



Biogeochemistry of Adjacent Conifer and Alder-Conifer Stands

Dan Binkley; Phillip Sollins; Randy Bell; Don Sachs; David Myrold

Ecology, Vol. 73, No. 6 (Dec., 1992), 2022-2033.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199212%2973%3A6%3C2022%3ABOACAA%3E2.0.CO%3B2-%23>

Ecology is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

BIOGEOCHEMISTRY OF ADJACENT CONIFER AND ALDER–CONIFER STANDS¹

DAN BINKLEY

Department of Forest Sciences, Colorado State University, Fort Collins, Colorado 80523 USA

PHILLIP SOLLINS, RANDY BELL, AND DON SACHS

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

DAVID MYROLD

Department of Crop and Soil Science, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. To determine the long-term effect of alder on soil fertility, biogeochemical fluxes were measured and calculated for two pairs of adjacent, 55-yr-old stands dominated by conifers, primarily Douglas-fir (*Pseudotsuga menziesii*), and by conifers and nitrogen-fixing red alder (*Alnus rubra*). At a low-fertility site in the Wind River Experimental Forest in southwestern Washington, biomass of the alder–conifer stand (289 Mg/ha) exceeded that of the conifer stand (171 Mg/ha), and the aboveground net primary production (ANPP) of the alder–conifer stand ($10.3 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) was more than twice that of the conifer stand ($4.8 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). At a more fertile site in the Cascade Head Experimental Forest in western Oregon, both biomass and ANPP were higher than at Wind River, and biomass and ANPP were higher in the conifer stand (584 Mg/ha and $19.2 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) than in the alder–conifer stand (342 Mg/ha and $10.7 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). Nitrogen accretion in the alder–conifer stand at Wind River averaged $54 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the 52 yr since stand establishment, with a current rate of N fixation of $\approx 75 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. For the alder–conifer stand at Cascade Head, N accretion averaged $73 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for 55 yr, with a current N-fixation rate of $85 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.

The cycling of all nutrients appeared very malleable under the influence of alder. At Wind River, return of nutrients in fine litterfall in the alder–conifer stand ranged from 1.5 (P) to 7.9 (N) times those in the conifer stand; whereas at Cascade Head, these ratios ranged from 1.7 (S) to 4.2 (N). Nutrient-use efficiencies (kilograms of ANPP per kilogram of nutrient uptake) were generally lower for the alder–conifer stands at both sites. Denitrification appeared negligible ($< 0.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) in all stands. Leaching of organic plus inorganic N ranged from $\approx 5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the conifer stand at Wind River, to $50 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the alder–conifer stand at Cascade Head.

Key words: denitrification; Douglas-fir; immobilization; mineralization; mixed-species stands; nitrification; nitrogen; nitrogen fixation; nutrient-use efficiency; Pacific Northwest; red alder.

INTRODUCTION

The ability of alder (*Alnus* spp.) to improve soil fertility has been recognized for centuries (reviewed by Tarrant and Trappe 1971). Alders were grown successfully in a nitrogen-free medium in the late 19th century (Hiltner 1896), the fixation of nitrogen (N_2) in root nodules was demonstrated with ^{15}N in the 1950s (Bond 1955), and the *Frankia* actinomycete responsible for the reduction of N_2 was isolated in the 1970s (Baker and Torrey 1979, Lechevalier and Lechevalier 1979). Despite this long history of interest in alders, long-term biogeochemical effects of alders have been examined in only a few case studies (reviewed by Van Miegroet et al. 1989a). On sites where the rate of N supply limits forest productivity, the addition of alders to conifer stands increased productivity, levels of N and exchangeable base (alkali + alkaline earth) cations,

and N availability, without decreasing soil pH. Where growth is less limited by N on fertile sites, forest N capital and availability have also increased, but with no corresponding increase in productivity. On these more fertile sites, N fixation has led variously to depletion of exchangeable base cations, high rates of nitrate leaching, and marked decreases in soil pH.

Within-ecosystem fluxes of nutrients other than N also increase under the influence of alder. For example, Cole et al. (1978) reported that the rate of calcium return in aboveground litterfall was almost 10 times greater under N-fixing red alder (*Alnus rubra* Bong.) than under an adjacent plantation of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], even though there was less exchangeable calcium in the soil under alder. The accelerated cycling of calcium was accompanied by a four-fold increase in the concentration of Ca^{2+} in soil solution under the alder (Van Miegroet 1986).

Objectives in this study were: (1) to characterize within-system nutrient fluxes in adjacent conifer and

¹ Manuscript received 7 January 1991; revised and accepted 10 January 1992.

alder-conifer stands at two sites, taking into account some processes not considered in earlier studies of alder forests; and (2) to examine effects of alder on nutrient-use efficiencies. Effects of the alder on soil chemistry and acidification at these sites were reported separately (Binkley and Sollins 1990).

METHODS

Site description

Both study sites are part of the USDA Forest Service system of Experimental Forests. C. Bernsten, J. Booth, S. Greene, L. Isaac, W. Meyer, R. Miller, M. Nance, and R. Tarrant have been instrumental in the establishment and maintenance of the stands we examined. The study site at the Wind River Experimental Forest is in southwestern Washington at ≈ 625 m elevation and $45^{\circ}49'$ N latitude. Precipitation averages 2500 mm/yr, of which about three quarters falls as snow between November and March. A snowpack of 1–2 m is common. The soil is a silty clay loam Andic Haplumbrept, unclassified as to series, which has developed in Tertiary andesitic or rhyolitic parent materials with some pumice and basaltic gravel of Pleistocene origin (Miller and Tarrant 1983). The site lies at the eastern edge of the 120 000-ha Yacolt Burn, which occurred in 1902, and burned again in 1922 and 1927 (Tarrant 1961, Tarrant and Miller 1963, Miller and Murray 1978). The terrain is rolling, with slopes ranging from 0 to 60%, and the site index (expected height of dominant tree species) for Douglas-fir in the absence of red alder is 25 m at 50 yr. The area was planted in 1929 with Douglas-fir seedlings from an off-site seed source at a density of 1700 trees/ha. In 1933 a 22-m wide strip was interplanted with 2-yr-old seedlings of red alder (also from an off-site seed source) at a density of 3000 trees/ha in order to provide a firebreak across the plantation (Tarrant 1978). Earlier reports on these plots provide information on mensuration (Tarrant 1961, Miller and Murray 1979), production (Binkley and Greene 1983), soil chemistry (Tarrant and Miller 1963), and Douglas-fir nutrition (Tarrant 1961, Reid 1983). Others describe effects of thinning and fertilization for the Douglas-fir portion of the plantation (Harrington and Reukema 1983, Miller and Tarrant 1983, Binkley and Reid 1984, 1985).

