Asymbiotic nitrogen fixation in litter from Pacific Northwest forests[1]

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Asymbiotic nitrogen fixation in litter was assayed by acetylene reduction across a range of 25 forested sites in the Willamette Valley and Oregon Cascade and Coast ranges and periodically over a year at two Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations in the Willamette Valley. Laboratory experiments showed that optimal conditions for N fixation by Douglas-fir litter were 200% moisture content and 22°C. Annual fixation was 1.08 ± 0.13 kg/ha at one Willamette Valley plantation, 0.39 ± 0.06 kg/ha at the other. Fixation rates at the other 23 sites, which were sampled less frequently, ranged from 0 to 5 g N ha^{-1} day^{-1} and exceeded trace levels at only six sites, indicating annual totals much less than those at the Willamette Valley plantations. At four coastal and valley sites sampled by litter layer, older L layer Douglas-fir litter fixed the most N per gram dry weight. Percent N, percent C, and the C:N ratio of that litter layer did not differ significantly among sites or correlate with N-fixation rates. Forest-floor litter in most Northwest forests fixes no more than trace amounts of N, at most ~1 kg N ha^{-1} $year^{-1}$. These amounts are smaller than N input from precipitation.

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La fixation de l'azote (N) asymbiotique dans la litière a été analysée par réduction de l'acétylène pour une variété de 25 stations forestières dans la vallée Willamette ainsi que dans les monts Cascade et côtiers de l'Orégon et de façon périodique durant 1 année dans deux plantations de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de la vallée Willamette. Les essais en laboratoire ont indiqué que les conditions optimales permettant la fixation de N par la litière de douglas étaient une teneur en humidité de 200% et une température de 22°C. La fixation annuelle était de 1,08 ± 0,13 kg/ha à une plantation de la vallée Willamette et 0,39 ± 0,06 kg/ha à l'autre. Les taux de fixation aux autres 23 stations, dont l'échantillonnage fut moins fréquent, ont varié de 0 à 5 g ha^{-1} $jour^{-1}$ de N et ont dépassé le niveau de traces à seulement six d'entre elles, indiquant par là les sommes bien inférieures à celles rencontrées dans les plantations de la vallée Willamette. À l'endroit de quatre stations côtières et de la vallée où l'échantillonnage se fit par couches de litière, les plus vieilles couches L de litière de douglas ont fixé le plus de N par gramme de poids sec. Le pourcentage de N, celui de C, ainsi que le ratio C : N de cette couche de litière ne différaient pas de façon significative parmi les stations et n'étaient pas corrélés avec les taux de fixation de N. La litière du parterre forestier dans la plupart des forêts du Nord-ouest américain ne fixe guère plus des quantités à l'état de traces de N et tout au plus 1 kg ha^{-1} an^{-1} de N. Ces quantités sont inférieures à l'intrant de N provenant des précipitations.

[Traduit par la revue]

Introduction

Because nitrogen limits tree growth at many sites in the U.S. Pacific Northwest (Ballard 1979), maintaining N reserves is of considerable interest to forest managers and ecologists. One-time occurrence of wildfire or logging and site preparation can remove 300–1000 kg/ha of N (Brown *et al.* 1973; Miller *et al.* 1976), whereas precipitation adds <200 kg/ha over the course of a 100-year rotation (Johnson *et al.* 1981). Early successional symbiotic N fixers, especially red alder (*Alnus rubra* Bong.) and ceanothus (*Ceanothus velutinus* Dougl.), may add 1000 to >5000 kg/ha over a rotation (Davey and Wollum 1979), but they do not occur at all sites. Where these symbiotic N fixers are absent, asymbiotic N fixers have sometimes been viewed as potential long-term sources of N that offset leaching, fire, and denitrification. Although asymbiotic fixation has been reported in soil, litter, and decaying wood and from foliage surfaces (Hardy *et al.* 1973; Larsen *et al.* 1978; Granhall and Lindberg 1978, 1980; Rennie and Rennie 1983), results vary widely when extrapolated to a yearly basis. Low rates of asymbiotic fixation (~1 kg ha^{-1} $year^{-1}$) occur in logs in the Pacific Northwest (Silvester *et al.* 1982), but rates in litter have not been measured.

