Nitrogen fixation in woody residue of northern Rocky Mountain conifer forests

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N fixation rates, as estimated by the acetylene reduction technique, were determined for large woody residues on four old growth conifer sites in western Montana and northem Idaho. Residue loadings ranged from <50 Mg ha^{-1} on a warm, dry Douglas-fir site in Montana to >150 Mg ha^{-1} on a highly productive, wet, cedar–hemlocksite in northern Idaho. Lignin and carbohydrate analyses indicated that wood on these sites was being decayed primarily by brown rot fungi. Ethylene production rates increased on all sites as wood decay progressed. Assuming that N-fixing bacteria were active for 180 days year^{-1}, N fixed in woody residues ranged from a high of nearly 1.5 kg ha^{-1} year^{-1} on a cedar–hemlocksite to a low of 0.16 kg ha^{-1} year^{-1} on a Douglas-fir site. The application of the N fixation results from this study to the northern Rocky Mountain region indicated that the majority of stands in the Douglas-fir, subalpine fir, and cedar–hemlockcover types would have N gains <0.5 kg ha^{-1} year^{-1}. However, in some areas where residue loadings are heavy, such as overmature stands on cool, moist sites, or following harvesting, N gains could be much greater.

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Les auteurs ont mesuré les taux de fixation d'azote par la technique de réduction de l'acétylène dans des résidus grossiers de bois dans quatre forêts matures de coniféres de l'ouest du Montana et du nord de l'Idaho. La masse des résidus variait de <50 Mg ha^{-1} dans une station chaude et sèche de douglas au Montana à >150 Mg ha^{-1} dans une station humide, tès productive, de cèdres et pruches du nord de l'Idaho. Des analyses de lignine et d'hydrates de carbone ont indiqué que le bois dans ces stations était décomposé principalement par des champignons de carie brune. Les taux de production d'éthyène ont augmenté dans toutes les stations avec la progression de la décomposition. En présumant que les bactéries fixatrices d'azote ont été actives durant 180 jours par année, l'azote fixé dans les résidus ligneux a varié de 1,5 kg ha^{-1} an^{-1} dans une station de cèdres-pruches à 0,16 kg ha^{-1} an-' dans une station de douglas. L'application des résultats de fixation d'azote de cette étude à la partie nord de la région Rocky Mountain indique que la majorité des peuplements des types forestiers de douglas, de sapins subalpins et de cèdres–pruches auraient un taux de fixation d'azote de <0.5 kg ha^{-1} an^{-1}. Cependant, dans certains endroits où les résidus de coupe sont importants, comme dans les peuplements surannés en stations humides et froides ou après une coupe, les gains d'azote du systéme pourraient être plus élevés.

[Traduit par la revue]

Large woody debris is a major component of western U.S. coniferous forests and may equal or surpass other biomass in the forest floor (Harmon *et al.* 1986). Such woody residues can have major impacts on stand growth and development by influencing tree seedling establishment, mycorrhizal root activity, incidence of certain tree diseases, and animal activity (Harvey *et al.* 1980; Maser and Trappe 1984; Harmon *et al.* 1986; Jurgensen *et al.* 1986). Woody residues also have an important role in ecosystem nutrient cycling, especially acting as reservoirs of N and P in the forest floor (Grier 1978; Covington 1981).

Nonsymbiotic N-fixing bacteria associated with wood decay can affect the N status of forest sites. N fixation has been found to occur in woody residues of both hardwoods and conifers (Cornaby and Waide 1973; Larsen *et al.* 1978; Granhall and Lindberg 1980; Roskoski 1980; Silvester *et al.* 1982; Jurgensen *et al.* 1984) Most of these studies examined N fixation rates associated with the decay of a particular species of wood or the activity of certain decay fungi. Only in the hardwood forests of New England has the significance of N fixation in wood been considered in relation to the N economy of a North American forest ecosystem (Roskoski 1980). Consequently, a study was conducted to estimate the contribution of nonsymbiotic N fixation in large woody residues to the N supply of four conifer sites in westem Montana and northern Idaho. These sites were selected to represent the wide range of moisture and temperature conditions characteristic of this region.

Study areas

The study was conducted at three sites on the Coram Experimental Forest of northwestern Montana and one site on the Kaniksu National Forest near Priest Lake in northern Idaho. Each site supported a mature, undisturbed stand of mixed conifers at least 250 years of age.. Habitat types were designated in Montana according to Pfister *et al.* (1977) and in Idaho according to Daubenmire and Daubenmire (1968).

