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Nitrogen Fixation Associated with Increased Wood Decay in Douglas-fir Residue

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ABSTRACT. Nitrogen fixation rates, as estimated by the acetylene reduction technique, were determined for four decay stages of down Douglas-fir logs on two old-growth sites in northwestern Montana. Acetylene reduction rates increased as wood decay progressed, but were not affected by site location. Wood carbohydrate, soluble sugar, total and soluble nitrogen, and moisture content also vaned among decay stages. Acetylene reduction rates were positively correlated with wood moisture content and nitrogen concentration, and negatively correlated with carbohydrate level. The annual nitrogen additions to the sites from nitrogen fixation in decaying Douglas-fir logs were small, 0.72 kg/ha/yr on the moister site and 0.26 kg/ha/yr on the drier site. These differences in nitrogen inputs were related to differences in residue loading between sites. Although small, such nitrogen gains may be significant over the rotation life of a stand. FOREST SCI. 30: 1038–1044.

ADDITIONAL KEY WORDS. Douglas-fir, acetylene reduction, *Fomitopsis pinicola,* wood carbohydrate, wood sugars.

FALLEN LOGS and other coarse woody materials are an important source of soil organic matter in many ecosystems. In forest stands of the Pacific Northwest such woody biomass can range from 6 to 200 Mg/ha (Grier and Logan 1977, Sollins 1982). In northern Rocky Mountain forests the quantity of woody residue is generally less, but on these sites decaying wood has been found to comprise from 15–25 percent of the surface 30 centimeters of soil (Harvey and others 1980). Similar amounts of woody material were found in the forest floor of a mixed conifer-hardwood stand in northern New York (McFee and Stone 1966).

The impacts of decaying wood on the forest soil ecosystem are various. Mycorrhizal root activity is favored in woody soil materials, particularly on dry sites (Harvey and others 1980). Decayed wood is also an excellent seedbed for conifer regeneration (Day and Duffy 1963), and may ameliorate soil nutrient losses following harvesting and other site disturbances (Triska and Cromack 1980).

The decay of woody residue may benefit the nitrogen status of a soil by favoring the activity of nitrogen-fixing microorganisms. Various nitrogen-fixing bacteria have been isolated from decaying wood (Aho and others 1974, Schink and others 1981, Spano and others 1982). Also, a number of investigators have demonstrated the occurrence of nitrogen fixation in woody substrates using acetylene reduction techniques (Cornaby and Waide 1973, Roskoski 1980, Larsen and others 1982, Silvester and others 1982). The amounts of nitrogen fixed in these studies were generally small, but they could partially alleviate some of the nitrogen losses from timber removal and post-harvest site preparation (Jur-

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gensen and others 1980). In only one of these studies (Roskoski 1980) was an attempt made to examine the effects of season and site on nitrogen fixation rates.

This paper reports the results of a study on nitrogen-fixation in decaying Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] logs in old-growth, mixed conifer forests of northwestern Montana. The objectives of the study were to: (1) estimate the rates of nitrogen fixation associated with wood decay on two sites with different temperature and moisture regimes; (2) determine the effects of wood chemical and moisture-holding properties on nitrogen fixation; and (3) evaluate the significance of these nitrogen gains and their impact on residue management practices.

Since nitrogen fixation activity in decaying wood has been shown to vary with the species of wood being decayed and with the fungi involved (Larsen and others 1978), this study was limited to the decomposition of Douglas-fir residue by *Fomitopsis pinicola* (Swartz: Fr.) Karst. This fungus is a basidiomycete frequently associated with a brown rot decay of conifer wood in the western United States.