Objectives of the current study were (*i*) to examine asymbiotic N-fixation rates in litter under various temperature–moisture regimes in the laboratory, and (*ii*) to survey asymbiotic N-fixation rates in litter across a variety of Pacific Northwest forest types, periodically in one habitat, and by litter layer.

Methods

Temperature–moisture experiments

So that proper incubation conditions for the rest of the study might be determined, effects of temperature and moisture on N fixation by litter layers were measured over a range of conditions in the laboratory.

Litter was collected from 10 randomly chosen locations in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantation near Adair, Oregon, on August 21, 1981. We separated litter into L and F layers. The L layer comprised L_1 litter, which consisted of freshly fallen, light golden-brown needles, resting on top of L_2 litter, which consisted of light grey needles. The F layer comprised F_1 litter, forming a dark grey crust (when dry) of partially decomposed needles that held together in cakes up to 10 cm in diameter when picked up, which overtopped F_2 litter, consisting of dark grey, loose, partially decomposed needles. Hereafter in

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TABLE 1. Descriptions of the 25 habitat-sampling sites and levels of nitrogen fixation by litter

Region by site name	Stand age or age-class (in 1982)	Dominant tree species[a]	Habitat type[a]	Elevation (m)	Reference[b]	N fixation[c]		Fig. 3 identifying letter
						Field	Optimal	
Willamette Valley								
Adair	24 year	Psme	Coco/Brvu	90	1	*	+ + + +	—
Monmouth	24 year	Psme	Coco/Brvu	120	1	*	+	—
Cascade Range								
H.J. Andrews Experimental Forest								
Reference stand 2	Old growth	Psme	Rhma-Bene	480	2	oto +	—	A
Reference stand 12	Old growth	Tshe	Abam/Vaal/Coca	1040	2	ooo	o	—
Lookout Creek	Mature	Alru	Rusp/Pomu	850	2	oooo	o	—
Suttle Lake	Old growth	Psme, Pipo	—	1130	—	+ to	+	B
Bull Run (Fox Creek)	Old growth	Tshe	Pomu/Oxor	670	1	oo	t	—
Squaw Creek	Old growth	Tshe	Rhma/Gash	1170	1	—	o	—
Mt. Rainier (Ipsut Creek)	Old growth	Tshe	Abam/Vaal	980	1	o	o	—
Wildcat Mt. RNA (silver fir)[d]	Old growth	Abam	Abpr/Clun	1370	1	ooo	o	—
Wildcat Mt. RNA (noble fir)	Old growth	Abpr	Abpr/Clun	1370	1	oott	+	—
Wolf Rock	Old growth	Abam	Abpr/Actr	1130	1	o	o	—
Metolius RNA (old)	Old growth	Pipo	Putr/Stoc	880	1	oooo	+ +	—
Metolius RNA (young)	Young	Pipo	Putr/Stoc	950	1	o	+ o	—
Warm Springs	Old growth	Pipo	—	—	—	—	+	—
Santiam Lava Flats	Mature	Pico	Aruv	1160	1	ooo	oo	—
Coast Range								
Marys Peak (Woods Creek)								
Douglas-fir (old)	Old growth	Psme	Coco/Adbi	610	3	ooo + +	+ t	C
Douglas-fir (mature)	Mature	Psme	Coco/Adbi	500	3	o +	—	D
Hemlock (old)	Old growth	Tshe	Acci/Pomu	610	3	oooo	tt	—
Hemlock (young)	<20 years	Tshe	Acci/Pomu	610	3	o	—	—
Alder	Mature	Alru	Rusp/Pomu	270	3	oooo	o	—
McDonald Forest	Old growth	Psme	Hodi	340	3	—	+	—
Black Rock	Mature	Psme	Gash-Pomu	270	1	t +	+	E
Neskowin Crest RNA	Old growth	Pisi	Tshe/Gash-Blsp	400	3	oot +	o	F
Cascade Head	Mature	Alru	Rusp	120	1	ooo	o	—