Our Cascade Head site lies within the Cascade Head Experimental Forest at ≈ 180 -m elevation near the coast of Oregon ($45^{\circ}03'$ N). Precipitation averages 2400 mm/yr, with very little falling as snow. Temperatures average about 20°C in July and 10°C in January; summer temperatures rarely exceed 27°C , and freezing temperatures are uncommon (Berntsen 1961). The soil, a well drained Typic Dystrandept of the Astoria series of silty clay loams, has developed from tuffaceous siltstone overlying basalt. The experimental plots are located within an 8-ha stand that occupies moderate slopes of $\approx 15\%$ with a southwesterly aspect. The site

index for Douglas-fir in the absence of alder is 40 m at 50 yr. The land was cleared for agriculture and then abandoned in 1925. By 1935 the naturally regenerated, 8-yr-old stand contained about 4500 conifers/ha—a mixture of Douglas-fir, western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Sitka spruce [*Picea sitchensis* (Bong.) Carr.]—and 3000 red alder/ha. A 0.2-ha plot (#17) was thinned in 1935 to a density of about 2800 stems/ha by removing all alders and many of the smaller conifers, and another 0.2-ha plot (#11) was left unthinned as control. Tree height and diameter have been measured periodically since the plots were established during 1935–1937 (Berntsen 1961). Information on soil chemistry (Franklin et al. 1968), litterfall (Tarrant et al. 1969), forest production (Binkley and Greene 1983), tree nutrition (Reid 1983), and soil physical structure (Strickland et al. 1988) is available.

Mass and nutrient content of vegetation and forest floor

At Wind River we established a 200-m transect through the middle of the alder-conifer strip, and placed a parallel transect 30 m to the west in the pure conifer stand. Ten variable-radius (prism) plots were located on alternate sides of the transect, at random distances from random points along each transect. The diameter (at 1.4 m height) of all trees within the prism field was measured. At Cascade Head we measured the diameters of all trees within each 0.2-ha plot. At both sites, understory biomass was determined by clipping and weighing all understory vegetation within 10 1-m² quadrats (located adjacent to soil pits, see below: *Soils*) in each of the two stands. Forest floor biomass was determined by weighing material collected within a 0.1-m² quadrat at 20 locations in each stand. All biomass values are ash-free, determined from loss-on-ignition (450°C , 4 h).

At Wind River, stand biomass in 1985 was calculated from the diameter of each tree included in the prism plots. At Cascade Head we used data from the 1985 remeasurement of the 0.2-ha plots. Regression equations relating biomass to diameter were available for all major species: Douglas-fir (Gholz et al. 1979), red alder (G. Koerper, *personal communication*), western hemlock (Sachs 1983), and Sitka spruce (B. Bormann, *personal communication*). All equations are on file at the Forest Science Department Data Bank, Oregon State University (Corvallis, Oregon, USA).

To determine the nutrient capital of each stand, we sampled the major components of each tree species in each stand, and multiplied measured nutrient concentrations times the biomass of the component. Foliage was obtained with a shotgun from 10 Douglas-fir and 10 red-alder branches in each stand. For the less important western hemlock and Sitka spruce, six foliage samples of each species were composited into three samples of each. Samples of wood, branches, and bark were obtained from nine trees of each species in each

stand, and composited into three samples per species, component, and stand for chemical analysis. Samples (0.250 g) were block-digested by adding 10 mL of ~ 9 mol/L H_2O_2 in three stages. H_2SO_4 and Na_2SO_4 were then added, and digestion continued at $365^\circ C$ for 6 h after clearing. The digests were analyzed for N with a Lachat Continuous Flow System (Lachat Instruments, Milwaukee, Wisconsin, USA), and for other elements by inductively coupled plasma spectrometry. Sulfur (S) was determined with a LECO S Analyzer (Leco Instruments, Saint Joseph, Michigan, USA). Recovery of elements from standard samples of *Pinus* needles from the U.S. National Bureau of Standards was always within 10% of the expected value, except for potassium (K), which was always within 20%. We found that complete recovery of N from woody materials [gauged by the recovery of N from wood standards (Sollins et al. 1987)] required prolonged digestion (6 h at $365^\circ C$ after clearing, with H_2O_2 added at .2 h after clearing) in a mixture of concentrated H_2SO_4 , $CuSO_4$, and K_2SO_4 . The average nutrient concentration should be accurate within 10% for foliage (except perhaps for K), and within 20% for woody materials.

Soils

Ten soil pits were dug in each stand at random distances (on alternate sides) from random points along a transect through the middle of each plot. The pits were $\approx 1 \times 0.5$ m, to a depth of > 1 m. Soil samples for chemical analysis were taken from 0.0–0.15 m, 0.15–0.40 m, 0.40–0.65 m, and 0.65–0.90 m depths at Wind River, and 0.0–0.15 m, 0.15–0.30 m, 0.30–0.60 m, and 0.60–0.90 m depths at Cascade Head. These depths corresponded roughly to the Ah, B1, B2, and C1 horizons. The volume of large rocks in the soil was calculated by measuring the mass of all rocks removed from each pit, and mass was then converted to volume on the basis of the density of a subset of the rocks. Bulk density of the rock-free soil was determined by weighing samples of known volume taken from the pit walls. Total soil C was determined with a LECO-12 carbon analyzer; total N by Kjeldahl digestion followed by ammonium analysis with a Science Associates (Pleasantville, New York, USA) autoanalyzer.

Litterfall and whole-tree mortality

The annual rate of fine litterfall (leaves, twigs < 20 mm diameter, and miscellaneous matter) was measured with 10 1-m^2 littertraps located adjacent to each soil pit in each stand. In addition, woody material (> 20 mm diameter) was collected monthly from 10 1-m^2 quadrats on the forest floor from which all woody litter had been removed initially. Fine and woody litterfall was collected monthly from 23 December 1985 through 31 January 1987 (≈ 13 mo) at Cascade Head, and from 20 April 1986 through 5 May 1987 (≈ 12 mo) at Wind River. The standard errors of the means for litterfall

mass were generally on the order of 5 to 15% of the means, so we are confident our estimates are good approximations of litterfall rates during our sampling period; we do not know the magnitude of annual variations in litterfall, so our rates may differ from long-term averages.

At Cascade Head, whole-tree mortality between 1980 and 1985 was determined from remeasurements of the permanent plots. Similar data were not available for Wind River, so we calculated mortality based on the change in the number of trees (assumed to be of average size) between 1980 and 1985 using our data for 1985 and values for stem density in 1980 from elsewhere in the same stands (R. Miller [USDA Forest Service], *personal communication*). The mortality estimates for Cascade Head should be very accurate, whereas those for Wind River are probably moderately accurate.