METHODS AND MATERIALS

The study was conducted in two old-growth Douglas-fir stands located on the Coram Experimental Forest in Northwest Montana. These stands were selected on the basis of soil moisture characteristics, associated vegetation, and tree growth to ensure site differences (Harvey and others 1979). The warm, dry site is 1,140 m in elevation with a southern aspect. Habitat type designation of the site was *Pseudotsuga menziesii/Physocarpus malvaceous* (Pfister and others 1977). The cool, moist site has an elevation of 1,460 m, an eastern aspect and a habitat type designation of *Abies lasiocarpa/Clintonia uniflora.* Climatic records for a lower elevation on the forest (ca. 1,067 m) give a mean annual precipitation of 79 cm, a mean annual temperature of 5.3°C, and a mean annual summer temperature of 16.1°C (Klages and others 1976).

Ten dead and down Douglas-fir trees ranging in diameter from 25 to 75 cm with multiple *F. pinicola* fruiting bodies were located on each of the two sites. The sample logs were cut with a chain saw to locate stages of wood decay. Four decay stages were examined in each log: (1) incipient, (2) intermediate, (3) light advanced, and (4) dark advanced. These decay stages were determined in the field on the basis of the following wood color and textural characteristics: incipient decay—light colored, relatively hard; intermediate decay—light gray to yellow in color, "punky" texture; light advanced decay—light yellowish-white in color, very brittle, fibrous, or cubicle; dark advanced decay—dark reddish brown in color, very brittle or cubicle. There was no relationship between decay stage and location in a log.

Preliminary analysis was conducted to determine the presence of active *F. pinicola* hyphae in the selected logs. Small pieces of woody tissue from each of the logs were transported to the laboratory, surface flame sterilized, placed in 2 percent malt agar (w/v) and incubated at 18°C. Fungal growth typical of F. pinicola confirmed the presence of the fungus within the substrates tested.

Five replicate samples of each decay type were taken from each log three times during the year—early June, early August, and early October. Each sample was placed in a 20 ml glass Vacutainer tube (Becton-Dickinson Div., Becton-Dickinson). Care was exercised to avoid incorporation of woody material from exposed surfaces. The temperature of each decay stage was recorded at time of sampling.

Nitrogen fixation rates were estimated using an adaptation of the acetylene reduction assay as discussed by Hardy and others (1968). Within 2 h after sampling the tubes were evacuated and flushed with argon five times and then filled with a mixture of 10 percent acetylene and 90 percent argon. One of the five replicate samples was not injected with acetylene to provide a control for monitoring endogenous ethylene production. The sample tubes were then incubated in the dark for 12 h at the temperature of each decay stage as determined in the field. These were as follows: June—incipient and intermediate 17°C, light and dark advanced 14°C; *August*—incipient and intermediate 14°C, light and dark advanced decay 12°C; October—all decay stages 10°C. No significant temperature differences were evident between sites.

Gas subsamples were removed from the 20 ml incubation tubes by 2 ml Vacutainer tubes and the woody material was oven dried at 105°C for determination of dry weight

TABLE 1. Acetylene reduction activity and moisture content of decaying Douglas-fir logs.[a]

Decay stage	Percent of samples exhibiting acetylene reduction	Acetylene reduction rate (nmoles C_2H_4/gm dry wgt/24 hr)				Moisture content (percent)
		June	August	October	Average	
Incipient	72	1.4	1.3	1.0	1.3[a]	46[a]
Intermediate	78	3.7	2.7	1.7	2.8[ab]	97[b]
Light advanced	78	4.6	4.0	2.8	3.9[b]	108[b]
Dark advanced	93	10.4	8.5	4.9	8.1[c]	277[c]
Average	80	5.0[x]	4.2[xy]	2.8[y]	4.1	135

[a] Values denoted by different letters are significantly different at the $P \leq 0.01$ level.

and moisture content. These gas subsamples were analyzed for acetylene and ethylene concentrations using flame ionization on a Varian Aerograph Series 2800 gas-liquid chromatograph fitted with an 80 to 100 mesh Poropak R column. The column temperature was maintained at 40°C with nitrogen as the carrier gas. Acetylene concentration was used as an internal standard to correct for air-space variations in the tubes and for gas leakage (McNabb and Geist 1979).