[a] Abbreviations as defined by Garrison *et al.* (1976).
[b] 1, Franklin and Dyrness 1973; 2, Hawk *et al.* 1978; 3, Juday 1976.
[c] —, No samples; o, no measurable activity; t, trace of activity; +, significant activity; *, significant activity on numerous sampling dates. Each symbol except asterisk indicates one sampling date. Field, samples incubated at ambient temperature and moisture; optimal, samples incubated at 22°C and 200% moisture content (optimum for Adair site Douglas-fir).
[d] RNA, Research Natural Area.

the temperature–moisture experiments, because the L layer included principally L_2 litter and only a small residual of L_1 litter, the designation L layer is used. The designation F layer refers to both F_1 and F_2 litter.

Litter was brought to the laboratory, air dried at 22°C for 5 days, and stored at 22°C for up to 4 weeks. Two parallel experiments were then conducted. Samples (90 for L layer, 156 for L + F; see Heath 1985) were incubated in 1-quart wide-mouth jars at the desired temperature (range, 0–40°C); a 20-g sample filled about one-third of each jar. Air-dried litter (three to four replicates) was brought to the desired moisture content (range, 10–250%) by adding the required amount of distilled water to each jar. So that water could soak in and the bacterial population stabilize its rate of N fixation, litter was preincubated at the desired temperature (±2.5°C) for 50–70 h. A 2-week time trial with four replicates showed that N fixation stabilized after 48 h except for a 4th-day peak 40% higher than the 2nd-day peak (Heath 1985). We found that 22°C and 200% moisture content were optimal incubation conditions for Douglas-fir litter from Adair, and used those conditions in habitat sampling under laboratory conditions and in litter-layer and soil sampling.

Habitat sampling

Litter was collected in 1981 and 1982 from 24 sites in Oregon and one (Mount Rainier) in Washington, spanning a range of climatic zones and forest types (Table 1). The litter was primarily leaves but also included small twigs, bud scales, insect frass, and moss, if present, and excluded woody debris >3 mm in diameter. The H layer, consisting of black organic matter in which needles were almost unrecognizable, was included where present. Most sites were sampled several times, and all except Squaw Creek, McDonald Forest, and Warm Springs were sampled at least once in spring or fall when litter was moist and litter temperature was >5°C. Two sites, Wildcat Mountain and Suttle Lake, were also sampled in winter under snow.

Litter samples from three or four randomly chosen points at each site were incubated in the laboratory under simulated field conditions. Litter temperature was measured at three points per site. Samples were stored in plastic bags in coolers from 1 to 48 h (except those from Mount Rainier and Bull Run, which were stored 3 weeks) at field litter temperature ±5°C and *in situ* moisture content until incubation. Samples were oven-dried after incubation to determine field moisture content.

An additional four litter samples per site were incubated in the laboratory under the conditions we had determined optimal (22°C, 200% moisture content). Samples were first air dried to standardize moisture content, then rewetted to 200%. Up to 3 weeks were required to air dry some samples. Some air-dried samples were stored for up to 1 additional month at 22°C before rewetting.

Periodic sampling

Litter from the Douglas-fir plantation near Adair was periodically collected and incubated during 1981 and 1982. Annual rainfall at nearby Hyslop Field Laboratory averages 108 cm, of which 6.1% falls between June and October, and mean annual air temperature is 11°C (Kelly Redmond, Oregon State University Climatic Research Institute, personal communication).

