The Nutritional Significance of Coarse Woody Debris in Three Rocky Mountain Coniferous Forests[1]

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Abstract

The contribution of coarse woody debris (CWD) to carbon, nitrogen, and phosphorus cycles was assessed in forests of lodgepole pine, white spruce-lodgepole pine, and subalpine fir-Engelmann spruce in southwestern Alberta. Mass loss and changes in C, N, and P concentrations in decomposing log segments were measured over a 14-year period. Organic matter input was measured during 10 years for CWD, 1 year for ground vegetation, and 5 years for other aboveground litter types. Carbon, N, and P release from decomposing litter were simulated for a period of 40 years to determine the relative contributions of each aboveground litter type, including CWD. After 14 years, pine log segments had lost 71 percent of their dry mass; spruce and fir lost 38 percent and 40 percent, respectively. The nitrogen (N) content of the logs increased in pine, changed little in spruce, and decreased by almost 30 percent in fir logs. Phosphorus (P) accumulated in decaying log segments of all three species, especially fir logs in which the P content was nearly five times the initial content after 14 years. Tree species with the lowest initial concentration had the greatest relative accumulation. Thus, wood decay organisms may compete with vegetation for limiting nutrients in these forests. The proportion of coarse woody debris (CWD) in aboveground litter input was 19 percent at the pine site, 3 percent at the spruce site, and 24 percent at the fir site. The contribution of CWD to N and P release was 2 percent or less, except at the fir site where CWD released 5 percent of the N. Coarse woody debris does not appear to make a significant contribution to N and P cycling in these forests.

Introduction

The role of coarse woody debris (CWD) as a critical habitat element for many species of organisms is well recognized (Freedman and others 1996), but less is known about the role of CWD in element cycling and productivity of forest ecosystems (Harmon and others 1986). Studies in the coastal forests of the Pacific Northwest, where CWD is particularly abundant and large (Harmon and others 1986, Keenan and others 1993, Sollins and others 1987), have suggested that CWD is an integral component of forest ecosystems, acting as a long term stabilizing storage pool for nutrients. In other coniferous forests, the role of CWD in nutrient cycling has been found to be small (Busse 1994). There is some controversy about the

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importance of CWD to forest productivity (Fahey 1983, Harmon and others 1986, Spies and others 1988).

Assessing the role of CWD in element cycling requires measurements of the rates of input and decomposition of CWD relative to other litter types. The long time span and considerable temporal variation make it difficult to directly measure CWD input and decomposition. Most previous studies have relied on indirect methods for estimating rates of decomposition and have usually involved chronosequence techniques. Decomposition estimates have usually been based on log inventories by using various backdating techniques (e.g., Brown and others 1998, Sollins and others 1987) that report changes in wood density, as the original mass of the logs was not known (Alban and Pastor 1993, Fahey 1983, Graham and Cromack 1982, Means and others 1985, Sollins and others 1987). In other studies, the mass of CWD was inventoried and rates of decay were estimated with the assumption of constant input (Sollins 1982). These rough estimates may be adequate for management guidelines, but ecosystem models require more precise information on the pattern of mass loss and nutrient release from CWD.

In this study, the rate of CWD input (treefall) was measured for 10 years in three Rocky Mountain forests: a self-thinning lodgepole pine *(Pinus contorta* Loud.) forest, a mature white spruce *(Picea glauca* [Moench] Voss) forest, and an old-growth forest of Engelmann spruce *(Picea engelmannii* Parry ex Engelm.) and subalpine fir *(Abies lasiocarpa* [Hook.] Nutt.). Mass loss and changes in C, N, and P concentrations were measured over a 14-year period in portions of recently fallen logs of the dominant species in each forest (pine, spruce, and fir, respectively). The role of CWD in nutrient cycling in these forests was assessed by determining 1) the proportion of the annual aboveground inputs of C, N, and P that is derived from CWD, and 2) the proportion of the C, N, and P released from aboveground litter that is derived from CWD during a simulated 40-year period.

