosilauke (New Hampshire)
(6) Means et al. 1992	Douglas-fir (<i>Pseudotsuga menziessi</i> (Mirb.) Franco)	183	Cascade Range (Oregon)
(7) Sollins et al. 1987	Douglas-fir	70	Cascade Range (Oregon and Washington)
	Western hemlock	49 [‡]	18
	Western red cedar (<i>Thuja plicata</i> Donn)	7	7

*Values in parentheses are used in the figure keys.

[†]Species pooled together.

[‡]Includes 17 class 5 logs of unknown species that we assumed to be primarily Douglas-fir.

Methods

We selected seven studies of coniferous CWD decomposition chronosequences in temperate forests (Table 1). All of these studies included N, P, K, Ca, and Mg analyses along with CWD bulk densities at each stage of decay. We used decay classes 1 through 5 (Triska and Cromack 1980), as a surrogate for CWD age because age was not well known in most studies. Decay class 1 represents freshly fallen, undecomposed CWD. In decay class 2, bark and heartwood are intact, but sapwood is beginning to decay. Decay class 3 is defined by loosening of the bark and further decay in the sapwood with heartwood still intact. In decay class 4, all bark is sloughed off, sapwood is severely decayed, and heartwood is no longer structurally sound. Decay class 5 CWD is highly decomposed throughout and may appear as a mound in the forest floor.

In studies that did not present their data using explicit decay classes (i.e., Grier 1978; Lambert et al. 1980), we derived estimates of decay class using the given bulk densities, CWD ages, and (or) decomposition descriptions. Grier (1978) presented data in terms of CWD age and density so we converted this data to decay class using age estimates and density values from western hemlock in Sollins et al. (1987). Lambert et al. (1980) did not explicitly state decay classes, but the decomposition descriptions they gave fit easily into the decay class definitions of Triska and Cromack (1980). Some studies did not include data for all decay classes, especially class 5, but were included in the analyses.

Volume adjusted concentration

The volume adjusted concentration method converts unadjusted mass-based nutrient concentrations (mass of nutrient per mass of CWD at the current decay class) to nutrient concentrations per mass of decay class 1 CWD, correcting for the effects of mass loss due to decomposition:

$$[1] \quad CVA_{\text{class}n} = C_{\text{class}n} \times \frac{B_{\text{class}n}}{B_{\text{class}1}}$$

where $CVA_{\text{class}n}$ is the volume-adjusted nutrient concentration (in μg nutrient/g CWD_{class1}), $C_{\text{class}n}$ is the unadjusted nutrient concentration of the CWD (in μg nutrient/g CWD_{classn}), $B_{\text{class}n}$ is the class n bulk density (in $\text{g CWD}_{\text{class}n}/\text{cm}^3$ CWD_{classn}), $B_{\text{class}1}$ is class 1 bulk density (in $\text{g CWD}_{\text{class}1}/\text{cm}^3$ CWD_{class1}), n is decay class 1

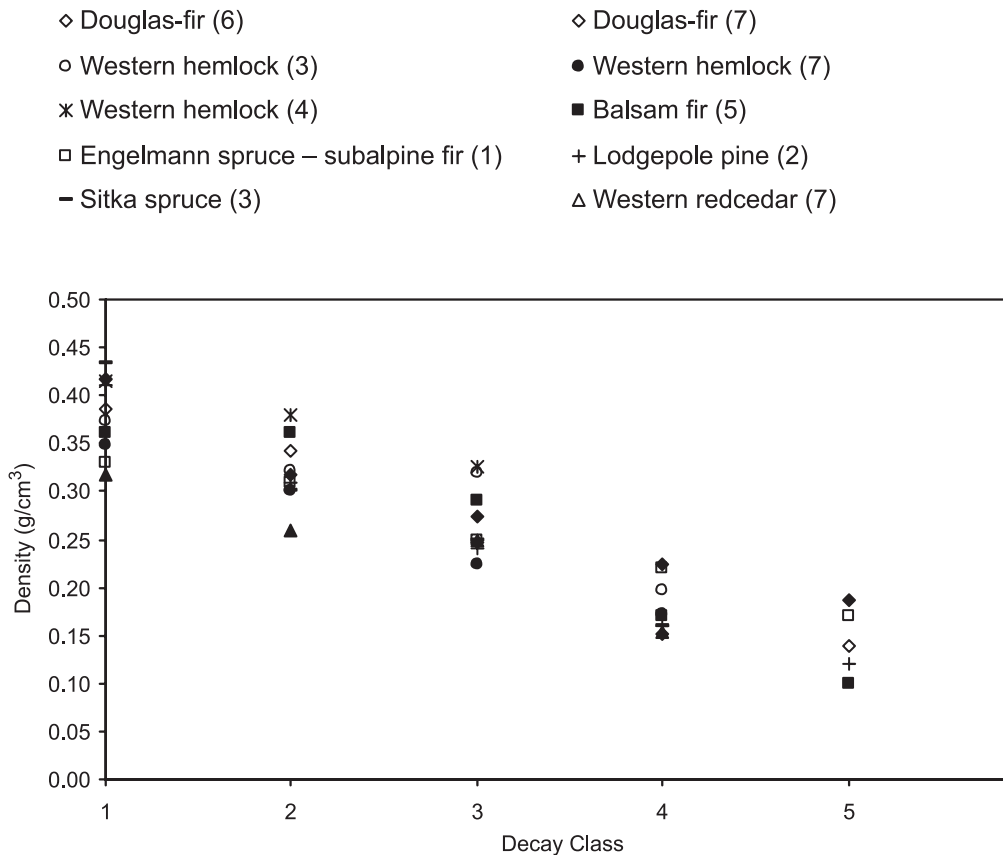
through decay class 5. This method requires only knowledge of the unadjusted nutrient concentration, the current CWD bulk density, and the bulk density of freshly fallen CWD. Results from the volume adjusted concentration method are similar to the volume-based concentrations (mass of nutrient per volume of CWD) used by a number of authors (e.g., Grier 1978; Sollins et al. 1987), except that the volume-adjusted concentration method facilitates direct comparison with unadjusted mass-based concentrations because results from the volume-adjusted concentration method are expressed as micrograms nutrient per gram of class 1 CWD. A similar method has been used in geochemical studies of saprolite weathering, where the saprolite maintains a semiconstant volume, and element dynamics are examined based on that volume (e.g., Gresens 1967).