The Adair stand, whose trees (2-0 stock, local seed source) were planted at 2.2-m spacings in March 1958, was chosen because the litter layer was nearly pure Douglas-fir needles and because the site was convenient to Corvallis. The Douglas-fir formed a closed canopy with little other vegetation beneath, although some Himalayan blackberry (*Rubus discolor* Weihe & Nees) had established in openings where trees had died. Nineteen percent of the area had a moss cover >75%. Large woody debris and large rocks were absent. The litter was a relatively uniform carpet of Douglas-fir needles on top of mineral soil with no humus. Mean litter conditions for the 302-day period during which N fixers were active were 7.6°C and 151% moisture content. We sampled in a flat 15 × 76 m portion of the stand buffered from surrounding fields on all sides by 2 to 20 rows of trees of the same seed source.

A Douglas-fir plantation near Monmouth, about 20 km north of Adair, provided a replicate site for periodic sampling. Planted at the same time as the Adair stand but from a different local seed source, the trees formed a closed canopy with little vegetation beneath. Unlike at Adair, trees had been pruned within the last 2 years, and slash covered the forest floor. Thirty-one percent of the area had a moss cover >75%. We sampled in a 17 × 17 m portion (7 × 7 rows of trees) buffered on all sides by two rows of trees from the same seed source.

Between August 1981 and 1982, litter was sampled on 23 dates at Adair and 18 dates at Monmouth. Samples were collected at 2- to 3-week intervals (up to 31 days when litter was frozen or dry) from 10 random locations at each site and stored in a cooler for 0.5–4 h before transfer to incubation chambers. Ambient temperature rocks were added to the cooler to stabilize the temperature. Litter moisture, temperature, and mass per area were measured on each sample date. To calculate annual N input at Adair and Monmouth, we divided the entire study period into intervals centered on each sampling date, multiplied the number of days in each sampling interval by the mean N-fixation rate for the sampling date, and then summed over the intervals. Zero values were assumed for two winter dates and when litter was dry.

Litter-layer and soil sampling

Litter (L, F, and H layers, as previously defined) and mineral soil were collected in late August and early September 1981 from three randomly chosen points at each of four sites — (*i*) Marys Peak (old-growth Douglas-fir with some western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)), (*ii*) Adair (young Douglas-fir plantation previously described), (*iii*) McDonald Forest (old-growth Douglas-fir with some grand fir (*Abies grandis* (Dougl.) Lindl.)), and (*iv*) Marys Peak (mature western hemlock) — so that N-fixation rates in the various litter layers might be differentiated. The mineral soil (below the H layer) was sampled to a depth of 5 cm.

Samples from each layer at each site were composited and then subsampled (three replicates). Each litter sample was air dried at 22°C for 2–12 days and then brought to 200% moisture content before incubation to allow the N-fixer population to stabilize. Mineral soil samples were incubated at three moisture levels (36%, field capacity; 45%, close to saturation; and 200%, under water) because we had not determined the optimal conditions for incubating mineral soil. Because mineral soil is denser than litter, 20-, 60-, and 200-g soil samples were incubated to provide a wide range of headspace volumes.

Acetylene reduction

N fixation was assayed by acetylene reduction, as described by Silvester *et al.* (1982). Acetylene (C_2H_2) generated with water and calcium carbide was injected through a serum stopper into each 1-quart jar containing litter, bringing the atmosphere to 10% C_2H_2. Jars were incubated in the dark for 6 h; tests comparing light with dark incubation showed no significant difference in fixation rates. After incubation, a gas sample was withdrawn from each jar, and ethylene and acetylene were measured with a Hewlett-Packard[4] 5830A gas chromatograph (GC) fitted with a flame-ionization detector and a 2-m, 80–100 mesh Poropak R column[3] at 70°C. N_2 (40 mL/min) served as carrier gas and acetylene as an internal standard (McNabb and Geist 1979). Ethylene standards were used to calibrate the GC. Endogenous ethylene production and background ethylene levels were checked routinely and subtracted from measured ethylene production values. Litter samples were oven-dried after incubation. Acetylene reduced was then converted to N fixed (per unit dry mass) by dividing by 3.52, a mean ratio determined by ^{15}N labelling of decaying boles at the H.J. Andrews Experimental Forest, Oregon (Silvester *et al.* 1982).