Study Sites

The study sites were in the Kananaskis Valley in the Front Range of the Rocky Mountains of southwestern Alberta (51°2'N, 115°3'W). Average monthly temperatures range from -10°C in January to 14°C in July. Average annual precipitation is 660 mm, of which 290 mm occurs as snow. Soils are well-drained brunisols overlying primarily limestone glacial deposits. The three study sites were within 5 km of one another in the Lusk Creek basin, adjacent to the Kananaskis Field Station of the University of Calgary. The sites were identified according to the dominant species of overstory tree in the stand, as pine, spruce, or fir (Prescott and others 1989a).

Methods

Wood Decomposition

Standing dead or recently fallen trees approximately 15 cm in diameter of the dominant species at each site were harvested and cut into segments 20 cm long. In September 1984, 70 log segments were placed on the litter surface at 3 m intervals within one 20 x 30 m plot at each site. Unused portions of the harvested logs were used to determine the average moisture content and C, N, and P concentrations—the original dry mass and C, N, and P content of each log segment.

Ten log segments were collected from each site after 2, 6, 10, and 14 years. Logs were cleaned of litter and vegetation, and end pieces were removed. Each piece was weighed fresh, dried at 80°C to constant mass, and weighed. The central pieces were then ground for C, N, and P analyses.

Litter Input

Input of CWD (treefall) was estimated on two 20 x 30 m plots at each site. All fallen trees were marked with paint in August 1984. New (unmarked) downed trees were checked annually for the first 5 years, and once again after another 5-year period. At each time, the species and decay class of each downed tree was recorded and their dbh and length (within the plot) measured. Decay classes were adapted from Triska and Cromack (1979). After calculating the stem volumes, the total dry mass and C, N, and P content of each log was estimated using average density values and nutrient concentrations for each species-decay class combination.

Input of "small woody litter" (i.e., twigs, branches, intact female cones, and bark) was harvested annually for 5 years on ten 3 x 3 m plots at each site. "Nonwoody litter" (i.e. needles, leaves, male cones, female cone scales, and seeds) was collected in fifteen 0.25 m^2 litter traps placed randomly in one 20 x 30 m plot at each site. The traps were emptied at least twice a year for 5 years. Litter input from ground vegetation was estimated during 1985 as described by Prescott and others (1989b). The litter samples were separated into components and dried to constant mass at 80°C.

Carbon, N, and P concentrations were analyzed in five composite samples of each litter type, and used to estimate the mass of nutrients in the annual inputs of each litter type. Samples were ground in a Wiley mill and C concentrations were measured with a Leco carbon analyzer. Nitrogen and P concentrations were analyzed with a Technicon II autoanalyzer after a sulphuric acid-hydrogen peroxide digestion in 360°C (Lowther 1980). Nutrient concentrations were measured only in the original and 14-year logs.

Statistical Analyses

Three equation types were tested to describe the pattern of mass loss from logs over time: linear, exponential and sigmoidal. Linear and exponential equations have been used in earlier studies of wood decomposition, and a sigmoidal curve was suggested by locally weighted regression procedures used for preliminary smoothing of the data. Statistical outliers in the wood decomposition data were identified and excluded from the regression analyses. Nonlinear estimation was done using a Gauss-Newton method and a least squares loss function (SYSTAT 6.0 for Windows 1996).[4] Final equation forms were selected after checking the residuals and assessing the bias of the estimates.

[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Decomposition and Nutrient Release Simulations

To examine the relative importance of the litter types in the nutrient cycles of these forests, organic matter accumulation and annual release of C, N, and P from each litter type were simulated for a period of 40 years. A 1-year time step was used; each year, the mean annual litter input of each litter type was added to the system. Mass loss equations from the log decomposition experiment were used for CWD. Decomposition of other litter types was simulated using the negative exponential decay model (e.g., Olson 1963):

$$\text{Mass remaining at time t / Initial mass} = \exp(-k \cdot t) \quad (1)$$

with the decomposition constants (k-values) presented in Taylor and others (1991). For materials for which decomposition data were not available, the k-value for a material most similar to it was used (e.g., k-values for *Epilobium angustifolium* were used for all herbaceous materials). Each litter cohort was progressively decomposed until the mass of the cohort became negligible or the simulation period ended. Organic matter accumulation was then calculated as the sum of the remaining mass of each cohort at each time step, and annual decomposition as the mass lost from each cohort between the time steps. Release of N and P was simplified by assuming nutrients were lost at the same rate as mass.