Two assumptions are necessary for this method: (i) the volume of a given section of wood in CWD does not change as the CWD decays (i.e., components of the wood structure remain sufficiently intact through the decomposition process to support the original wood shape), and (ii) the bulk density of current decay class 1 CWD is equal to the bulk density of each piece of CWD at the time it fell.

Statistics

Because of the subjectivity related to assigning CWD to decay classes, we investigated the relationship between decay class and CWD bulk density using a one-way ANOVA followed by Tukey's HSD multiple-comparison test (SYSTAT version 7.0). For the nutrient concentrations, we chose to present the entire range of the data and look for apparent trends between decay classes, species, nutrients, and locations. We omitted error bars from the figures, because overlapping caused them to be confusing. The coefficient of variation in the studies we examined was usually 10–20% although often lower and occasionally higher. (See the original papers for precise error values.) We did not present species averages, because the total number of studies for any individual species was usually only one. For those species with replicate studies, results often varied widely among sites leading to a large potential for bias towards the locations of the studies that we examined. Similarly, an overall average has the problem of low sample size and bias towards the locations and species of the studies we examined. Averages could also be misleading. For example, the CWD in some studies had large systematic increases in Mg, while others had systematic de-

Fig. 1. Log bulk density (g/cm^3) versus decay class. Each pairwise comparison by decay class was significantly different ($p < 0.01$) except decay class 4 versus decay class 5 ($p = 0.42$). Reference numbers from Table 1 are given in the key in parentheses.



creases in Mg averaging to no change, although Mg may differ by site or species. Since this study was limited to CWD in non-randomly selected temperate coniferous forests primarily in western North America, extrapolation of our results outside of this scope of inference should be made with extreme caution.

Results

We found a significant difference between the bulk densities of the decay classes (one-way ANOVA, $p < 0.001$, $df = 39$). Furthermore, multiple comparison testing showed a significant decrease in bulk density as decay class increased for each pairwise comparison ($p < 0.01$, Tukey's HSD) except decay class 4 versus decay class 5 ($p = 0.42$, Tukey's HSD) (Fig. 1).

The unadjusted mass-based nutrient concentrations (mass of nutrient per mass of CWD) generally increase or do not change through the decay classes for Ca, N, P, and Mg (Figs. 2A, 3A, 4A, and 6A). This suggests that CWD mass loss is greater than or equal to the loss of these nutrients or that the nutrients are being imported into CWD. Conversely, unadjusted concentrations of K decrease rapidly (Fig. 5A), indicating that K is lost at a greater rate than bulk CWD mass.

In contrast, the volume-adjusted concentration method showed losses of many nutrients. Ca (Fig. 2B) and K (Fig. 5B) both showed clear trends of net nutrient loss for most species through class 4. CWD lost 5–75% of Ca and 40–85% of K. These losses were maintained in class 5 for