[4]Mention of trade names or commercial products does not constitute endorsement by the authors or Oregon State University.

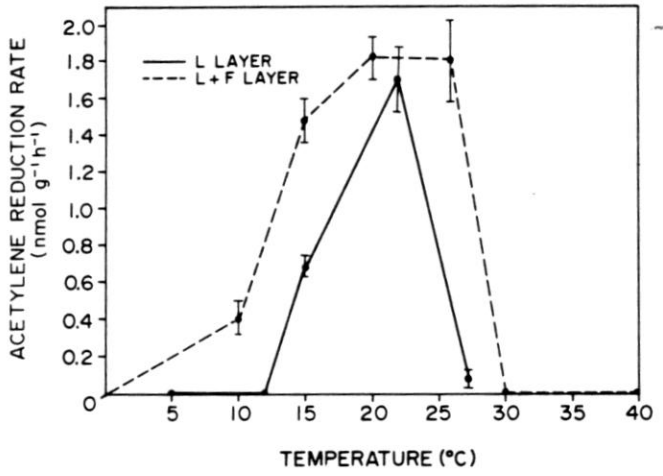

FIG. 1. Effect of temperature on acetylene reduction in L layer and combined L and F layer litter gathered in August 1981 from the Douglas-fir plantation at Adair, Oregon. Values for the L layer are means over four moisture contents (50, 100, 150, 200%); those for the L + F layer are means over five moisture contents (50, 90, 130, 170, 210%). Error bars indicate 1 SE.

Results

Temperature-moisture experiments

L layer litter reduced less acetylene than the L + F layer at most temperature and moisture levels (Figs. 1, 2). L layer acetylene reduction (AR) peaked at 22°C and was sharply lower at 27°C. AR by the L + F layer maintained a constant high rate between 20 and 26°C. A moisture threshold for AR in both the L and L + F layers was evident between 10 and 50% (Fig. 1). (Data from periodic sampling confirmed that this threshold was about 35%.) Above that moisture threshold, AR increased and then, except for samples at 23°C, leveled out above about 170%. When moisture content was below 130%, AR by the L + F layer was negligibly affected by temperature between 15 and 26°C.

Habitat sampling

Litter reduced more than trace amounts (<0.2 nmol g^{-1} h^{-1}) of acetylene under simulated field conditions at only 8 of 25 sites sampled (Table 1). Seven of the eight sites were dominated by Douglas-fir, one by Sitka spruce. Ponderosa pine and noble fir litter reduced small amounts, and western hemlock litter trace amounts, when incubated under the conditions we had determined to be optimal.

Periodic sampling

No acetylene was reduced at Adair when litter was dry, i.e., from July to late September 1981, and again in late July 1982 (Fig. 3). AR rate was assumed to be zero in late December and January 1981 when litter was frozen, on the basis of results from the temperature–moisture experiments and because samples collected in spring and incubated in the laboratory under snow we brought in did not reduce acetylene. AR rate fluctuated erratically during other times of year (Fig. 3). Rates at Monmouth were consistently lower than at Adair, although litter temperature and moisture conditions were similar (Fig. 4). In all, litter temperature and moisture conditions explained 69% ($p < 0.01$; $n = 18$) of the annual variation in AR rate at Adair and Monmouth. At Adair, litter dry mass averaged 18.3 ± 0.6 Mg/ha (95% confidence interval) with 31 ± 7% C and 0.9 ± 0.2% N,