After dry weight values were obtained from wood samples, the five replicates were composited and sent to the U.S. Forest Products Laboratory in Madison, Wisconsin, for nitrogen and carbohydrate determinations. Total carbohydrate contents were obtained using the procedure described by Moore and Johnson.[1] The Kjeldahl method, as described by Broadstreet (1940), was used for total nitrogen determination. Soluble sugars and soluble nitrogen values were determined by a modification of the TAPPI standard method T-207 (TAPPI 1975).

The statistical test used to analyze the effects of decay stage, site, and sampling date on acetylene reduction rates was the 3 way analysis of variance using the F-test for significance. If significant differences were found, the Duncan Multiple Range Test was used for grouping data. Regression analysis using the product moment correlation coefficient (r) was used to determine if significant relationships existed between acetylene reduction rates and moisture availability, wood carbohydrate, soluble sugar, total and soluble nitrogen.

Results and Discussion

Nitrogen Fixation Rates.—Nitrogen fixation, as expressed by acetylene reduction analysis, occurred in all stages of decay. Little difference was found between the amount of acetylene reduction occurring on the two sites. All decay stages combined on the dry site showed acetylene reduction frequency of 82 percent (354 samples) and, on the moist site, a frequency of 79 percent (417 samples). However, frequency of occurrence in the samples as well as rates of fixation varied among the different decay stages (Table 1). These results show the increasing incidence of acetylene reduction as wood decay progressed. A similar decay relationship was observed by Roskoski (1980) but the overall acetylene reduction activity in the wood litter she examined was only 25 percent, as compared to 80 percent in our study. This difference appears related to size of woody material sampled and its effect on wood moisture content. We used samples from fallen logs having a minimum diameter of 25 cm, while Roskoski (1980) tested all wood materials ranging from tree boles to twig fragments. However, in her study the large majority of active samples came from large size classes.

The strong relationship between wood decay stage and acetylene reduction capacity was again shown when a three-way analysis of variance was used to test the effects of decay stage, site, and sampling date on acetylene reduction rates. Both decay stage and period of

[1] Moore, W. E., and D. B. Johnson. 1967 (revised). Procedures for the chemical analysis of wood and wood products (as used at the U.S. Forest Products Laboratory). U.S. Forest Service, Madison, WI (unpublished).

sampling were significantly ($P < 0.01$) related to acetylene reduction, but no significant difference was found between sites or for the interaction between decay stage and site. This lack of a site effect on acetylene reduction rates was somewhat unexpected considering the overall climatic and vegetation conditions of each location. However, little difference in log moisture contents were found between the sites. Decaying wood has been shown to be much less affected by daily or even seasonal moisture changes than surface soil horizons (Hungerford 1980). Although rainfall data was not available for each study site, the occurrence of above normal rainfall on the Experimental Forest during the study period may have contributed to the similar moisture patterns.

The use of Duncan's multiple range test to group the combined acetylene reduction data from both sites by decay stages indicated that acetylene reduction rates increased significantly as the log decayed (Table 1). This was particularly evident in the dark advanced decay, which had acetylene reduction rates far higher than any other decay stage. The moisture content of the wood also increased as decay progressed (Table 1) indicating a possible moisture/acetylene reduction interaction. A low linear correlation ($r = 0.430$) was found between acetylene reduction rate (Y) and wood moisture content (X), but the curvilinear form $Y = aX^b$ gave a much better result ($r = 0.877$). This curvilinear relationship indicates a proportionally greater increase in acetylene reduction rates as wood moisture content increases.

All acetylene reduction values, including zero, were used in establishing the wood moisture correlations shown above, even though each wood sample would have a threshold moisture content below which the nitrogen-fixing bacteria could not function. Consequently, wood moisture contents below this threshold value would show no correlation to acetylene reduction no matter how widely they might differ. Roskoski (1980) tried to overcome this problem by considering all samples yielding less than 0.5 nm C_2H_4/g/h as not having any nitrogen-fixing activity. However, the reason for selecting this value was not stated.