Nitrogen fixation

Nitrogen fixation in the alder–conifer stands was calculated from data on nodule biomass and from measurements of acetylene reduction repeated six times between 30 May 1986 and 10 October 1986 for Wind River by us, and eight times between 21 April 1985 and 16 February 1986 for Cascade Head by Kim (1987). Nodule biomass was determined by sieving the soil removed from the 10 soil pits in each alder–conifer stand. Acetylene reduction was determined at each sampling time by incubating 10 to 30 nodulated root segments (≈ 20 mm in length) in 1-L jars for 1 h in 10% acetylene (McNabb and Geist 1979). After incubation a headspace gas sample was collected and analyzed for ethylene and acetylene with a gas chromatograph. To calculate N fixation we multiplied the nodule biomass by the average rate of acetylene reduction, assuming a ratio of 3 mol C_2H_4 per mole of N_2 fixed, then multiplied the average rate per hour by the mass of nodules per hectare and the number of hours in 4 mo (at Wind River) or 6 mo (at Cascade Head). Ethylene was not detectable when non-nodulated roots were incubated with acetylene. Given the multiple estimates involved in the N-fixation estimate, we expect the acetylene-reduction estimates of N-fixation to be within about 50% of the true rates.

Denitrification

On four dates, denitrification was assayed by pounding 20 polyvinyl chloride (PVC) plastic tubes into the soil in each stand to a depth of 0.15 m, capping the tubes, extracting 10 mL of air, and replacing it with 10 mL of C_2H_2 (pulling and pushing the syringe to distribute the C_2H_2 [after Robertson and Tiedje 1984]). The soil cores were incubated in the field for 20 h, and headspace samples were analyzed for N_2O by gas chromatography. Given our limited sampling periods and intensities, and the very high temporal and spatial variations commonly found for denitrification (e.g., Rob-

ertson and Tiedje 1984, Struwe and Kjoller 1991), we hope our estimates are within a factor of 2 of the true rates.

Solution sampling

Soil solution was collected at a depth of 0.7–0.8 m with tension-free lysimeters in each of the 10 pits per stand. Our first design for tension-free lysimeters used 0.30-m lengths of 0.15 m diameter PVC tubes, cut in half longitudinally to form a trough. These troughs were capped on one end, a small drip tube was inserted through the cap, and the other sharpened end was pounded into the pit walls at a slight uphill angle. Almost none of these lysimeters collected water even after heavy rainfall, so a second design was used: square pans (0.25 × 0.25 m and 0.10 m deep) made of stainless steel, covered with a fiberglass mesh screen (Radulovich and Sollins 1987). Each lysimeter was installed in a pit wall by excavating a cavity, forcing the lysimeter upward against the ceiling of the cavity so that the rim penetrated about 10 mm upward into the soil, and then packing soil beneath the lysimeter to hold it in place. Leachate collected in the lysimeters and dripped through a small tube into 4-L plastic bottles. Samples were collected monthly from September 1986 through November 1987, and analyzed for ammonium, nitrate, and organic N. Organic N was determined as Kjeldahl N minus ammonium N; recovery of organic N from EPA water standards was 95%.

We did not attempt to measure the flux of water past 0.80 m depth. Instead, we used estimates of evapotranspiration for nearby watersheds to convert nutrient concentrations to nutrient fluxes. At Fox Creek, a gauged USDA Forest Service watershed at 840–1070 m elevation ≈ 50 km south of the Wind River site, evapotranspiration averages ≈ 650 mm/yr (Harr 1976). Precipitation at Wind River during 1987 was 1500 mm (about 65% of the long-term average), and we therefore estimated that leaching past 0.80 m depth was ≈ 850 mm (1500 mm minus 650 mm of evapotranspiration). At the Alsea watershed, at 135–490 m elevation and ≈ 50 km inland from the Cascade Head site, evapotranspiration averages ≈ 500 mm/yr (Harr 1976). Precipitation at Cascade Head was 2120 mm during 1987 (about 88% of the long-term average), so we estimated that ≈ 1620 mm of water leached past 0.80 m depth. Uncertainty in estimates of nitrogen leaching derives mainly from errors in estimating annual average concentrations in leachates; we expect errors in the estimate of quantity of water leaching to be less critical. We expect the overall leaching estimates to be within 50% of the true values.

Aboveground net primary production (ANPP) and nutrient uptake

Aboveground net primary production (ANPP) was calculated as the tree increment between 1980 and 1985 divided by the number of years, plus the annual pro-

duction of alder leaves (=all leaf biomass) and conifer leaves (assumed to average 20% of total foliage biomass for all species; Grier and Logan 1977). Note that mortality was not added to this sum because biomass increments were based on within-tree changes of trees present in 1985, rather than on differences in total stand biomasses for the two periods. Tree increments between 1980 and 1985 were calculated for Wind River from the radial growth measured on cores from each tree in the prism plots. For Cascade Head, tree increments were calculated from the diameters measured in 1980 and 1985. We have high confidence in the accuracy of biomass and increment estimates at both locations.

Nutrient content of annual biomass production was calculated by multiplying biomass production times concentration for each tissue type. Nutrient uptake was calculated as the sum of nutrients in annual production of woody materials plus the nutrient content of fine litterfall (Cole and Rapp 1981). The difference between the nutrient uptake and the quantity needed to produce biomass is presumably met from retranslocation or other sources. The estimate of uptake therefore depends upon the accuracy of each component of the calculation, and year-to-year variations in litterfall nutrient content may introduce substantial errors. Nonetheless, we are confident that the calculations we present allow realistic comparisons across the four stands in our study, and also comparisons with other studies that have used the same approach (e.g., Cole and Rapp 1981, Johnson and Lindberg 1992).

RESULTS

Biomass and nutrient content

At Wind River the overstory biomass and nutrient content in the alder–conifer stand exceeded that in the adjacent conifer stand (Table 1). The biomass of conifers alone was greater in the alder–conifer stand (177 Mg/ha) than in the conifer stand (151 Mg/ha); adding the alder biomass (92 Mg/ha) raised the total biomass of the alder–conifer stand to nearly twice that of the conifer stand. For the understory, the pattern was reversed. In fact, the salal (*Gaultheria shallon* Pursh) understory in the conifer stand contained half as much N as the overstory.