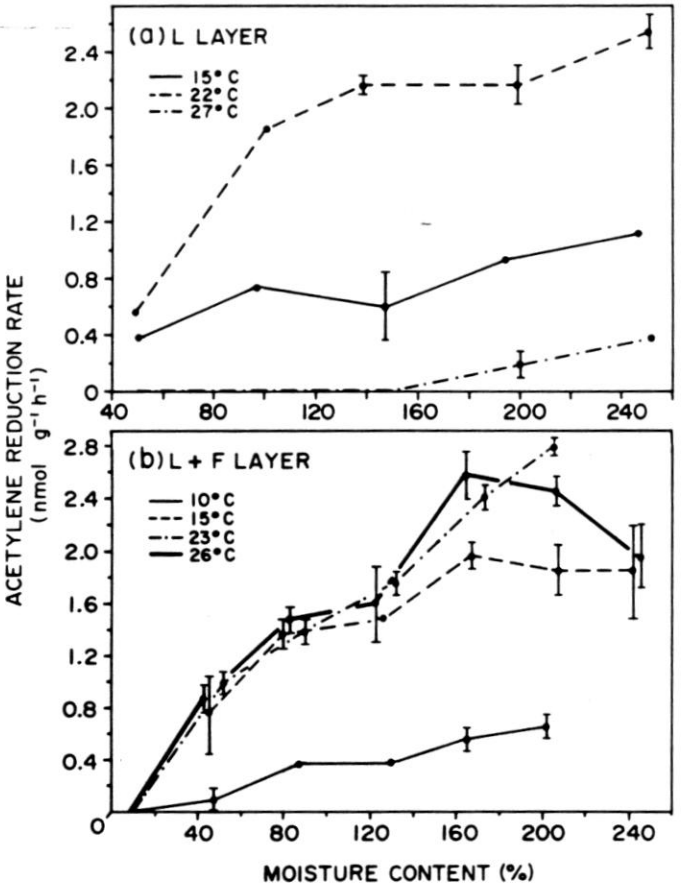

FIG. 2. Effect of moisture on acetylene reduction in (*a*) L layer litter and (*b*) combined L and F layer litter gathered in August 1981 from the Douglas-fir plantation at Adair. Rates at 5, 8, and 12°C for *a* and 2, 30, and 40°C for *b* were zero, irrespective of moisture content. Error bars indicate 1 SE. Error bars were omitted when SE was too small to be shown clearly.

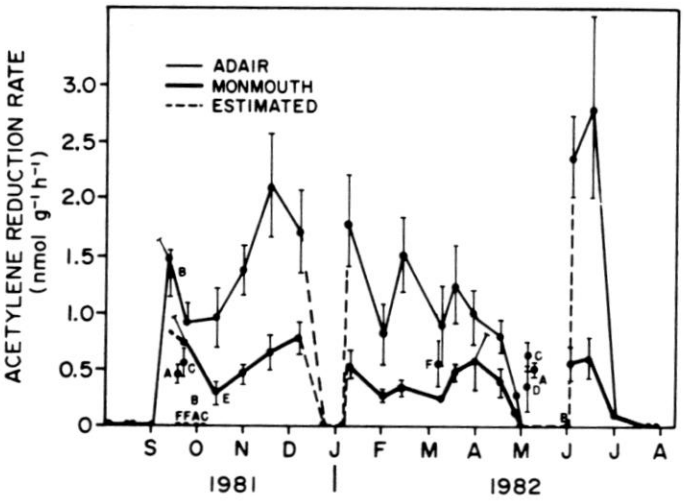

FIG. 3. Seasonal pattern of acetylene reduction in litter from the Douglas-fir plantations at Adair and Monmouth, Oregon. Each point is the mean of 10 samples. Additional sites, sampled less frequently, are denoted by letters A–F (as listed in Table 1). Error bars indicate 1 SE.