Douglas-fir climax (Montana)

This site was the driest and warmest of the ecosystems studied. The stand was made up almost entirely of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with an occasional western larch (*Larix occidentalis* Nutt.) present. Stand volume estimates averaged 243 m^3

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ha^{-1}. Habitat type designation was *Pseudotsuga menziesii/Physocarpus malvaceus* (PSME/PHMA). This site was located on a 25% south-facing slope at an elevation of 1140 m.

Cedar–hemlock climax (Montana)

Located on a north-facing slope, this site was wetter than the Douglas-fir climax. Site elevation was 1115 m with a slope of 15%. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir dominated the site with some western larch and western red cedar (*Thuja plicata* Donn ex D. Don) also present. Habitat type designation was *Tsuga heterophylla/Clintonia uniflora* (TSHE/CLUN). Stand volume averaged 439 m^3 ha^{-1}.

Subalpine fir climax (Montana)

At an elevation of 1465 m and on a 55% east-facing slope, this was the coolest, wettest site studied in Montana. Douglas-fir, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Englemann spruce (*Picea engelmannii* (Parry)), and western larch dominated the site. Stand volume averaged 300 m^3 ha^{-1}. Habitat type designation was *Abies lasiocarpa/Clintonia uniflora* (ABLA/CLUN).

Cedar–hemlock climax (Idaho)

This was the wettest and the most productive site studied with a stand volume of 850 m^3 ha^{-1}. Dominant trees were western hemlock and western red cedar with a scattering of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and Douglas-fir. Habitat type designation was *Tsuga heterophylla/Pachistima myrsinites* (TSHE/PAMY). The site had a **10–20%** northeast-facing slope at an elevation of 1200 m.

Methods

Wood samples were obtained around 10 permanent points evenly distributed throughout each study area. A random transect was run from each point to the nearest piece of downed woody residue (>7.62 cm). Three stages of wood decay were obtained for each piece of residue: (*i*) incipient, (*ii*) intermediate, and (*iii*) advanced. These decay stages were separated in the field on the basis of wood color and textural characteristics (Jurgensen *et al.* 1984). Five replicate samples of each decay type were placed in 20-mL glass Vacutainer tubes (Becton-Dickenson Division, Becton-Dickenson). Care was exercised to avoid incorporation of woody material from exposed surfaces. The temperature of each decay stage was recorded at time of sampling. Woody residues on all four sites were sampled in June, July, August, and September of 1977. The three sites in Montana were also sampled in September 1976. A total of 2850 wood samples were obtained over the course of the study. Woody residue weights on each study 'area were estimated using the planar intersect method described by Brown (1974).

N fixation rates were estimated using an adaption of the acetylene reduction assay (Hardy *et al.* 1973). Since the N-fixing bacteria associated with wood decay are reported to be either microaerophilic or anaerobic (Aho *et al.* 1974; Schink *et al.* 1981; Silvester *et al.* 1982; Spano *et al.* 1982), atmospheric oxygen introduced when the logs were cut open and wood decay stages sampled had to be removed. Within **2** h after sampling. tubes were evacuated and flushed with argon five times and filled with a mixture of 10% acetylene and 90% argon. This evacuation–flushing technique lowered oxygen concentrations in the tubes to the 1–3% range. One of the five replicate samples of each decay stage was not injected with acetylene to provide a control for monitoring endogenous ethylene production. The sample tubes were incubated in the dark for 24 h at temperatures measured in the residue at the time of sampling. Gas samples were removed from the 20-mL incubation tubes by 2-mL Vacutainer tubes and the wood sample was oven dried at 105°C for determination of dry weight and moisture content. The nature and extent of residue decomposition was determined by analyses for lignin, carbohydrate, and alkali soluble content on a composite of the five replicates for each decay class (Effland 1977; TAPPI 1983).

The gas samples were analyzed for acetylene and ethylene concentrations using a Varian Aerograph Series 2800 gas–liquid chromatograph fitted with an 80–100 mesh Poropak R column. The column