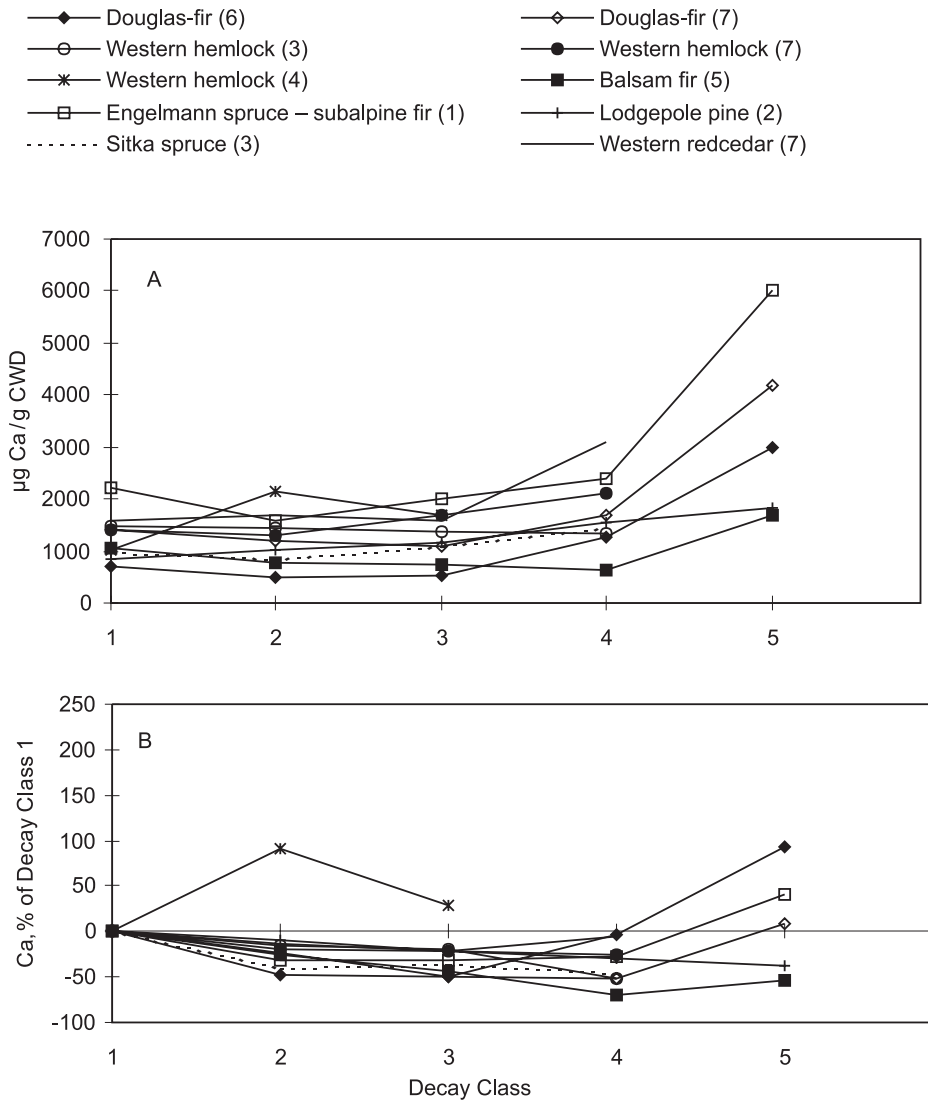
K, while CWD often had moderate net gains of 5–75% for Ca or at least no further loss in class 5 logs. The western hemlock studied by Grier (1978) was an outlier with a relatively large increase in Ca.

Most CWD had no change in the amount of N (Fig. 3B) through class 3, where N generally began to increase with a range of –5 to 50% change in class 4 and 20–150% increase in class 5. CWD had a similar pattern for P (Fig. 4B) as that of N, except that CWD had moderate losses of 0–50% through class 3, followed by general increases with a range of –25 to 50% in class 4 and 5–150% in class 5. CWD had diverging trends for Mg (Fig. 6B), with some studies showing gains and others showing losses. Both Douglas-fir studies and one western hemlock study had net gains of Mg from 150 to 200%, while the other western hemlock and the remaining species had losses of 25–50%. Similar to Ca, the Mg data from Grier (1978) were a high outlier.

Discussion

Potential inputs of the nutrients in CWD include precipitation or throughfall inputs (Harmon et al. 1986), dry deposition, litter fall, root ingrowth, fungal translocation (Frey et al. 2000), animal inputs, and asymbiotic N_2 fixation (Silvester et al. 1982; Sollins et al. 1987). Soil could also become mixed with CWD during class 4 and 5. Nutrient loss pathways could include leaching (Yavitt and Fahey 1985), animal transfer out (Edmonds and Eglitis 1989), fungal translocation (Harmon et al. 1994), nutrient volatilization

Fig. 2. (A) Unadjusted calcium concentration ($\mu\text{g Ca/g CWD}$) versus decay class. (B) Volume-adjusted calcium concentration as a percent of decay class 1 logs versus decay class (calculated using eq. 1). Reference numbers from Table 1 are given in the key in parentheses.



(e.g., ammonia loss or denitrification), plant uptake, and CWD fragmentation. Although several studies have examined these potential source and loss pathways individually, the importance of each flux remains unclear, especially since they could vary between species and sites. Nutrients present in CWD were primarily derived from within a given site, so CWD should not be considered a true “source” of nutrients, because the nutrients in CWD are themselves the product of past nutrient additions to a given site.