Results

Wood Decomposition

Mass loss during the 14 years averaged 71 percent in pine logs, 38 percent in spruce logs and 40 percent in fir logs. Carbon concentrations in the decaying log segments changed little during the 14 years, whereas N and P concentrations increased *(table 1).* There was an average net import of 0.78 mg N per g remaining mass in each pine log, and net releases of 0.05 and 0.65 mg N g^{-1} from spruce and fir logs, respectively *(fig. 1).* Phosphorus accumulated in decaying wood of all three species, particularly in fir logs; the amounts of P imported into the logs after 14 years were 0.02, 0.03, and 0.07 mg P g^{-1} in pine, spruce, and fir logs, respectively. For both N and P, the increases in nutrient content during decay were greatest in logs with the lowest initial concentration (pine logs for N and fir logs for P).

Table 1—*Carbon, nitrogen, and phosphorus concentrations of the log segments initially and after 14 years of decomposition.*

Site	Percent C	mg N g^{-1}	mg P g^{-1}
Initial			
Pine	47.76 ± 0.44	0.61 ± 0.12	0.04 ± 0.02
Spruce	49.07 ± 0.82	0.88 ± 0.20	0.03 ± 0.00
Fir	49.76 ± 0.59	1.55 ± 0.35	0.01 ± 0.01
14-year			
Pine	49.77 ± 1.65	2.78 ± 1.08	0.16 ± 0.06
Spruce	50.84 ± 1.08	1.53 ± 0.92	0.08 ± 0.04
Fir	48.44 ± 0.91	2.03 ± 0.94	0.09 ± 0.05

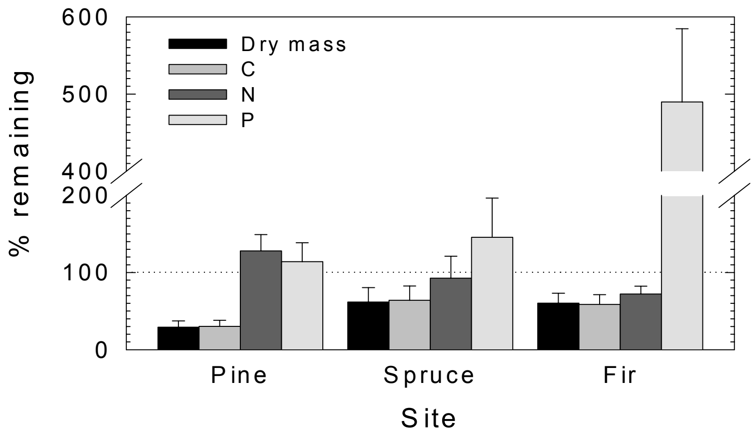

Figure 1—Dry mass, C, N, and P contents of 20-cm log segments of lodgepole pine, white spruce, and subalpine fir after decomposing for 14 years at the pine, spruce, and fir sites, respectively. Values are relative to the initial content: values more than 100 percent indicate net import; values less than 100 percent indicate net release. Each value is the mean of 10 log segments; error bars are one standard deviation.

Litter Input

Total aboveground litter input averaged 362 g m^{-2} $year^{-1}$ at the pine site, 237 g m^{-2} $year^{-1}$ at the spruce site, and 205 g m^{-2} $year^{-1}$ at the fir site. Foliar litter (needles and leaves) made up the greatest proportion of the litter input at all sites *(fig. 2).* CWD input accounted for 19 percent of the litter input at the pine site, 3 percent at the spruce site, and 24 percent at the fir site. For C, the values were 18, 3, and 23 percent, respectively. CWD accounted for 2.6, 0.4, and 5.1 percent of the annual aboveground N input and 1.4, 0.5, and 2.2 percent of the annual aboveground P input at the pine, spruce, and fir sites, respectively.

Decomposition and Nutrient Release Simulations

Nonwoody litter (mostly foliage and cone scales) also dominated release of C, N, and P *(figs. 3-5).* CWD accounted for 18 percent of the total C released from decomposing litter at the pine site, 2 percent at the spruce site, and 20 percent at the fir site. The contribution of CWD to N and P release was 2 percent or less, except at the fir site where CWD released 5 percent of the N.