The concept of nitrogen fixation/wood moisture thresholds was tested using the partial correlation method (Neter and Wasserman 1974). The partial correlation coefficient (p) was used to determine if the acetylene reduction/wood moisture correlation improved as various threshold values were included in the model $Y = aX^b$.[2] Acetylene reduction values from 0 to 0.5 nm of C_2H_4/g/day were tested as possible moisture threshold levels. The model was fit using each threshold level and the level which resulted in the greatest value of the partial correlation coefficient (p) was taken to be the threshold level indicated by the data. The highest correlation of wood moisture content and acetylene reduction was obtained when 0.3 nm of C_2H_4/g/day was used as the threshold value ($r = 0.971$).

Acetylene reduction rates were highest in June and lowest in October (Table 1). This difference appears related to variations in log temperature rather than moisture. Log moisture contents did not vary significantly among the three sampling times, but log temperatures showed a seasonal decrease similar to the acetylene reduction rates: June 15.8°C, August 13.2°C, and October 10.0°C. A similar temperature effect on acetylene reduction activity in wood residue was also noted by Roskoski (1980).

The relationship between acetylene reduction and wood decay has been reported by other investigators (Cornaby and Waide 1973, Larsen and others 1978, Roskoski 1980). Cornaby and Waide (1973) reported average acetylene reduction rates of over 30 nm C_2H_4/g/day for decaying chestnut logs, while Roskoski (1980) found acetylene reduction values ranging from 20 to 80 nm C_2H_4/g/day during summer months for mixed hardwood-conifer residue. Acetylene reduction values from our study are generally low when compared to these results. The likely predominance of white rot decay systems in the hardwood residues examined in these studies (Larsen and others 1980), as contrasted with a brown rot decay of conifer wood in our study, may at least partially account for such differences in acetylene reduction rates.

While the fungi involved and type of decay seem important to acetylene reduction activity, the species of wood being decayed may also be significant. In an earlier study (Larsen and others 1978), little difference was observed in acetylene reduction rates between the white rot decay of white birch (*Betula papyrifera* Marsh.) by *Fomes fomentarius* (Fr.)

[2] Acetylene reduction values below or above a determined level were added to the model as an indicator value (which takes on the value of 0 if acetylene reduction was equal to or below the determined level or 1 if above the determined level).

TABLE 2. Carbohydrate, sugar, and nitrogen contents of decaying Douglas-fir logs.[a]

Decay stage	Total carbohydrate	Soluble sugar	Total nitrogen	Soluble nitrogen
	Percent			
Incipient	58.3a	3.1e	0.006l	0.010w
Intermediate	55.8a	2.4f	0.090m	0.014x
Light advanced	43.7b	2.5f	0.171n	0.022y
Dark advanced	29.1c	1.8g	0.152n	0.017z

[a] Combined values from both the moist and dry site expressed on a dry weight basis.
Values denoted by different letters for soluble sugar are significantly different at the $P \leq 0.05$ level, the others are significantly different at the $P \leq 0.01$ level.

Michx. and the brown rot decay of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) by F. pinicola. In contrast, much higher acetylene reduction activity was associated with F. pinicola decay of Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). These latter results compare favorably with the acetylene reduction rates found in our study.

Carbohydrate-Nitrogen Relationships. — Chemical analyses of wood samples indicated that total carbohydrate, total nitrogen and soluble nitrogen levels differed significantly among decay stages, but not between logs on the moist vs. logs on the dry site (Table 2). Soluble sugar was found to have a significant site relationship, but only for the incipient and intermediate decay stage. However, as seen below, this difference of approximately 0.7 percent more soluble sugar in the dry site samples was not reflected in acetylene reduction activity.