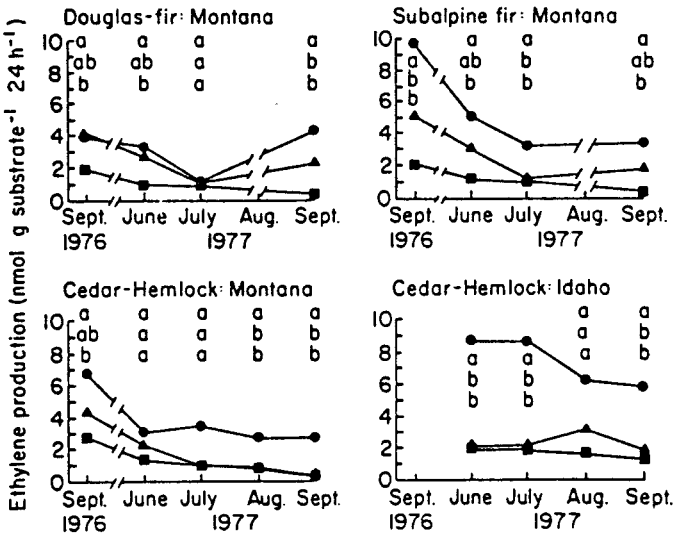

FIG. 1. Seasonal ethylene production rates in woody residues on four old growth conifer sites in western Montana and northern Idaho. ■, incipient decay; ▲, intermediate decay; ●, advanced decay.

temperature was maintained at 40°C with N 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). Endogenous ethylene production in the controls was subtracted from ethylene produced in the acetylene-injected samples. The possible error in background ethylene correction reported by Nohrstedt (1983) was not found when tested under the experimental conditions used in this study.

Analysis of variance was used to analyze the data. Decay class, site location, and sampling date were independent variables; ethylene production was the dependent variable. Scheffé's multiple comparison procedure was used to separate the means of the independent variables.

Results and discussion

N fixation rates

N fixation rates, as measured by ethylene production, were strongly related to the decay stage of the woody residues on all four sites. Ethylene production increased significantly as residue decay progressed (Fig. 1, Table 1). This pattern was evident at each sampling time. Wood moisture content also increased as decay progressed (Table l), indicating a positive relationship between moisture content and ethylene production. A similar wood moisture - ethylene production interaction has been found in other studies (Larsen *et al.* 1978; Roskoski 1980; Silvester *et al.* 1982; Jurgensen *et al.* 1984). Increased moisture levels with advancing decay would favor the activity of the anaerobic or microaerophilic N-fixing bacteria.

Ethylene production rates in woody residues were highest on the cedar-hemlock site in Idaho, but only minor differences were evident among the three Montana sites (Table 1). This was somewhat surprising considering the range of moisture and temperature conditions associated with these Montana habitat types. However, insignificant differences in the moisture contents of wood residues were found among the sites (Table 1). This lack of a site–moisture relationship may have been caused by above normal rainfall in this region of Montana during the study period. Decaying wood has also been shown to be much less affected by daily or even seasonal moisture changes than underlying soil horizons (Hungerford 1980).

Ethylene production rates from this study are similar to other reports for westem conifer ecosystems (Larsen *et al.* 1978;

TABLE 1. Ethylene production and moisture content in woody residues on four old growth conifer sites in western Montana and northern Idaho

Decay class	Douglas-fir (Montana)	Cedar–hemlock (Montana)	Subalpine fir (Montana)	Cedar–hemlock (Idaho)	Average
			Ethylene production (nmol C_2H_4 g^{-1} 24 h^{-1})		
Incipient	0.7*a*	0.8*a*	0.7*a*	1.7*b*	1.1*A*
Intermediate	2.1*m*	1.4*m*	2.0*m*	2.3*m*	1.9*B*
Advanced	3.0*s*	2.8*s*	3.9*s*	7.3*t*	4.4*C*
Average	2.0*x*	1.7*x*	2.3*x*	3.8*y*	
			Moisture content (%)		
Incipient	28*a*	34*a*	34*a*	31*a*	32*A*
Intermediate	57*m*	36*m*	54*m*	50*m*	46*A*
Advanced	134*s*	131*s*	191*s*	168*s*	155*B*
Average	75*x*	68*x*	96*x*	80*x*	

NOTE: Values are averaged over all sampling dates in 1977. Values followed by different letters are significantly different at the $P \leq 0.05$ level.

TABLE 2. Chemical properties of woody residue on old growth forest sites in western Montana and northern Idaho

	Decay class		
Chemical property	Incipient (%)	Intermediate (%)	Advanced (%)
Lignin	33.9*a*	36.0*a*	47.9*b*
Carbohydrate	60.0*l*	57.3*l*	43.3*m*
NaOH soluble	25.1*x*	29.0*x*	39.6*y*

NOTE: Values are averages for the four sites. No significant differences in the chemical properties of woody residue were found among sites. Values followed by different letters in the same row are significantly different at the $P \leq 0.05$ level.