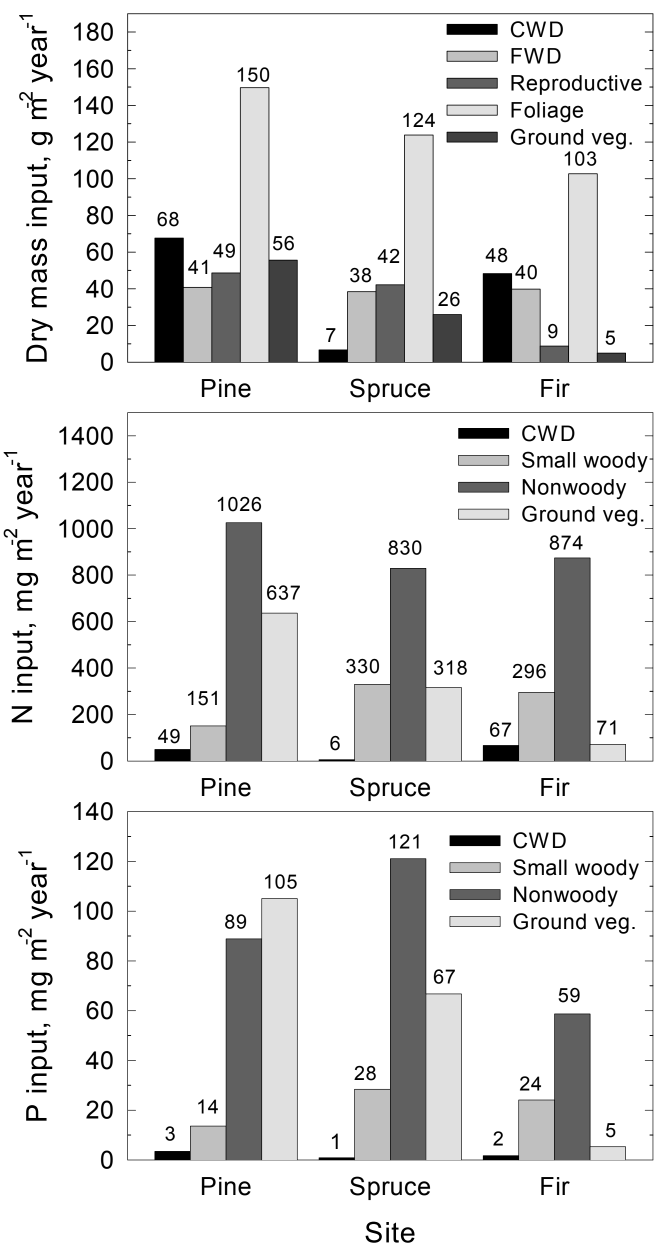

Figure 2—Average annual inputs of dry mass, C, N, and P in each litter type at the pine, spruce and fir sites. CWD = coarse woody debris; FWD = fine woody debris.