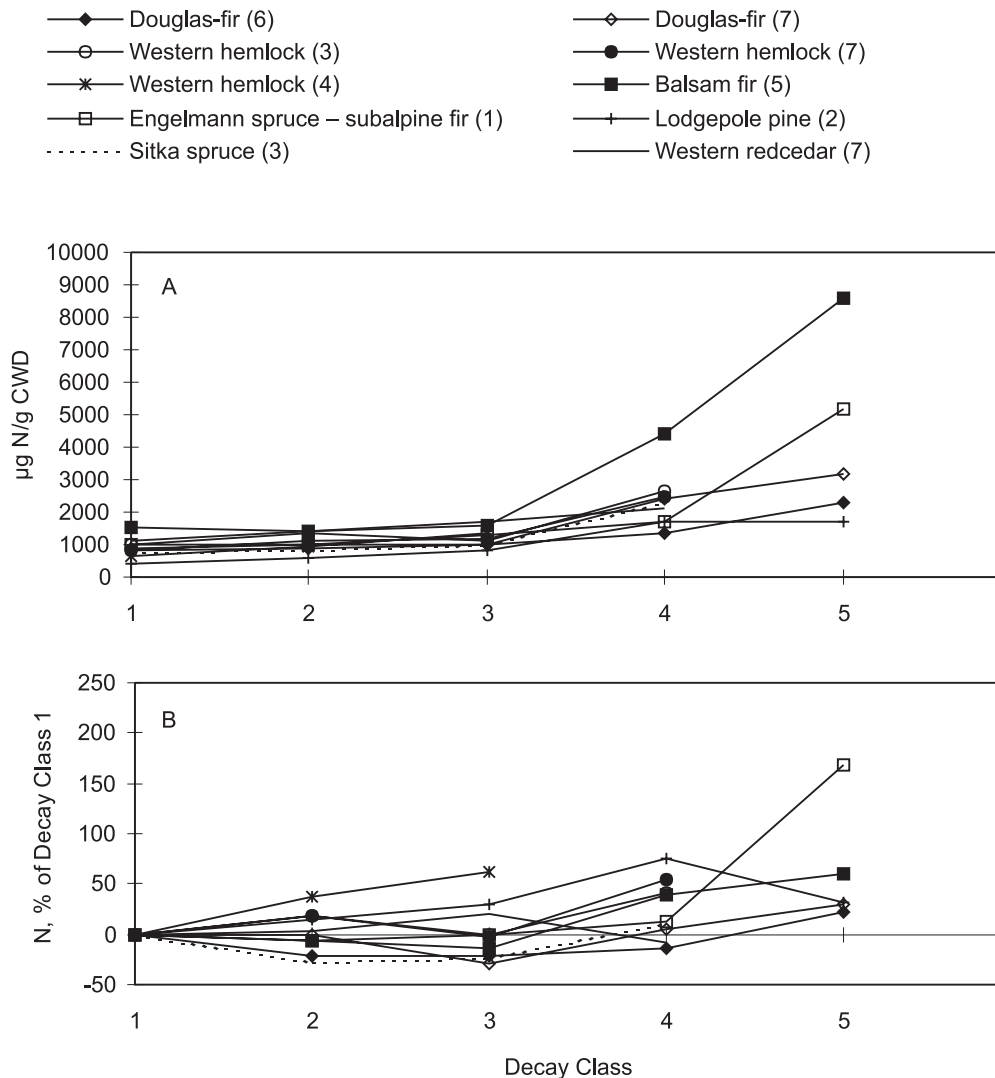
The losses observed for Ca (Fig. 1) could be due to leaching of the labile Ca substances from within the vascular components of the wood, while structural Ca is retained. Most studies appear to lose Ca between class 1 and 2 and maintain the same amount through class 4. The increase in Ca and most other nutrients at class 5 was likely due to a violation of the constant volume assumption at late stages of decay.

Nitrogen (Fig. 2) had mixed results from class 1 to class 3 but in almost all cases increased from class 3 to class 5. Nitrogen is known to be limiting to plant growth in most temperate forest ecosystems (Date 1973), and in some situations

it may limit microbial growth as well (Hart and Stark 1997). To degrade the C in a log, microbes must obtain N to manufacture decomposition enzymes. Therefore, fungi and bacteria that retain, import, or manufacture new N in CWD would have an advantage in terms of the ability to obtain energy from the C in CWD. Fungi have been shown in an agricultural setting to import N into straw at rates of about $40 \mu\text{g N}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ (Frey et al. 2000). Asymbiotic N_2 -fixers have also been observed to reduce acetylene, a surrogate for N_2 , in the range of $0\text{--}230 \text{ nmol C}_2\text{H}_2\cdot(\text{g CWD})^{-1}\cdot\text{day}^{-1}$ in decaying logs (Harmon et al. 1986). Using a ratio of about four acetylene reduced to one N_2 (Liengen 1999), the amount of N fixed could be up to $3 \mu\text{g N}\cdot(\text{g CWD})^{-1}\cdot\text{day}^{-1}$. While N_2 fixation in CWD is about 13 times smaller than the N translocated by fungi into straw, the N added by N_2 -fixation contributes a “new” source of N to the ecosystem instead of merely transporting existing N from one pool to another.