At Wind River the organic matter content of vegetation plus forest floor in the alder–conifer stand was nearly twice (1.7 times) that in the conifer stand (Table 1). The ratio for Ca was the same as for biomass, whereas the ratios for N, S, Mg, and K were higher, and the ratio for P was lower. The difference between stands in amounts of cations in vegetation and forest floor was small, and probably of little ecological significance.

At Wind River the forest floor and mineral soil were much richer in N where alder was present, whereas amounts of other nutrient elements differed little (Table 1). From the difference in N content of the mineral

TABLE 1. Biomass and nutrient contents of the Wind River (Washington) stands, with 10 plots/stand.

Component	Organic matter (Mg/ha)		Mean nutrient contents (kg/ha)					
	\bar{X}	SE	N	P	S	Ca	Mg	K
Conifer stand								
Foliage	7.6	0.5	67	22.5	13.1	87	9.0	58
Branches	17.5	1.2	22	5.5	3.5	80	5.6	24
Stems	126	10.5	20	5.9	12.6	36	3.4	5
Understory	4.7	0.9	52	0.6	...	36	8.6	12
Forest floor								
>4 mm	10.4	0.9	55	0.6	6.6	64	20.9	12
<4 mm	5.2	0.4	49	0.3	4.5	32	10.3	4
Vegetation + forest floor	171		265	35.4	40.3	335	57.8	115
Soil (0–0.9 m)†	156		1960	12 800	5520	6240
Alder–conifer stand								
Alder								
Foliage	1.0	0.2	28	1.7	1.7	10	3.8	18
Branches	11.3	2.2	44	6.0	5.7	25	4.9	28
Stems	79.4	12.7	118	11.6	39.7	100	21.4	81
Douglas-fir								
Foliage	7.0	0.7	85	9.9	7.2	68	11.8	55
Branches	17.8	1.6	21	3.4	2.7	60	7.2	12
Stems	152	12	40	13.4	15.2	36	2.9	6
Understory	0.6	0.2	7	0.9	...	4	1.0	4
Forest floor								
>4 mm	20.2	3.0	200	0.9	17.1	120	40.3	20
<4 mm	9.1	0.9	150	0.3	9.6	56	18.2	8
Vegetation + forest floor	289		693	48.1	98.9	479	111.5	232
Soil (0–0.9 m)†	212		4340	12 800	5760	5460

* No data.

† From Binkley and Sollins (1990); assumes soil organic matter is 50% C.

soil in the two stands, we calculated an average N accretion rate of $45 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the alder–conifer stand during the 52 yr since its establishment. A similar value, $41 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, was reported for the stand at age 26 (Tarrant and Miller 1963). Taking account of the difference in biomass and forest-floor N in the two stands raises our accretion estimate for the 52-yr period to $54 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.

At Cascade Head the aboveground biomass of the alder–conifer stand was much less than that of the pure conifer stand (Table 1), owing in large part to high rates of self-thinning mortality in the very dense alder–conifer stand early in its development (Binkley and Greene 1983). Conifer biomass in the alder–conifer stand (154 Mg/ha) was $<1/3$ that of the conifer stand (530 Mg/ha). Even including the biomass of alders (164 Mg/ha), the total biomass of the alder–conifer stand was only 60% that of the conifer stand.

At Cascade Head the organic-matter content of vegetation plus forest floor in the alder–conifer stand was slightly more than half (59%) that in the conifer stand (Table 2). The corresponding ratios for P and Ca were close to that for organic matter, whereas the ratios for the other nutrients were larger: 1.3 for S and 1.1 for N and Mg. The small difference of $\approx 8 \text{ kmol}$ of charge/ha in the base cations in vegetation plus forest floor

was negligible (within measurement error) relative to the charge difference of 290 kmol/ha in the exchangeable base cations in the soil. Assuming the soils in the conifer and alder–conifer stands were similar 55 yr ago, the lower level of base cations in the soil in the alder–conifer stand indicates substantial cation leaching (discussed by Binkley and Sollins 1990).

At Cascade Head the presence of alder raised the N content of the mineral soil. On the basis of the difference in N content of the mineral soil, plus a small difference in N content of the vegetation, we calculate an N accretion rate of $73 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in the alder–conifer stand during the 55 yr since its establishment. This rate is >2.5 times that calculated by Franklin et al. (1968) for the same stand at age 40 yr. Our values for soil N content are lower than theirs for both stands, but the precision of their estimates is likely low. They sampled soils from only three pits per stand, and estimated bulk density from only one pit per stand (bulk density values were not reported).

Nitrogen fixation

Current rates of N fixation (based on acetylene reduction assays) in the alder–conifer stands were $75 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for Wind River and $85 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for Cascade Head. Nodule biomass averaged 325 ± 155

TABLE 2. Biomass and nutrient content of the Cascade Head (Oregon) stands.

Component	Organic matter (Mg/ha)	Mean nutrient contents (kg/ha)					
		N	P	S	Ca	Mg	K
Conifer stand							
Alder							
Foliage	0.4	10	0.6	0.7	1	0.8	4.7
Branches	5.6	22	1.3	2.8	5	1.7	7.5
Stems	22	31	3.2	4.4	9	4.6	18.5
Douglas-fir							
Foliage	12	150	21.5	12.3	74	21.6	81.4
Branches	36	52	9.1	9.5	61	9.5	27.9
Stems	362	98	28.2	30.8	38	4.7	14.5
Western hemlock							
Foliage	1.6	18	2.7	1.6	7	2.2	9.8
Branches	0.6	1	0.2	0.1	2	0.2	0.9
Stems	37	11	13.3	3.1	20	3.8	24.2
Sitka spruce							
Foliage	3.1	32	5.2	2.9	12	3.4	29.4
Branches	8.3	13	2.4	2.2	35	2.6	9.1
Stems	69	25	7.8	6.0	52	4.8	4.6
Understory	1.1	13	2.2	...*	0	0	0
Forest floor							
>4 mm	18	131	13.7	5.4	108	36.0	18.0
<4 mm	8	112	10.1	5.7	48	16.0	8.0
Vegetation + forest floor	585	719	121.5	87.5	472	111.9	258.5
Soil (0–0.9 m)†	468	9800	3680	4560	1599
Alder–conifer stand							
Alder							
Foliage	2.1	57	3.5	3.4	21	7.7	36.9
Branches	25	97	13.2	11.6	56	10.8	62.6
Stems	137	202	19.9	66.6	172	36.7	139.2
Douglas-fir							
Foliage	3.2	40	4.7	3.2	32	5.4	25.8
Branches	9	14	2.2	1.6	31	2.4	8.4
Stems	85	22	7.5	7.1	20	1.6	3.4
Western hemlock							
Foliage	0.7	7	1.1	0.6	3	0.9	4.1
Branches	0.3	0	0.1	0.0	1	0.1	0.4
Stems	1.4	0	0.5	0.1	1	0.2	0.9
Sitka spruce							
Foliage	2.8	29	4.7	2.9	10	3.1	26.6
Branches	5.8	9	1.7	1.7	24	1.8	6.3
Stems	46	17	5.3	4.6	35	3.3	3.1
Understory	2.4	26	4.3	...	18	4.3	21.8
Forest floor							
>4 mm	12	119	7.4	5.1	72	24.0	12.0
<4 mm	9	182	10.2	6.6	54	18.0	9.0
Vegetation + forest floor	342	821	86.3	115.1	550	120.3	360.5
Soil (0–0.9 m)†	518	13 720	2520	1776	1755

* No data.