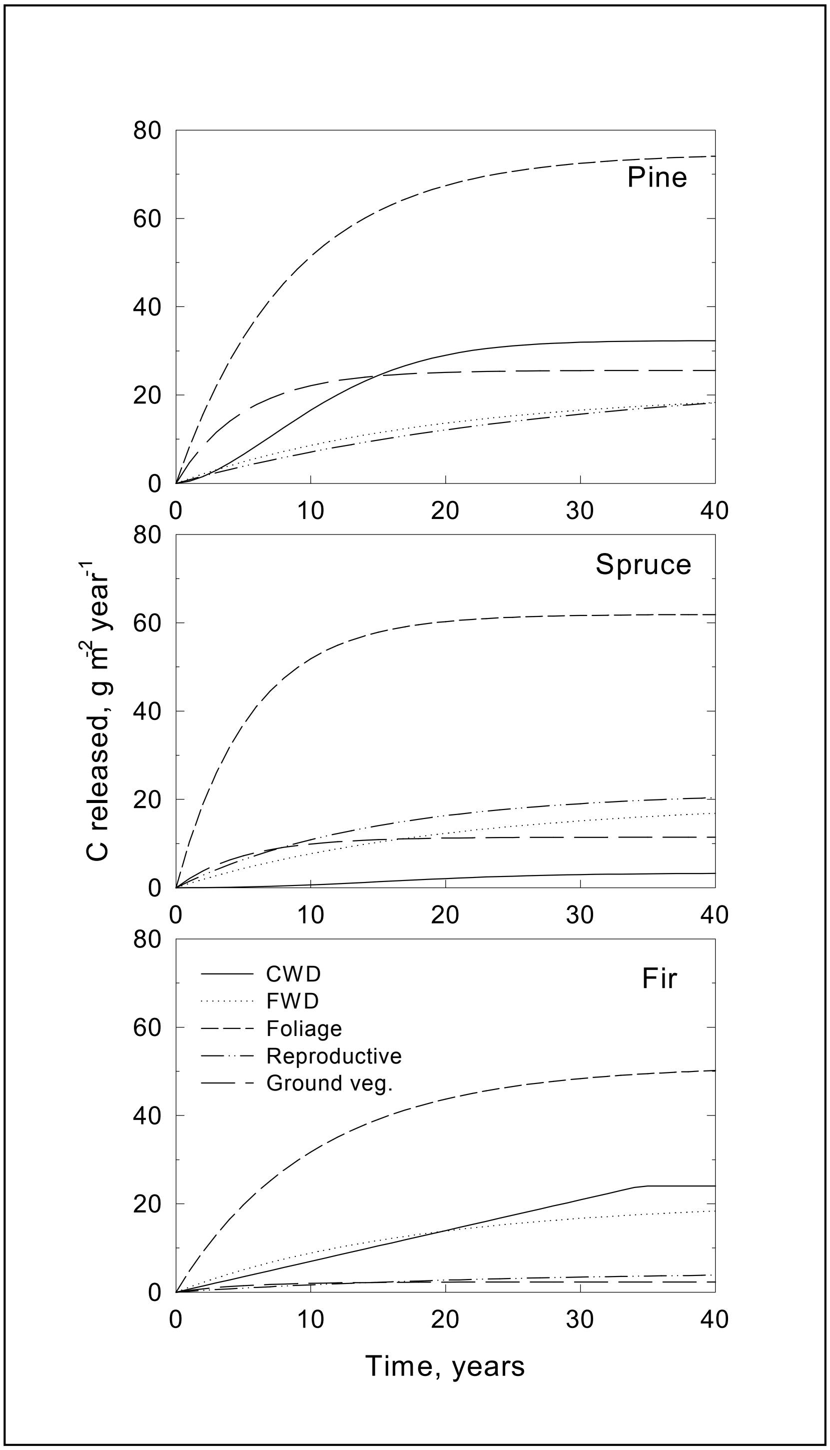

Figure 3—Contributions of the various litter types to annual C release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