Phosphorus (Fig. 3), also an important plant and microbial nutrient, has a similar pattern to N, only with a slightly higher initial losses. Because P is usually not the limiting

Fig. 3. (A) Unadjusted nitrogen concentration ($\mu\text{g N/g CWD}$) versus decay class. (B) Volume-adjusted nitrogen concentration as a percent of decay class 1 logs (calculated using eq. 1) versus decay class. Reference numbers from Table 1 are given in the key in parentheses.



nutrient in temperate terrestrial ecosystems, microbes may not absorb all available P, which facilitates P leaching from the CWD initially. Perhaps increased microbial demand for P in later decay classes contributed to the observed increase in P.

Potassium (Fig. 4) is a highly mobile cation and, as expected, was lost rapidly from logs in all studies. This trend is apparent even before any mass related corrections are applied (Fig. 4A), which indicates that K is lost at faster rates than microbially respired CO_2 mass losses.

Some studies found systematic increases in Mg, while others found systematic decreases (Fig. 6B). The studies that increased in Mg over decay class included all of the Douglas-fir, two of three western hemlocks and the only western redcedar. These species are also among the lowest in initial Mg concentration (Fig. 6A), indicating that perhaps microbes in these logs are importing Mg to meet a nutrient requirement and that microbes in the other species have a reduced need for Mg resulting in Mg leaching. This is in contrast to the similarly charged Ca where the CWD in most studies maintained losses, indicating that Ca may be in

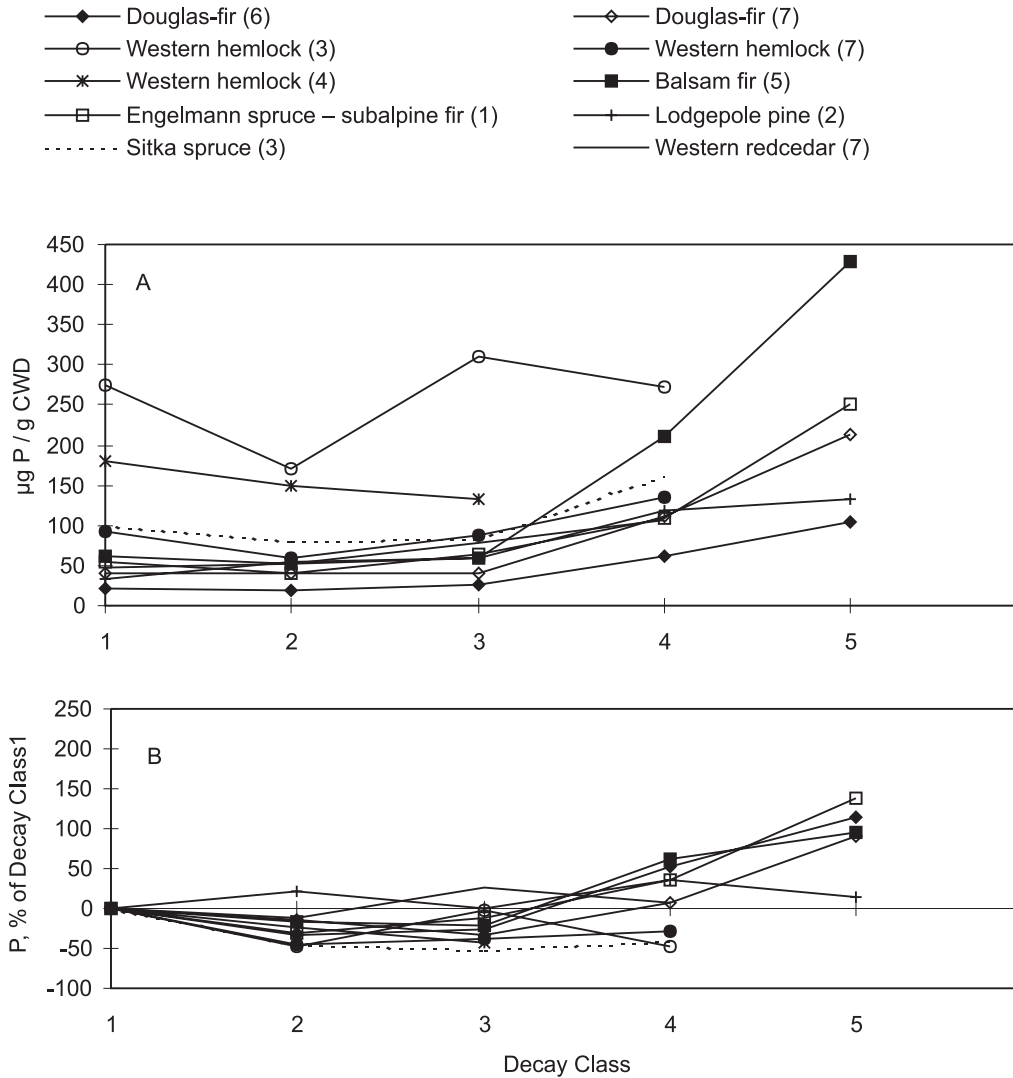
lower microbial demand. Other unidentified differences between species or sites may be responsible as well.