TABLE 3. Woody residue weights and associated N additions from nonsymbiotic N fixation on four old growth forest sites in western Montana and northern Idaho

	Douglas-fir (Montana)		Cedar–hemlock (Montana)		Subalpine fir (Montana)		Cedar–hemlock (Idaho)	
Decayclass	Mg*	g N†	Mg	g N	Mg	g N	Mg	g N
Incipient	11.1	13	24.0	34	61.5	77	6.9	19
Intermediate	16.0	55	34.8	80	35.3	119	47.8	181
Advanced	18.0	91	24.4	115	48.9	319	99.6	1228
Total	45.1	159	83.2	230	145.7	515	154.3	1428

*Dry weight ha^{-1} of woody residues >7.6 cm in diameter.
†Total N fixed ha^{-1} in woody residue over a 180-day period.

Silvester *et al.* 1982; Jurgensen *et al.* 1984) but are much lower when compared with results from eastern forests. Cornaby and Waide (1973) reported average ethylene production rates of over 30 nmol C_2H_4 g^{-1} day^{-1} for decaying chestnut (*Castanea dentata* (Marsh) Borkh.) logs in North Carolina, while Roskoski (1980) found ethylene production values ranging from 20 to 80 nmol $C_2H_4g^{-1}$ day^{-1} during the summer for mixed hardwood –conifer residue in New England.

Lignin, carbohydrate, and alkali solubility analysis of the residues on all the sites indicated that the wood was being primarily decayed by brown rot fungi (Table 2). This group of fungi typically removes cellulose and hemicellulose while leaving lignin. Consequently, lignin concentration and alkali solubility increases and carbohydrate content decreases as wood decay progresses. In contrast, wood decay in eastern hardwood forests is primarily caused by white rot fungi (Jurgensen *et al.* 1986). These fungi generally degrade cellulose and lignin at the same rate and thus cause little change in the relative proportions of these wood components during decay (Larsen *et al.* 1980). Since N-fixing bacteria are unable to use these substrates as energy sources directly, they are dependent on low molecular weight carbon compounds produced by other microorganisms during wood decay. Differences in the metabolic processes and rates between brown rot and white rot fungi would likely affect

TABLE 4. Annual N gains reported in wood residues from nonsymbiotic N fixation

Location	Stand	Age (year)	Residue loading (Mg ha^{-1})	N gain (kg ha^{-1})
Montana[a, b]	Cedar–hemlock	>250	83	0.2
	Subalpine fir	>250	146	0.5
	Subalpine fir	>250	114	0.7
	Douglas fir	>250	49	0.3
	Douglas fir	>250	45	0.2
Idaho[a]	Cedar–hemlock	>250	154	1.4
Wyoming[c]	Lodgepole pine	110	20	<0.2
Sweden[d]	Scots pine	15	24	<0.1
	Scots pine	120	11	0.1
	Scots pine–N. spruce	160	4	<0.1
N. Carolina[e, f]	Mixed hardwoods	—	12	0.9
	Oak–hickory	—	—	1.6
N. Hampshire[g]	Northern hardwoods	4	39	2.2
		8	28	0.9
		18	7	<0.2
		40	8	0.4
		57	15	0.5
		>200	23	1.7

[a]Residue >7.5 cm in diameter (this study).
[b]Residue >7.5 cm in diameter (Jurgensen *et al.* 1984).
[c]Highly decomposed woody litter (Fahey *et al.* 1985).
[d]Twigs, branches, logs, and stumps (Granhall and Lindberg 1980).
[e]Values only for chestnut (*Castenea dentata*) logs (Cornaby and Waide 1973).
[f]Twigs, branches, and logs (Todd *et al.* 1975).
[g]All size residue from twigs to boles (Roskoski 1980).

the activity of N-fixing bacteria and may account for the regional differences in residue N fixation rates discussed earlier.

N gains from woody residue

Additions of N from nonsymbiotic N fixation associated with woody residue decay on these four conifer sites may be approximated by using the ethylene production rates and woody residue weights obtained in this study. A 3:1 conversion factor of ethylene production to N fixation was used for comparison with other studies, even though this ratio may give an overestimate of N gains (Roskoski 1981; Silvester et al. 1982). Estimated residue loadings ranged from <50 Mg ha^{-1} on the warm, dry Douglas-fir site in Montana to >150 Mg ha^{-1} on the wet cedar–hemlock site in northern Idaho (Table 3). Assuming that N-fixing bacteria are active for 180 days year, N fixed in woody residues ranged from a high of nearly 1.5 kg ha^{-1} year^{-1} on the cedar–hemlock site in Idaho to a low of 0.16 kg ha^{-1} year^{-1} on the Montana Douglas-fir site (Table 3). In Montana, N additions increased from the Douglas-fir site to the cool, moist, subalpine fir site. These increases were due mostly to increasing stand residue loadings and not to variations in the N fixation rate. In contrast, the large N gain in Idaho was caused by both high residue loadings and high N fixation rates.