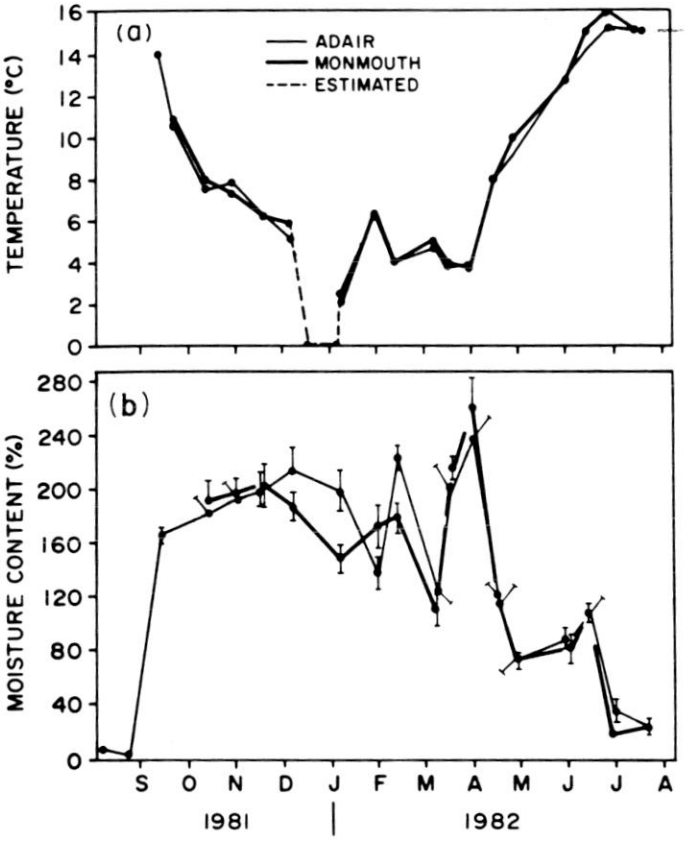

FIG. 4. Seasonal pattern of (*a*) temperature and (*b*) moisture content of litter from the Douglas-fir plantations at Adair and Monmouth. (*a*) Each point is the mean of three values; SE is $<1°C$ for all points. (*b*) Error bars indicate 1 SE.

giving a C:N ratio of 33 ± 6 (Heath 1985). At Monmouth, litter dry mass averaged 12.3 ± 0.8 Mg/ha with 31 ± 2% C and 0.9 ± 0.1% N, giving a C:N ratio of 34 ± 2. At both sites, AR rates >0.023 kg ha^{-1} day^{-1} were associated with higher C levels ($p = 0.06$) and with higher C:N ratios ($p = 0.08$). On the basis of an N fixation to AR ratio of 3.52, N fixation totalled 1.08 ± 0.13 kg ha^{-1} year^{-1} at Adair and 0.39 ± 0.06 kg ha^{-1} year^{-1} at Monmouth (95% confidence interval).

Moss-covered litter usually reduced less acetylene than did surrounding litter. Sixty (25%) of the samples collected after December 21, 1981, at Adair and Monmouth had moss cover >75%. Of those, 49 reduced acetylene at a rate below the mean AR rate for that day, 10 clustered around the mean, and 1 reduced acetylene at 151% of the mean.

Litter-layer sampling

AR was restricted, for the most part, to the L_2 layer at all four sites sampled by litter layer (Table 2). Trace activity in adjacent layers could have been due to incomplete separation of the layers during sampling. The L + F layer at Adair reduced acetylene at a rate about equal to that of the L_2 layer in the litter-layer sampling despite dilution by the other more massive but less active layers.

Discussion

Our habitat and periodic sampling produced little evidence that asymbiotic N fixation by litter accounts for significant N input in Pacific Northwest forests. Even at Adair and Monmouth, where fixation was readily measurable, the input was only 0.4–1.1 kg ha^{-1} year^{-1}, barely enough to offset amounts of N typically lost in leaching (Johnson *et al.* 1981; Sollins and McCorison 1981). Litter at the other sites appeared to fix even less N, although it is hard to know for certain because we sampled at only a few points in time (Fig. 3). Several sites had values as high as or higher than those at Adair and Monmouth, but most of these sites were at high elevation where cold winters are likely to inhibit N fixation during much of the year. The large seasonal variability (Fig. 3) suggests that many values reported from other forests worldwide should be viewed with caution because they are often based on material collected at only one point in time (e.g., Jorgensen and Wells 1971; Cornaby and Waide 1973; Jorgensen 1975; Silvester 1978; Larsen *et al.* 1978), although some have used an experimentally determined Q_{10} to take into account annual variation in temperature (e.g., Granhall and Lindberg 1978, 1980).