Outliers

Balsam fir (Lambert et al. 1980) showed large losses of Ca and Mg outside of the range of the rest of the species. In their discussion, Lambert et al. (1980) proposed that the balsam fir logs were small and in a wet, high-N environment, which could increase decomposition and thus increase base cation leaching. The N and P concentration increases are muted, however, when the volume-adjusted correction is applied, indicating that balsam fir boles reach lower densities at the later decay classes than other species (Fig. 1). This lower density signifies greater decomposition and further supports the hypothesis that the high base cation leaching is related to more advanced decomposition (Lambert et al. 1980).

The western hemlock studied by Grier (1978) showed the highest increase in volume-adjusted Ca (Fig. 2B), N (Fig. 3B), and Mg (Fig. 6B) concentrations. Because of its location near the Pacific Ocean, Grier (1978) suggested sea

Fig. 4. (A) Unadjusted phosphorus concentration ($\mu\text{g P/g CWD}$) versus decay class. (B) Volume-adjusted phosphorus concentration as a percent of decay class 1 logs (calculated using eq. 1) versus decay class. Reference numbers from Table 1 are given in the key in parentheses.



spray as the cause of unusually high Na concentrations in CWD at his site. Sea spray alone, however, cannot explain the increase in Ca, N, and Mg, since these elements are found at 10–100 times smaller concentrations than Na in seawater (Faure 1998). The data extracted from Grier was not in the standard decay class format, which could lead to a certain degree of error in our calculations, but this does not explain the relatively large increases in Ca and Mg when all other studies showed decreases. The underlying reason for the discrepancy is unclear, barring site liming or N fertilization.

The unadjusted P concentration in western hemlock from Graham and Cromack (1982) is much higher than the P concentrations for other hemlocks and the rest of the species. In the same study, Sitka spruce P concentrations were consistent with the rest of the studies that we examined. It is unclear why this discrepancy exists.

Method assessment

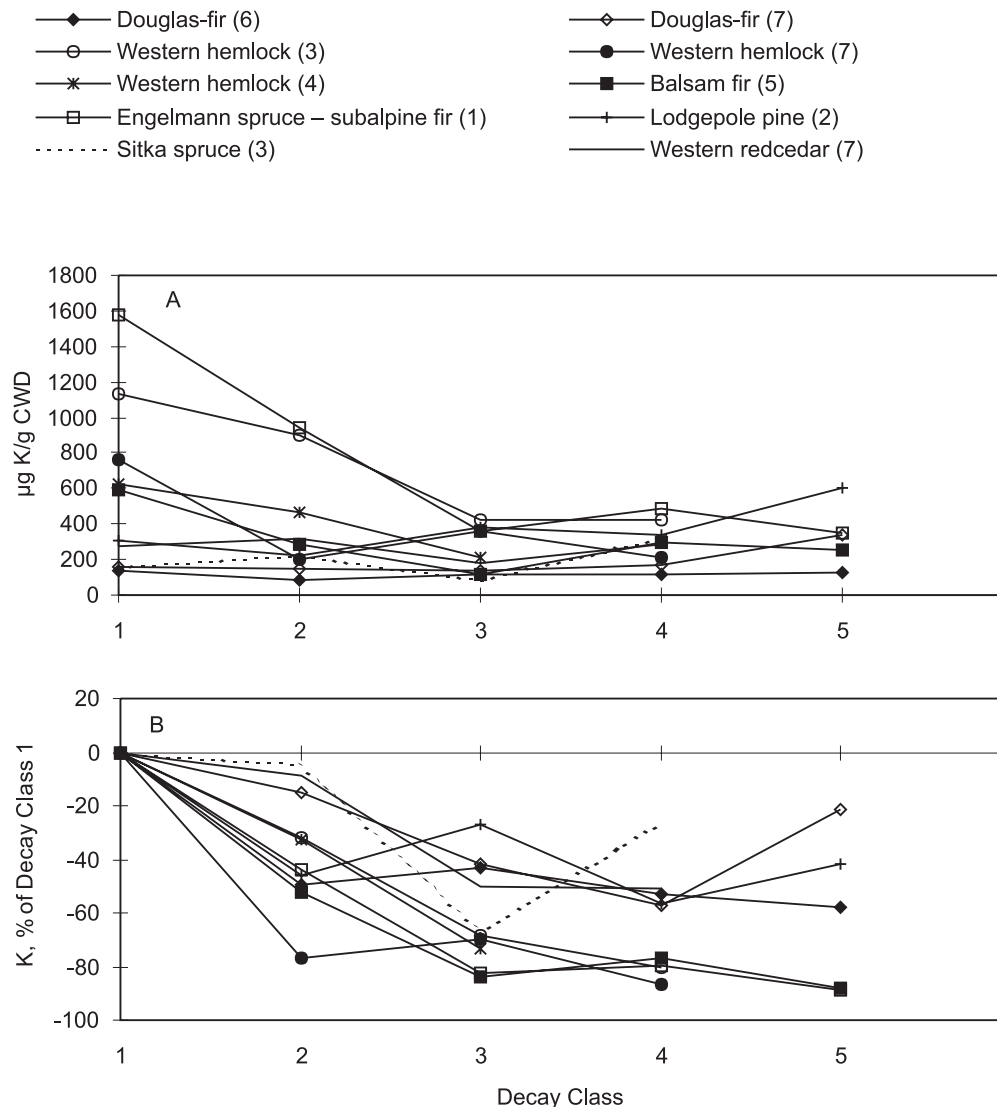
Based on the decay-class definitions given by Triska and Cromack (1980), the assumptions of the volume-adjusted