Total carbohydrate and soluble sugar contents decreased as wood decay progressed, while total and soluble nitrogen showed a reverse pattern (Table 2). Such a lowering in wood carbohydrate level is characteristically associated with the activity of brown rot fungi (Larsen and others 1980). The increased nitrogen contents in the more advanced decay stages may be due to (1) a concentrating of residual nitrogen as other components of the log are removed, (2) a translocation of nitrogen from surrounding materials into the log by decay fungi, or (3) to the activity of nitrogen-fixing microorganisms (Cowling and Merrill 1966, Grier 1978).

When wood chemical properties were related to acetylene reduction rates determined for each decay stage, a strong curvilinear relationship of the form $Y = aX^{\beta}$ was found: total carbohydrate ($r = -0.930$), soluble sugar ($r = -0.837$), total nitrogen ($r = 0.913$), soluble nitrogen contents ($r = 0.930$). The inverse relationship between acetylene reduction and soluble sugar level was unexpected, since nitrogen-fixing bacteria presumably require low molecular weight sugars and other metabolites produced by decay fungi. The high nitrogen contents in more decayed wood would also tend to inhibit nitrogen fixation (Jurgensen 1973). Consequently, other factors, particularly moisture content, appear to overweigh the seemingly negative effects of low carbohydrate and high nitrogen levels for nitrogen fixation in advanced decayed wood. Increased moisture levels associated with advanced decay (Table 1) would result in an overall lowering of the oxygen values in the wood. This should favor nitrogen-fixing bacteria present in wood, which are either anaerobic or microaerophilic (Aho and others 1974, Schink and others 1981, Silvester and others 1982, Spano and others 1982). Reduced competition from other wood-inhabiting microorganisms at low oxygen levels may also benefit the nitrogen-fixing bacteria.

Nitrogen Gains in Woody Residue. — By using the acetylene reduction data obtained in this study an approximation of nitrogen gains associated with woody residue decay on these two Douglas-fir sites may be calculated. Since the wood decay stages used for the acetylene reduction tests could not be easily measured for residue inventory purposes, all logs on the sites were classified as either sound or rotten. By averaging the results for the incipient and intermediate decay type shown in Table 1, an acetylene reduction rate of 2.0 nm C_2H_4/gm of wood/day was calculated for the sound residue. A value of 5.7 nm of C_2H_4/gm/day

for acetylene reduction was calculated for rotten wood by averaging the light and dark advanced decay rates. The theoretical conversion factor of acetylene reduction to nitrogen fixation of 3:1 was used as a basis for comparison to other studies, even though this value may overestimate nitrogen conversion (Roskoski 1981, Silvester and others 1982).

The woody residue loading (> 7.6 cm in diameter) was 114 metric tons/ha on the moist site and 49 metric tons/ha on the dry site. Conservatively assuming that nitrogen-fixing bacteria are active for 120 da/year, the nitrogen fixed in decaying logs was calculated to be 0.72 kg/ha/yr on the moist site, and 0.26 kg/ha/yr on the dry site. These results compare favorably with nitrogen gains of 0.4 kg/ha/yr reported for a 160-year-old pine stand in Sweden containing 20 metric tons of pine stumps and logs (Granhill and Lindberg 1980).

Higher nitrogen additions than reported above for conifers have been associated with hardwood decay. In the southern United States, 0.89 kg/ha/yr of nitrogen was added by only 11 tons of chestnut logs decaying on hardwood sites (Cornaby and Waide 1973). In New England hardwood forests Roskoski (1980), using an acetylene/nitrogen conversion ratio of 8.5 to 1, reported nitrogen gains from woody residue to range from a high of 2.2 kg/ha/yr in a 4-year-old stand to less than 0.2 kg/ha/yr in an 18-year-old stand. In an old-growth stand similar in age to our Montana sites, she calculated nitrogen fixation additions of 1.7 kg/ha/yr from 23 metric tons of woody residue. When these values are recalculated with the 3:1 acetylene/nitrogen conversion ratio used in our study, the nitrogen gains amounted to 6.2 kg/ha/yr in the 4-year-old stand, 0.6 kg/ha/yr in the 18-year-old stand, and 4.8 kg/ha/yr in the old growth forest. These differences in nitrogen additions with stand age were related to the amounts of woody residue present on the sites, not to variations in the nitrogen fixation rate. This finding is similar to our results for Douglas-fir sites.