† From Binkley and Sollins (1990); assumes soil organic matter is 50% C.

kg/ha (mean \pm 1 SE) at Wind River and 250 ± 75 kg/ha) at Cascade Head. The rate of acetylene reduction to ethylene averaged about $8.3 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ for 4 mo at Wind River (Fig. 1), where moisture stress in July and August is common. At the wetter Cascade Head site the acetylene reduction rate remained high throughout the summer, averaging $8.5 \mu\text{mol} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ for 6 mo. Given the multiple uncertainties in the over-

all estimates of annual N fixation rates, we expect the true values are within 40 kg/ha of the estimates.

Net primary production and nutrient uptake

At Wind River the ratio of ANPP in the alder–conifer stand to that in the conifer stand was 2.1 (Table 3). Ratios of nutrient uptake in the alder–conifer stand to uptake in the conifer stand were: 8.3 for N, 1.6 for

P, 6.0 for S, 2.2 for Ca, 3.3 for Mg, and 5.5 for K. At Cascade Head the ANPP was lower in the alder-conifer stand than in the conifer stand (a ratio of 0.6, Table 4), which was opposite the pattern at Wind River. Despite the lower productivity of the alder-conifer stand, uptake was greater in the alder-conifer stand for most elements, especially N (ratio of 3.4), K (3.1), and Mg (2.1). Across all four stands the uptake of N (from the soil and from N-fixation) to produce aboveground biomass ranged from a low of $5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the Wind River conifer stand to a high of $83 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the alder-conifer stand at Cascade Head.

Litterfall and mortality

At Wind River the mass of fine litterfall (needles plus twigs and other small materials) in the alder-conifer stand was 2.6 times that in the conifer stand (Table 5). The P content of litterfall differed less than litterfall mass between the stands, whereas the differences in litterfall nutrient contents were much greater than the mass difference for the other elements. The

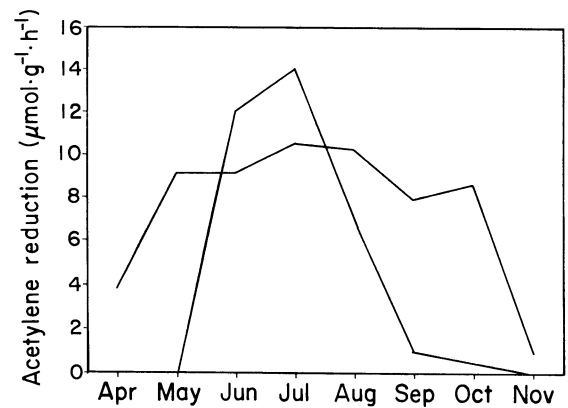


FIG. 1. Seasonal course of acetylene reduction activity in alder-conifer stands at Wind River, Washington (line commencing in May) and Cascade Head, Oregon (commencing in April).

ratios (alder-conifer stand to conifer stand) were 7.9 for N, 6.0 for S, 2.6 for Ca, 3.3 for Mg, and 4.5 for K. Unless decomposition were limited by P availability, the higher concentrations of nutrients in litterfall in the

TABLE 3. Annual production and nutrient flux for the Wind River (Washington) stands.

Component	Organic matter (Mg/ha)	Nutrient flux (kg/ha)					
		N	P	S	Ca	Mg	K
Conifer stand							
Litterfall							
Foliage + twigs	1.2	4.8	4.0	0.7	10.8	1.4	2.5
Woody	2.8	4.9	1.2	0.8	7.6	0.6	1.5
Total	4.0	9.7	5.2	1.5	18.4	2.0	4.0
Whole-tree mortality	0.3	0.0	0.0	0.0	0.1	0.0	0.0
Aboveground net primary production							
Foliage	1.5	13.9	4.7	2.9	18.2	1.9	12.1
Branches	0.2	0.2	0.1	0.1	0.4	0.0	0.1
Stems	1.9	0.3	0.1	0.2	0.6	0.1	0.1
Understory	1.2	3.5	0.6	0.0	0.0	0.0	0.0
Total	4.8	17.9	5.5	3.2	19.2	2.0	12.3
Uptake	...	5.3	4.2	1.0	11.8	1.5	2.7
Alder-conifer stand							
Litterfall							
Foliage + twigs	3.1	37.8	5.9	4.2	28.0	4.6	11.3
Woody alder	3.9	23.7	2.4	1.1	22.0	1.9	3.5
Woody conifer	2.7	13.0	1.8	0.8	8.8	1.1	1.9
Total	9.7	74.5	10.1	6.1	58.8	7.6	16.7
Whole-tree mortality	2.5	3.4	0.4	1.1	2.9	0.6	2.3
Aboveground net primary production							
Alder							
Foliage	1.0	27.6	1.7	1.7	10.4	3.8	18.0
Branches	0.2	0.7	0.1	0.1	0.4	0.1	0.4
Stems	2.6	3.8	0.4	1.3	3.2	0.7	2.6
Douglas-fir							
Foliage	1.5	18.6	2.2	1.7	14.9	2.5	12.1
Branches	0.4	0.6	0.1	0.1	1.3	0.1	0.4
Stems	4.4	1.2	0.4	0.4	1.0	0.1	0.2
Understory	0.2	0.1	0.1	0.0	0.3	0.1	0.4
Total	10.3	52.6	5.0	5.3	31.5	7.4	34.1
Uptake	...	44.1	6.9	6.0	32.9	5.6	14.9

TABLE 4. Annual production and nutrient flux of the Cascade Head (Oregon) stands.