concentration method are well met in decay classes 1 through 3, so we presume that the method works well over this decay range. By late class 4 and class 5, however, the assumptions become less valid, because the structure of the class 5 CWD sags as the structural components decay. This increases the volume of original CWD per volume of class 5 CWD (Lambert et al. 1980), thereby creating artificially high volume-adjusted concentrations. Increases in the volume-adjusted concentration in class 4 and 5 CWD may be caused by the nutrient inputs mentioned previously. Therefore, a decrease in CWD volume and an increase in nutrient inputs could be working independently or synergistically to cause the nutrient increases observed in class 4 and 5. Fragmentation of CWD also occurs at the later stages of decay and can cause a loss of nutrients not measured by the volume adjusted concentration method.

Other methods

With the data given, we could determine only the net fluxes, as opposed to gross fluxes, of nutrients into and out

Fig. 5. (A) Unadjusted potassium concentration ($\mu\text{g K/g CWD}$) versus decay class. (B) Volume-adjusted potassium concentration as a percent of decay class 1 logs (calculated using eq. 1) versus decay class. Reference numbers from Table 1 are given in the key in parentheses.



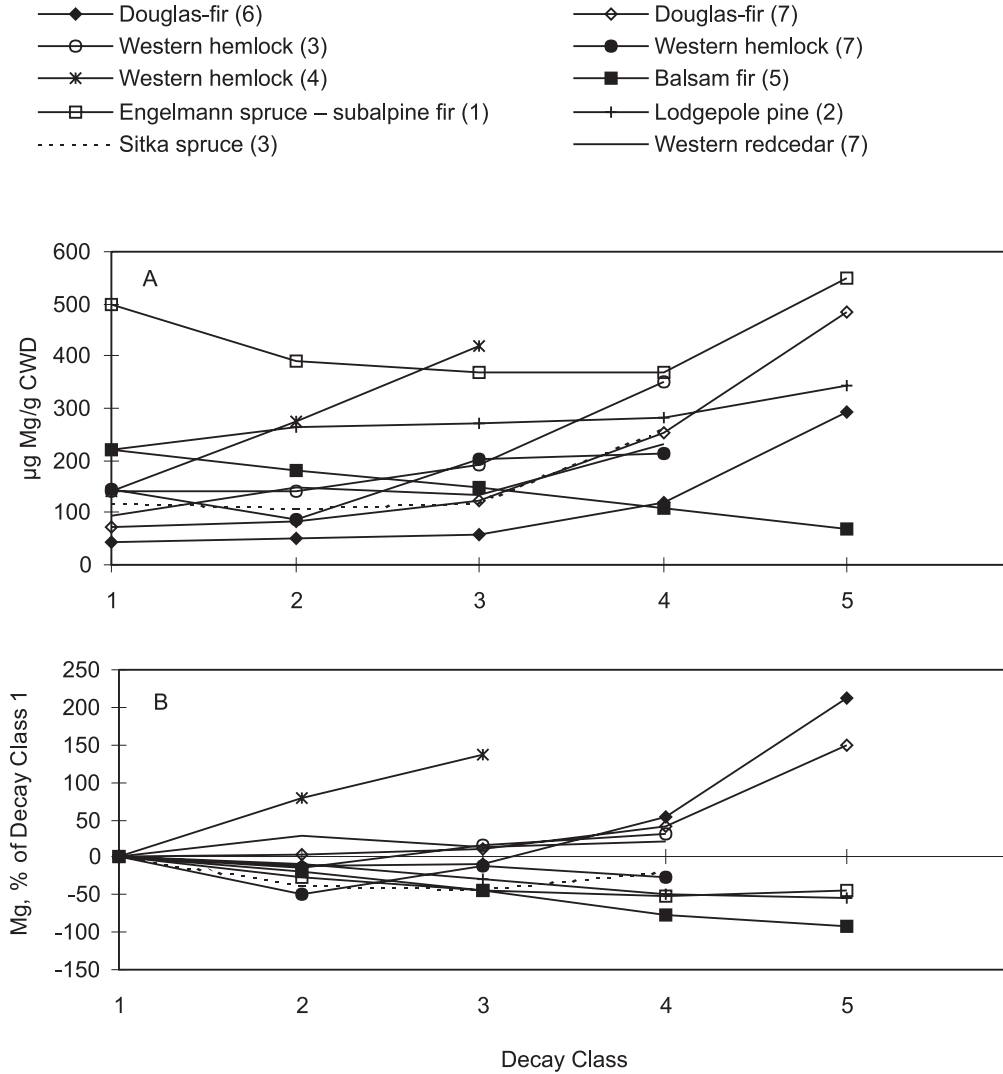
of CWD over time. In the studies we examined there was no way to determine the origin of the nutrients that reside in CWD at any given decay class, nor can we determine the fate of the nutrients that originated in CWD and have subsequently been lost by various pathways. However, the origin and fate of nutrients, and thus gross fluxes, could be explored using stable or radioactive isotope tracers (e.g., Berg 1988). This method would be difficult and time consuming, however, because growing trees in an isotopically enriched environment and transporting the CWD to a site that has not been isotopically enriched would require an enormous amount of time and resources. The results obtained from such a study would be invaluable in terms of understanding CWD nutrient dynamics.