N additions indicated in our study are similar to the amounts reported by other investigators for conifer residue but are lower than values found in hardwood stands (Table 4). All of these N gains were based on the theoretical 3: 1 ethylene to N conversion ratio, except Roskoski (1980) who used an ethylene to N ratio of 8.5:1. When her values were recalculated using the 3:1 conversation ratio, N additions ranged from a high of 6.2 kg ha^{-1} year^{-1} in the 4-year-old stand to a low of 0.6 kg ha^{-1} year^{-1} in the 18-year-old stand.

The application of the N fixation results from this study to a wider geographic area must necessarily account for the wide variation in site residue loadings found in this region. Residue weights on all the study sites were higher than regional averages but nowhere near the maximum for these forest cover types (Table 5). Regional estimates of N fixation in rotten wood were calculated using the ethylene production rates for the advanced decay stage and an average of the ethylene values for the incipient and intermediate decay stages was applied to the sound residue. Two estimates were obtained for the cedar–hemlock cover type by using ethylene rates from both the Montana and Idaho sites.

Since residue weights were related to forest cover type, N fixation showed the same pattern (Table 5). Even with these differences, the majority of stands in these northern Rocky Mountain cover types would have N gains <0.5 kg ha^{-1} year^{-1}. However, in some areas where residue loadings are heavy, such as overmature stands on cool, moist sites or following a timber harvest, N gains could be much greater. These N gains also did not include N fixation in tree stumps, which may be greater than that occurring in residues (Granhall and Lindberg 1980).

These estimates of N fixation in woody residue were based on ethylene production rates from 1977. Although it is not possible to determine how representative this year was of long-term N fixation gains on each site, considerably higher ethylene production on the Montana sites for September 1976 compared with September 1977 indicated that annual N additions could vary considerably (Fig. 1). However, even if the N fixation rates in residues were doubled or tripled, N additions would be low compared with the possible contributions from nodulated N-fixing plants such as *Ceanothus* or *Alnus* (Youngberg and Wollum 1976).

N-fixing plants are an important component of some northern Rocky Mountain forest ecosystems but may be lacking or be of low frequency on many other sites (Jurgensen *et al.* 1979). On

TABLE 5. Possible N additions to three northern Rocky Mountain forest types from nonsymbiotic N fixation in woody residues[a]

Cover type	Residue weight (Mg ha^{-1}) Mean	Residue weight (Mg ha^{-1}) Range[b]	Advanced decayed wood (%)	N added (g N ha^{-1}/180 days^{-1}) Mean	N added (g N ha^{-1}/180 days^{-1}) Range
Douglas-fir	28.9	0–248	63	116	0–995
Subalpine fir	53.4	0–369	52	240	0–1660
Cedar–hemlock	65.9	0–512	57	230[c]	0–1790
				557[d]	0–4325

[a]Woody residues >7.6 cm in diameter in National Forests on the west side of the Continental Divide (from Brown and See 1981).
[b]Maximum value of residue loading estimated to be three standard deviations of the highest mean from National Forests on the west side of the Continental Divide (from Brown and See 1981).
[c]Using ethylene production rates from cedar–hemlock site in Montana.
[d]Using ethylene production rates from cedar–hemlock site in Idaho.

these sites, the replacement of N losses due to fire, timber removal, or soil leaching would have to come from nonsymbiotic N fixation in soil and wood, N present in rainfall, or fertilizer applications. The amounts of N fixed in the soil are similar to N gains in woody residues (Jurgensen *et al.* 1979). N additions in precipitation can add in excess of 50 kg ha^{-1} year^{-1} near urban or industrialized areas, but these values normally average between 0.5 and 2 kg ha^{-1} year^{-1} in the northern Rocky Mountains (Tiedemann *et al.* 1978; Clayton and Kennedy 1985).

Assuming an average stand rotation age of 150 years, the N gains from nonsymbiotic N fixation and precipitation would replace N losses from most conventional timber harvests in the region (Stark 1979; Clayton and Kennedy 1985). However, the trend toward increased residue utilization will remove greater amounts of N and reduce nonsymbiotic N fixation in both wood and soil (White and Harvey 1979; Jurgensen *et al.* 1980). These N losses would be greater on sites where fire is used as a site preparation technique or after a wildfire (Wells *et al.* 1979; Harvey *et al.* 1987) and should be considered when evaluating the environmental impacts of such management practices.

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