Component	Organic matter (Mg/ha)	Nutrient flux (kg/ha)					
		N	P	S	Ca	Mg	K
Conifer stand							
Litterfall							
Foliage + twigs	2.4	18.2	4.0	2.0	10.0	2.3	4.4
Woody	4	11.8	2.4	1.5	9.2	1.9	3.1
Total	6.4	29.4	6.5	3.6	19.2	4.1	7.6
Whole-tree mortality	0.4	0.4	0.1	0.1	0.2	0.1	0.2
Aboveground net primary production							
Foliage	5.5	69.2	9.3	6.2	28.9	8.9	40.4
Branches	1.1	1.8	0.3	0.3	2.5	0.3	1.0
Stems	14.0	4.1	1.5	1.4	3.2	0.4	1.5
Understory	0.3	0.8	0.1	0.0	0.6	0.1	0.6
Total	19.2	95.1	11.2	7.9	35.2	9.7	43.5
Uptake	...	24.1	5.6	3.4	13.8	3.0	6.5
Alder-conifer stand							
Litterfall							
Foliage + twigs	4.2	77.0	8.4	3.3	12.8	5.5	17.2
Woody alder	12.0	47.6	4.7	3.3	20.4	5.3	8.4
Woody conifer	5.1	19.6	3.1	1.4	10.0	2.4	3.8
Total	21.3	144.2	16.2	8.0	43.2	13.2	29.4
Whole-tree mortality	1.8	2.0	0.3	0.6	2.3	0.3	1.2
Aboveground net primary production							
Alder							
Foliage	2.2	60.0	3.7	3.8	22.5	8.2	39.1
Branches	0.5	1.8	0.2	0.2	1.0	0.2	1.1
Stems	1.5	2.2	0.2	0.7	1.9	0.4	1.5
Conifers							
Foliage	1.8	21.0	2.8	2.0	13.1	2.6	14.9
Branches	0.4	0.5	0.1	0.1	1.3	0.1	0.4
Stems	3.7	1.1	0.4	0.4	1.4	0.1	0.2
Understory	0.6	0.2	0.2	0.0	1.1	0.2	1.2
Total	10.7	86.8	7.6	7.2	42.3	11.8	58.4
Uptake	...	82.6	9.3	4.7	18.4	6.3	20.4

alder-conifer stand should allow substantially faster mineralization of nutrients from the litter.

At Cascade Head the mass of fine litterfall in the alder-conifer stand was 1.7 times that in the conifer stand (Table 6). Corresponding ratios for major nutrient elements were 4.2 for N, 2.1 for P, 1.7 for S, 1.3 for Ca, 2.4 for Mg, and 3.9 for K.

Woody litter accounted for a major portion of litterfall biomass and nutrient content, with the greatest rates in the alder-conifer stand at Wind River (biomass: 17 Mg·ha⁻¹·yr⁻¹; N: 37 kg·ha⁻¹·yr⁻¹). A single severe windstorm yielded more than half of the woody litterfall collected at Cascade Head, and we expect the long-term average rate for woody litterfall may be somewhat lower than the rate we measured.

Whole-tree mortality was low in the conifer stand at Wind River, 0.3 Mg·ha⁻¹·yr⁻¹ (equalling about 6% of ANPP; Table 5). Mortality was much greater in the alder-conifer stand, where deaths primarily of alders gave a rate of 2.5 Mg·ha⁻¹·yr⁻¹ (24% of ANPP). At Cascade Head, mortality was very low in the conifer

stand (0.4 Mg·ha⁻¹·yr⁻¹, 2% of ANPP), and moderate in the alder-conifer stand (1.8 Mg·ha⁻¹·yr⁻¹, 17% of ANPP).

Outputs

Denitrification rates were low relative to other N fluxes in all stands (Table 5). Averaging the monthly rates by quarterly periods and then summing gave values ranging up to 0.21 kg·ha⁻¹·yr⁻¹ for the alder-conifer stand at Wind River. Such low rates clearly fall within the uncertainty in values for most other N fluxes. It is possible that high rates may have occurred at microsites not sampled in the 20 cores per stand, or at time points between our sampling occasions, but we of course have no data to examine these possibilities.

Leaching of N past 0.80 m depth in the soil ranged from a low of 5 kg·ha⁻¹·yr⁻¹ for the Wind River conifer stand to 50 kg·ha⁻¹·yr⁻¹ for the Cascade Head alder-conifer stand (Table 6). Dissolved organic N accounted for ≈80% of the total N leached from the stands at

TABLE 5. Denitrification rates.

Forest	Daily rate (mg·ha ⁻¹ ·day ⁻¹)								Annual rate* (kg·ha ⁻¹ ·yr ⁻¹)
	Apr. 1986		Aug. 1986		Nov. 1986		Feb. 1987		
	\bar{X}	1 SE	\bar{X}	1 SE	\bar{X}	1 SE	\bar{X}	1 SE	
Wind River, Washington									
Conifer stand	900	225	125	85	40	15	···†		0.10
Alder-conifer stand	1500	390	155	110	55	40	···		0.21
Cascade Head, Oregon									
Conifer stand	500	180	200	40	125	55	30	15	0.08
Alder-conifer stand	900	225	340	55	125	55	225	110	0.14

* Annual rate derived as simple average of the 4 periods (with a rate of 0 assumed for winter at Wind River) times 365 d/yr.

† No data.

Cascade Head, and 20–35% of the total N leached from the stands at Wind River.

DISCUSSION

N fixation

Our estimates of current rates of N fixation (≈ 75 kg·ha⁻¹·yr⁻¹) at Wind River and Cascade Head are consistent with the long-term rate of N accretion, and also fall within the range of 55–110 kg·ha⁻¹·yr⁻¹ reported for alder-conifer mixtures worldwide (summarized by Binkley 1981). The seasonal average fixation rate of ≈ 8 μmol of C₂H₂ reduced per gram of nodule per hour is remarkably similar to other reported values for alders past age 15: 5–10 $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for Sitka alder [*Alnus sinuata* (Regel.) Rydb.] and red alder (Binkley 1981), 9 $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for grey alder (*Alnus incana* L.; Johnsrud 1978), and 5–8 $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for black alder (*Alnus glutinosa* L.; Akkermans 1971).

The continued high rate of N fixation at age 55 yr counters earlier speculation that alders fix little N after age 20 yr (Newton et al. 1968), but is consistent with more recent studies, both laboratory (Ingestad 1981) and field (Luken and Fonda 1983), that showed no drop in N fixation by alder despite increasing availability of N. The continued expenditure of energy to fix N at sites where nitrate is abundant may appear inefficient. Schubert (1982) estimated the costs of N assimilation (not counting synthesis of the carbon skeletons of amino acids) at 0.1 mole of glucose per mole of N from ammonium, 0.33 mol from nitrate, and 0.38–0.50 mol from N₂ (depending on amount of H₂ evolved and recovered during N fixation). Ammonium absorption would appear to be the most energy-efficient way to obtain N, followed by nitrate uptake and reduction, and then by N₂ fixation. However, the mobility of these molecules in soils follows the reverse trend, and it is possible that N₂ may be the most economical source of N if the cost of root growth and replacement is taken into account (Gutschick 1981). Research on the relative costs of N acquisition from these various sources appears warranted.