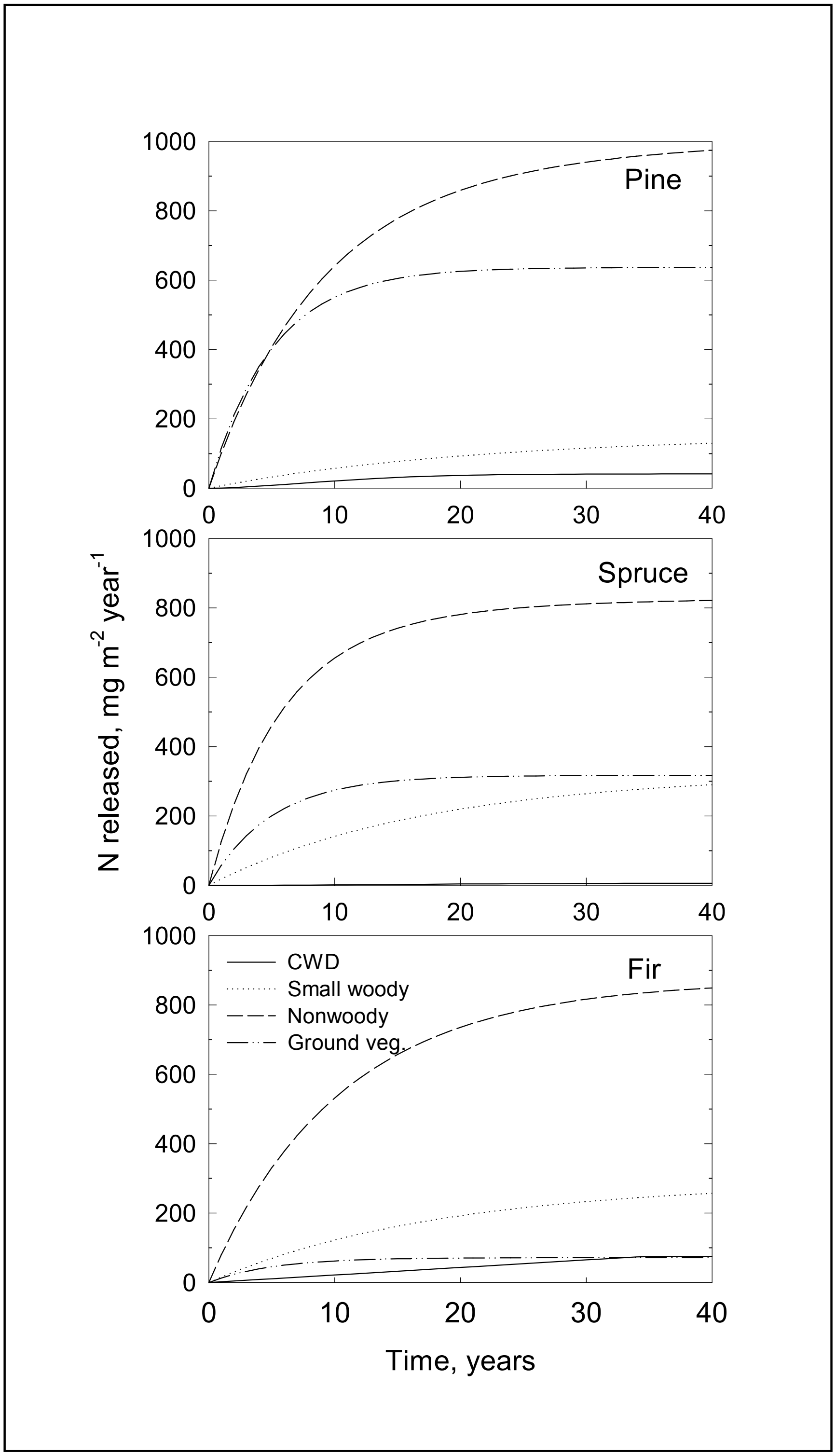

Figure 4—Contributions of the various litter types to annual N release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