While amounts of nitrogen fixed in decaying wood are low when compared to nitrogen gains from nodulated nitrogen-fixing plants such as *Ceanothus* or *Alnus* (Youngberg and Wollum 1976), total nitrogen additions over the life of the stand could be appreciable. Assuming a rotation age of 150 years, the nitrogen fixed in woody residue on the moist Douglas-fir site would replace the nitrogen removed by a conventional timber harvest (Stark 1979). Gains in wood nitrogen content could also increase the activity of the wood-decaying fungi (Kaarik 1974). Cornaby and Waide (1973) calculated that annual additions from nitrogen fixation amounted to 4.1 percent of the total nitrogen in decaying chestnut logs. Nitrogen inputs into the Douglas-fir logs we assayed were much less, ranging from 0.2 to 0.5 percent of the wood nitrogen content. Thus, greater nitrogen input from nitrogen-fixing bacteria may be a factor in the speed by which white rot fungi decay hardwood slash, as compared to the slower brown rot decay of conifer wood (Larsen and others 1980).

The current trend toward increased utilization of logging residue will reduce the amounts of large diameter woody material left to decay on site. This study has shown that the annual input of nitrogen associated with decaying wood would be small on the Douglas-fir sites studied. However, even a small nitrogen gain, coupled with the importance of decayed wood for mycorrhizae development and soil nutrient cycling, make such woody materials an important factor to be considered in site productivity studies.

Literature Cited

Aho, P. E., R. J. Seidler, H. J. Evans, and P. N. Rajau. 1974. Distribution, enumeration and identification of nitrogen-fixing bacteria associated with decay in living white fir trees. Phytopathology 64:1413–1420.

Broadstreet, R. B. 1940. A review of Kjeldahl determination of organic nitrogen. Chem Rev 27: 331.

Cornaby, B. S., and J. S. Waide. 1973. Nitrogen fixation in decaying chestnut logs. Plant and Soil 39:445–448.

Cowling, E. B., and W. Merrill. 1966. Nitrogen in wood and its role in wood deterioration. Can J Bot 44:1539–1554.

Day, R. J., and P. J. B. Duffy. 1963. Regeneration after logging in the Crowsnest Forest. Can Dep For Publ 1007, 31 p.

Granhall, V., and T. Lindberg. 1980. Nitrogen input through biological nitrogen fixation. *In* Structure and function of northern coniferous forests—an ecosystem study (T. Persson, ed), p 333–340. Ecol Bull (Stockholm) 32, 609 p.

Grier, C. C. 1978. A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can J Forest Res 8:198–206.

GRIER, C. C., and R. S. LOGAN. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol Mag 47:373–400.

HARDY, R. W. F., R. D. HOLSTEIN, E. J. JACKSON, and R. C. BURNS. 1968. The acetylene-ethylene assay for N-fixation: laboratory and field evaluation. Plant Physiol 43:1185–1207.

HARVEY, A. E., M. J. LARSEN, and M. F. JURGENSEN. 1979. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. Forest Sci 25:350–358.

HARVEY, A. E., M. J. LARSEN, and M. F. JURGENSEN. 1980. Ecology of ectomycorrhizae in northern Rocky Mountain forests. *In* Environmental consequences of timber harvesting in Rocky Mountain coniferous forests, p 188–210. USDA Forest Serv Gen Tech Rep INT-90, 526 p.

HUNGERFORD, R. D. 1980. Microenvironmental response to harvesting and residue management. *In* Environmental consequences of timber harvesting in Rocky Mountain coniferous forests, p 37–74. USDA Forest Serv Gen Tech Rep INT-90, 526 p.