A conservative element ratio would provide an index of nutrient loss or gain by calculating the ratio of a given nutrient to an immobile element and observing the change in that ratio over time or in a CWD chronosequence. The ideal conservative element would be tightly held in CWD throughout

decomposition, have no biological activity, and have no outside inputs, but all of these criteria are difficult to meet simultaneously. Of the commonly measured elements in CWD decomposition (N, P, K, Ca, Mg), we considered Ca to be the best candidate. A nutrient to Ca ratio has been used previously as an index of nutrient translocation in leaves (Vitousek and Stanford 1986). With its +2 valence charge, Ca might be expected to bind to cation exchange sites in organic matter (Ferguson and Ballard 1976) and to be maintained as a component of cell wall structure (Kozłowski and Pallardy 1997). However, since Ca inputs are possible and the volume adjusted concentration method showed Ca losses, we determined Ca to be inappropriate as a conservative tracer. We ruled out N, P, K, and Mg for similar reasons.

Rock weathering and environmental monitoring studies often use niobium (Nb^{+5}), zirconium (Zr^{+4}), titanium (Ti^{+4}), aluminum (Al^{+3}), or some other immobile metal as a conservative element with which other elements are compared (e.g., Beavers et al. 1963; Sudom and St. Arnaud 1971;

Fig. 6. (A) Unadjusted magnesium concentration ($\mu\text{g Mg/g CWD}$) versus decay class. (B) Volume-adjusted magnesium concentration as a percent of decay class 1 logs (calculated using eq. 1) versus decay class. Reference numbers from Table 1 are given in the key in parentheses.



Summers et al. 1996; Kurtz et al. 2000). Because of their high ionic charge, these elements will form strong bonds to cation exchange sites in CWD. They are also only sparingly soluble in water, which should reduce losses from CWD as well as inputs from precipitation or throughfall, although dust inputs could pose a potential problem. Despite the relative insolubility of Nb, Zr, and Ti compounds, plants have been shown to contain small (0.05, 0.1, and 5 $\text{mg}\cdot\text{kg}^{-1}$ dry mass, respectively) but measurable amounts of these elements in their tissue (Kabata-Pendias and Pendias 1992; Markert 1992). Aluminum is found in at much higher concentrations in plants ($\sim 80 \text{ mg}\cdot\text{kg}^{-1}$) (Markert 1992) and could work equally as well as Nb, Zr, and Ti under the proper conditions. Further studies of CWD nutrient dynamics using Nb, Zr, Ti, and Al as conservative elements appear warranted.

Conclusion

The volume adjusted concentration method can provide useful insight into the nutrient dynamics occurring in CWD

by correcting for the mass lost during decomposition. Using this methods we determined that (i) the amount of N in CWD generally increased through time; (ii) Ca was lost at least through class 4 logs; (iii) P was lost initially followed by gains; (iv) CWD Mg concentrations showed no large changes overall, although some individual studies showed gains while others showed losses; and (v) K was lost rapidly in large amounts.

Like any method used to examine CWD chronosequence data, the volume adjusted concentration method has limitations to its applicability. We suggest that the volume adjusted concentration method be used in combination with other methods such as isotopic tracers and conservative element tracers for a more accurate examination of nutrient dynamics in CWD.

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