Factors accounting for the large AR differences among sites across the Pacific Northwest are unclear. The two most active sites, Adair and Monmouth, were young, monospecific, single-provenance stands at low elevation in the Willamette Valley. Yet even these apparently similar stands had annual fixation patterns that barely overlapped. Spatial variability in acetylene reduction was substantial (SEs were 10–40% of the mean, $n = 10$) and might be even greater in multispecies stands on complex topography.

We found some evidence that N fixers at Adair adapted to seasonal changes in climate, although they may simply have responded to changing substrate composition. The temperature threshold differed considerably in summer and winter. Summer L layer litter at Adair fixed only trace amounts of N below 12°C (Fig. 1), whereas L + F litter gathered in winter remained active down to 2.5°C (Fig. 3). More data are needed to confirm this change. Further evidence for adaptation can be seen by comparing N fixation by Adair litter collected in late summer and incubated under "laboratory" conditions with that collected periodically and incubated under "field" conditions (Table 3). AR rates became higher under field than laboratory conditions as the season progressed. Studies that measure annual N fixation should account for seasonal changes in substrate and bacterial population behavior.

More sampling in young stands elsewhere in the Pacific Northwest and in mixed stands in and adjacent to the Willamette Valley might yield N fixation rates as high as those at Adair and Monmouth. Stands without western hemlock would be good candidates to examine because hemlock may allelopathically inhibit N fixation (Rose *et al.* 1983); in fact, the Suttle Lake site, which lacked hemlock, yielded the highest single fixation rate of all Cascade and Coast Range sites. The coastal Sitka spruce forest, which also produced a few high values, might be favorable because it lacks the cold winters and dry summers of most of the other sites. Although N fixation in litter varies greatly among Pacific Northwest habitats, 1 kg ha^{-1} year^{-1} appears to be close to the maximum.

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TABLE 2. Acetylene reduction (nmol g^{-1} h^{-1}, mean ± 1 SE) by litter and soil for the four sites surveyed by litter layer

Source	Marys Peak (Douglas-fir + hemlock)	Adair (Douglas-fir plantation)	McDonald Forest (Douglas-fir + grand fir)	Marys Peak (hemlock)
Litter layer				
L_1	No layer	0.6 ± <0.1	No layer	No layer
L_2	0.9 ± <0.1	2.8 ± 0.1	0.6 ± 0.1	<0.2
F_1	0.3 ± <0.1	0.3 ± <0.1	<0.2	No sample
F_2	No layer	0.9 ± <0.1	<0.2	No sample
H	<0.2	No layer	<0.2	No sample
Total litter profile	<0.2	2.8 ± 0.1	No sample	<0.2
Mineral soil (top 5 cm)	<0.2	<0.2	<0.2	No sample

TABLE 3. Acetylene reduction (AR) rates (nmol g^{-1} h^{-1}) for litter collected in August and for litter collected periodically at Adair and incubated under comparable temperature and moisture conditions

Laboratory conditions (August litter)		Field conditions (periodically collected litter)			
°C/% moisture	AR rate[a]	Date	°C/% moisture	AR rate[b]	AR rate difference
15.0/168	2.0	27 Sept. 1981	14.1/165	1.5	−0.5
9.5/166	0.6	8 Oct. 1981	10.6/173	0.9	0.3
9.5/166	0.6	28 Oct. 1981	7.5/181	0.9	0.3
2.0/210	0.0	21 Jan. 1982	2.5/199	1.8	1.8
9.5/131	0.4	13 Feb. 1982	6.3/135	0.8	0.4
2.0/210	0.0	25 Feb. 1982	4.0/223	1.5	1.5
15.0/80	1.4	15 June 1982	12.9/88	2.4	1.0
15.0/126	1.5	27 June 1982	14.1/107	2.8	1.3
15.0/22	0.0	4 Aug. 1982	15.0/22	0.0	0.0

[a] Data from Figs. 1 and 2.
[b] Data from Fig. 3.

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