Nutrient-use efficiency

Nutrient-use efficiency (kilograms of ANPP per kilogram of nutrient taken up) may be expected to drop as utilization of that nutrient increases, because availability of some other resource (such as water, energy, or light) limits production (Melillo and Gosz 1983, Bloom et al. 1985). The nutrient-use efficiencies at both locations were generally consistent with this hypothesis. At Wind River the nutrient-use efficiencies were much lower in the alder-conifer stand than in the conifer stand for all elements except P (Table 7). The alder-conifer stand as a whole used nutrients less efficiently, largely because red alder was less efficient than the conifers. At Cascade Head all nutrient-use efficiencies were lower for the alder-conifer stand than for the conifer stand, a pattern again consistent with the expectation that efficiency should decrease with increasing rates of uptake.

N outputs

We expected that denitrification might constitute an important N output from our alder-conifer stands, given the high availability of nitrate and frequently moist soils. Rates were low, however, as has been reported for some other nitrate-rich sites (Davidson and Swank 1987, Wells et al. 1989, Davidson et al. 1990), and our results provide no evidence that denitrification is important as a vector of N loss from these forests.

TABLE 6. Nitrogen leaching past 0.80-m depth in soil.

Forest	Nitrogen leaching (kg·ha ⁻¹ ·yr ⁻¹)			
	NH ₄ ⁺	NO ₃ ⁻	Organic-N*	N sum
Wind River, Washington				
Conifer stand	0.6	0.4	4.1	5.1
Alder-conifer stand	3.8	2.5	19.6	25.9
Cascade Head, Oregon				
Conifer stand	6.3	7.8	7.3	21.4
Alder-conifer stand	3.6	35.8	10.6	50.0

* Kjeldahl-N minus ammonium-N.

TABLE 7. Nutrient-use efficiencies, calculated as the annual production of biomass per unit mass of nutrient taken up.

Forest	Nutrient-use efficiency (kg/kg)					
	N	P	S	Ca	Mg	K
Wind River, Washington						
Conifer stand	910	1140	4800	410	3200	1780
Alder-conifer stand	230	1490	1720	310	1840	690
Cascade Head, Oregon						
Conifer stand	800	3430	5650	1390	6400	2950
Alder-conifer stand	130	1150	2280	580	1700	525

The factors regulating N leaching are not well understood. The "N saturation hypothesis" (e.g., Aber et al. 1990) suggests that N leaching should be well correlated with both total soil N and N availability. In our four stands N leaching was directly correlated with soil N capital and indirectly with the C-to-N ratio, but was not correlated consistently with any of several measures of N mineralization (Binkley et al. 1992). The difficulty of predicting N leaching is illustrated by studies showing that very high rates of nitrate leaching from red alder forests (N loss rates 50–140 kg·ha⁻¹·yr⁻¹) drop to nearly zero within 1 or 2 yr after logging (Bigger and Cole 1983, Van Miegroet et al. 1989b). The mechanisms underlying this response remain unexplained (see discussion by Johnson 1992).

Our leaching estimates also underscore the importance of dissolved organic N (DON) as an avenue of N loss. DON accounted for a large proportion (20–80%) of the total N leached from our four stands. The dominance of DON has been reported for many other temperate forests: for example, more N leached as DON than as ammonium in 14 of 15 of the diverse forest sites included in the Integrated Forest Study (Johnson and Lindberg 1992), and more N leached as DON than as inorganic N (ammonium + nitrate) in 8 of those 15 sites.

Malleability of nutrient cycles

The presence of N fixers, such as alders, generally increases rates of uptake and return of all nutrients (Binkley 1992). Two explanations are possible: (1) more rapid cycling of N increases the rate of supply (net mineralization plus weathering) for nutrients other than N, or (2) the rates of supply of nutrients other than N exceed the rates of uptake and return in forests without N fixers. If the first explanation is true, then what is the mechanism by which N cycling affects the rate of supply of other nutrients? If the second explanation is true, then what mechanisms prevent leaching of large amounts of nutrients (other than N) from forests without N fixers?

The higher rate of P return in litterfall in alder forests probably results from an increase in the rate of P supply, attributable to geochemical and biological factors. Potential geochemical factors include rhizosphere acid-

ification (Gillespie and Pope 1989), and biological factors include rooting depth (Malcolm et al. 1985), soil enzyme activity (Ho 1979), and organic chelates (Ae et al. 1990). The higher rate of S return may relate to higher rates of uptake from solution, rather than to any difference in the rate of supply (Van Miegroet 1986). Faster cation cycling probably involves two mechanisms that are important on different time scales: faster decomposition on an annual time scale, and either depletion of exchangeable pools or increased mineral weathering in the longer term. Biogeochemical cycles are thus remarkably malleable under the influence of species (and perhaps management activities). Case studies with N-fixing alders demonstrate the magnitude of this malleability, but extensive experimentation on the mechanisms that give rise to this malleability is needed for a predictive understanding.

ACKNOWLEDGMENTS

We thank Carol Glassman for assistance in the laboratory and Amy Horne for her help in the field. Special thanks are due to Ute Riesenkonig, who bore responsibility for the majority of the data analysis. R. Miller, G. P. Robertson, and several anonymous reviewers provided helpful comments on earlier drafts. Funding was provided by NSF grant BSR-841678, by the Electric Power Research Institute and Oak Ridge National Laboratory as part of the Integrated Forest Study of the Effects of Acidic Deposition, and by McIntire-Stennis Project 0133245. This paper is a contribution of the Andrews Ecosystem Research Group.