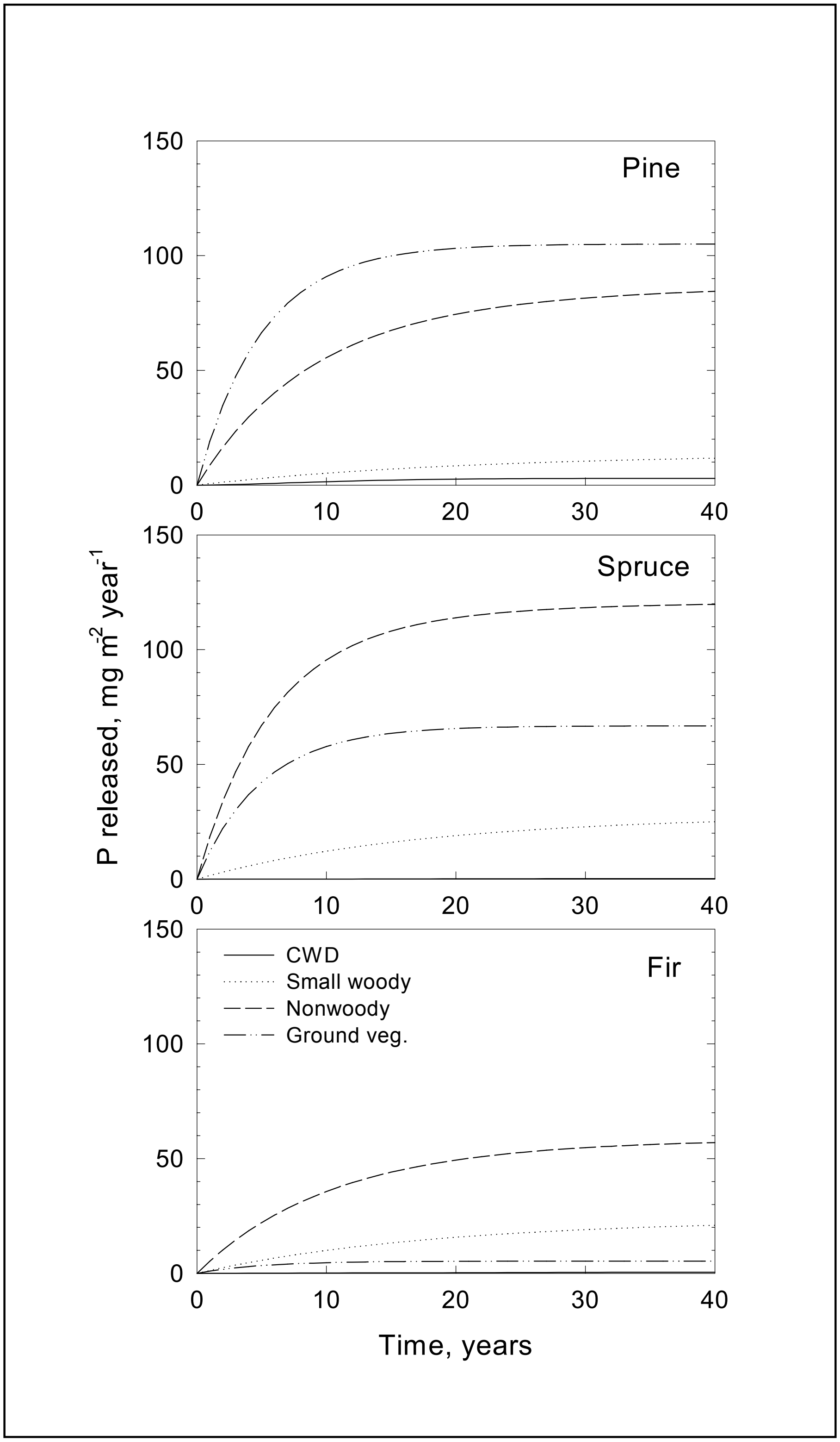

Figure 5—Contributions of the various litter types to annual P release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

Discussion

Our results indicate that CWD contributed a maximum of 5 percent of the N and P returned in annual aboveground litter and a maximum of 5 percent of the N and P released during decomposition. Other studies have also indicated that the contribution of CWD to nutrient cycling in undisturbed forests is relatively minor. Downed wood comprised less than 3 percent of the soil nutrient pools in lodgepole pine stands in central Oregon (Busse 1994). Fahey and others (1985) found that downed wood accounted for less than 3 percent of the soil N pool in two lodgepole pine ecosystems in Wyoming. In an old-growth mixed conifer forest in central Oregon, well-decayed logs contributed only 4 to 6 percent of annual plant N uptake (Hart 1999).

CWD was clearly more important for the C flows, accounting for 18, 3, and 23 percent of the C returned in aboveground litter, and 18, 2 and 20 percent of the C released during decomposition at the pine, spruce, and fir sites, respectively.

Our observation that logs with the lowest initial concentrations of N or P immobilized the greatest amount of N or P during decomposition has implications as to the role of CWD as a nutrient source in these forests. The initial concentrations of N and P in the logs corresponded to the availability of the nutrient at the site, as determined in previous studies (Prescott and others 1992). For example at the fir site, availability of N was high and P was low, and the logs released N and immobilized P during decomposition. In contrast, N availability was lowest at the pine site, and the logs at this site were the only ones to immobilize N. Release dynamics of N and P in other litter types have been found to depend on the initial concentrations (Prescott and others 1993), and a similar pattern has been noted for decaying wood (Alban and Pastor 1993). Wells and Boddy (1990) and Wells and others (1990) have shown that wood-decaying fungi translocate P from surroundings to the substrate they are colonizing. Our findings of greatest N import into logs at the pine site and greatest P import at the fir site suggest that wood decay organisms may be competing with vegetation for limiting nutrients.

Our estimates are only valid for these forests at the time of measurements, but the sites represent a variety of common forest types and stand development stages: a dense self-thinning lodgepole pine stand, a mature post-thinning spruce stand, and an old-growth spruce-fir stand.

In conclusion, our findings indicate that CWD is not a significant source of available N and P in these forests; it may actually compete with vegetation for limiting nutrients. Guidelines for management of CWD should be based on management objectives related to other potential values, rather than its role in N and P cycling.

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