JURGENSEN, M. F. 1973. Relationship between nonsymbiotic nitrogen fixation and soil nutrient status—a review. J Soil Sci 24:512–522.

JURGENSEN, M. F., M. J. LARSEN, and A. E. HARVEY. 1980. Microbial processes associated with nitrogen cycling in northern Rocky Mountain forests soils. *In* Environmental consequences of timber harvesting in Rocky Mountain coniferous forests, p 175–187. USDA Forest Serv Gen Tech Rep INT-90, 526 p.

KAARICK, A. A. 1974. Decomposition of wood. *In* Biology of plant litter decomposition. Volume One (C. H. Dickinson and G. J. F. Pugh, eds), p 129–174. Academic Press, London, 246 p.

KLAGES, M. G., R. C. MCCONNELL, and G. A. NIELSON. 1976. Soils of the Coram Experimental Forest. Mont Agric Exp Stn Res Rep 91, 43 p.

LARSEN, M. J., A. E. HARVEY, and M. F. JURGENSEN. 1980. Residue decay processes and associated environmental functions in northern Rocky Mountain forests. *In* Environmental consequences of timber harvesting in Rocky Mountain coniferous forests, p 157–174. USDA Forest Serv Gen Tech Rep INT-90, 526 p.

LARSEN, M. J., M. F. JURGENSEN, and A. E. HARVEY. 1978. N_2-fixation associated with wood decayed by some common fungi in western Montana. Can J Forest Res 8:341–345.

LARSEN, M. J., M. F. JURGENSEN, and A. E. HARVEY. 1982. N_2-fixation in brown-rotted soil wood in an intermountain cedar-hemlock ecosystem. Forest Sci 28:292–296.

MCFEE, W. W., and E. L. STONE. 1966. The persistence of decaying wood in humus layers of northern forests. Proc Soil Sci Soc Am 30:513–516.

MCNABB, D. H., and J. M. GEIST. 1979. Acetylene reduction assay of symbiotic nitrogen fixation under field conditions. Ecology 60:1070–1072.

NETER, J., and W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, Ill. 842 p.

PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO, and R. C. PRESBY. 1977. Forest habitat types of Montana. USDA Forest Serv Gen Tech Rep INT-34, 172 p.

ROSKOSKI, J. P. 1980. Nitrogen fixation in hardwood forests of the northeastern United States. Plant and Soil 54:33–44.

ROSKOSKI, J. P. 1981. Comparative C_2H_2 and $^{15}N_2$ fixation in deciduous wood litter. Soil Biol Biochem 13:83–85.

SCHINK, B., J. J. WARD, and J. G. ZEIKUS. 1981. Microbiology of wet wood: role of anaerobic bacterial populations in living trees. J Gen Microbiol 123:313–322.

SILVESTER, W. B., P. SOLLINS, T. VERHOEVEN, and S. P. CLINE. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. Can J Forest Res 12:646–652.

SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can J Forest Res 12:18–28.

SPANO, S. D., M. F. JURGENSEN, M. J. LARSEN, and A. E. HARVEY. 1982. Nitrogen-fixing bacteria in Douglas-fir residue decayed by *Fomitopsis pinicola*. Plant and Soil 68:117–123.

STARK, N. M. 1979. Nutrient losses from timber harvesting in a larch/Douglas-fir forest. USDA Forest Serv Res Pap INT-231, 41 p.

TAPPI. 1975. Water solubles in wood and pulp. TAPPI Standard Method T-207.

TRISKA, F. J., and K. CROMACK, JR. 1980. The role of wood debris in forests and streams. *In* Forests: fresh perspectives from ecosystem analysis (R. H. Waring, ed), p 172–190. Proc 40th Annu Biol Coll, Oreg State Univ, Oreg State Univ Press, Corvallis, 199 p.

YOUNGBERG, C. T., and A. G. WOLLUM II. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. Proc Soil Sci Soc Am 40:109–112.