LITERATURE CITED

- Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1990. Nitrogen saturation in northern forest ecosystems. *Bioscience* 39:378–386.
- Ae, N., J. Arihara, K. Okada, T. Yoshihara, and C. Johansen. 1990. Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian subcontinent. *Science* 248: 477–480.
- Akkermans, A. D. L. 1971. Nitrogen fixation and nodulation of *Alnus* and *Hippophae* under natural conditions. Dissertation. University of Leiden, Leiden, The Netherlands.
- Baker, D., and J. Torrey. 1979. The isolation and cultivation of actinomycetous root nodule endophytes. Pages 38–56 in J. Gordon, C. Wheeler, and D. Perry, editors. Symbiotic nitrogen fixation in the management of temperate forests. Proceedings of a workshop 2–5 April 1979. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Berntsen, C. 1961. Growth and development of red alder

- compared with conifers in 30-year-old stands. United States Forest Service PNW Research Paper Number 38.
- Bigger, C., and D. Cole. 1983. Effects of harvesting intensity on nutrient losses and future productivity in high and low productivity red alder and Douglas-fir stands. Pages 167–178 in R. Ballard and S. Gessel, editors. IUFRO symposium on forest site and continuous productivity. United States Forest Service General Technical Report PNW-163.
- Binkley, D. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B.C. Canadian Journal of Forest Research 11:281–286.
- . 1992. Ecology of mixtures of nitrogen-fixing trees and other species. Pages 99–123 in M. Cannell, editor. Ecology of mixed species stands. Cambridge University Press, Cambridge, England.
- Binkley, D., R. Bell, and P. Sollins. 1992. Soil nitrogen transformations in adjacent conifer and alder/conifer forests. Canadian Journal of Forest Research, *in press*.
- Binkley, D., and S. Greene. 1983. Production in mixtures of conifers and red alder: the importance of site fertility and stand age. Pages 112–117 in R. Ballard and S. Gessel, editors. IUFRO symposium on forest site and continuous productivity. United States Forest Service General Technical Report PNW-163.
- Binkley, D., and P. Reid. 1984. Long-term responses of stem growth and leaf area to thinning and fertilization in a Douglas-fir plantation. Canadian Journal of Forest Research 14: 656–660.
- Binkley, D., and P. Reid. 1985. Long-term increase of nitrogen availability from fertilization of Douglas-fir. Canadian Journal of Forest Research 15:723–724.
- Binkley, D., and P. Sollins. 1990. Acidification of soils in mixtures of conifers and red alder. Soil Science Society of America Journal 54:1427–1433.
- Bloom, A., F. S. Chapin III, and H. Mooney. 1985. Resource limitation in plants—an economic analogy. Annual Review of Ecology and Systematics 16:363–392.
- Bond, G. 1955. An isotopic study of the fixation of nitrogen associated with nodulated plants of *Alnus*, *Myrica*, and *Hippophae*. Journal of Experimental Botany 6:303–311.
- Cole, D., S. Gessel, and J. Turner. 1978. Comparative mineral cycling in red alder and Douglas-fir. Pages 327–336 in D. Briggs, D. DeBell, and W. Atkinson, editors. Utilization and management of alder. United States Forest Service General Technical Report PNW-70.
- Cole, D., and M. Rapp. 1981. Elemental cycling in forest ecosystems. Pages 341–409 in D. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, England.
- Davidson, E., and W. Swank. 1987. Factors limiting denitrification in soils from mature and disturbed southeastern hardwood forests. Forest Science 31:135–144.
- Davidson, E. A., D. D. Myrold, and P. M. Groffman. 1990. Denitrification in temperate forest ecosystems. Pages 196–220 in S. P. Gessel, D. S. Lacate, G. F. Weetman, and R. F. Powers, editors. Sustained productivity of forest soils. University of British Columbia, Faculty of Forestry Publications, Vancouver, British Columbia, Canada.
- Franklin, J., C. Dyrness, D. Moore, and R. Tarrant. 1968. Chemical soil properties under coastal Oregon stands of alder and conifers. Pages 157–172 in J. Trappe, J. Franklin, R. Tarrant, and G. Hansen, editors. Biology of alder. United States Forest Service, Portland, Oregon.
- Gholz, H., C. Grier, A. Campbell, and A. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Research Paper 41. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Gillespie, A. R., and P. E. Pope. 1989. Alfalfa N₂-fixation enhances the phosphorus uptake of walnut in interplantings. Plant and Soil 113:291–293.
- Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs 47:373–400.
- Gutschick, V. 1981. Evolved strategies in nitrogen acquisition by plants. American Naturalist 118:607–637.
- Harr, R. D. 1976. Forest practices and streamflow in western Oregon. United States Forest Service General Technical Report PNW-49.
- Harrington, C., and D. Reukema. 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. Forest Science 29:33–46.
- Hiltner, L. 1896. Über die Bedeutung der Wurzelknöllchen von *Alnus glutinosa* für die Stickstoffernährung dieser Pflanze. Die Landwirtschaftlichen Versuchs-Stationen 46: 153–161.
- Ho, I. 1979. Acid phosphatase activity in forest soil. Forest Science 25:567–568.
- Ingestad, T. 1981. Growth, nutrition, and nitrogen fixation in grey alder at varied rates of nitrogen addition. Physiologia Plantarum 50:353–364.
- Johnson, D. 1992. Nitrogen retention in forest soils. Journal of Environmental Quality 21:1–12.
- Johnson, D., and S. Lindberg, editors. 1992. Atmospheric deposition and nutrient cycling in forest ecosystems. Springer-Verlag, New York, New York, USA.
- Johnsrud, S. C. 1978. Nitrogen fixation by root nodules of *Alnus incana* in a Norwegian forest ecosystem. Oikos 30: 475–479.
- Kim, D. Y. 1987. Seasonal estimates of nitrogen fixation by *Alnus rubra* and *Ceanothus* species in western Oregon forest ecosystems. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Lechevalier, M., and H. Lechevalier. 1979. The taxonomic position of the actinomycetous endophytes. Pages 111–123 in J. Gordon, C. Wheeler, and D. Perry, editors. Symbiotic nitrogen fixation in the management of temperate forests. Proceedings of a workshop 2–5 April 1979. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Luken, J., and R. Fonda. 1983. Nitrogen accumulation in a chronosequence of red alder communities along the Hoh River, Olympic National Park, Washington. Canadian Journal of Forest Research 13:1228–1237.
- Malcolm, D. C., J. Hooker, and C. Wheeler. 1985. *Frankia* symbioses as a source of nitrogen in forestry: a case study of symbiotic nitrogen-fixation in a mixed *Alnus-Picea* plantation in Scotland. Proceedings of the Royal Society of Edinburgh 85B:263–282.
- McNabb, D., and J. Geist. 1979. Acetylene reduction assay of symbiotic N₂ fixation under field conditions. Ecology 60: 1070–1072.
- Melillo, J. M., and J. Gosz. 1983. Interactions of biogeochemical cycles in forest ecosystems. Pages 177–221 in B. Bolin and R. Cook, editors. The major biogeochemical cycles and their interactions. John Wiley & Sons, New York, New York, USA.
- Miller, R., and M. Murray. 1978. The effects of red alder on growth of Douglas-fir. Pages 283–306 in D. Briggs, D. DeBell, and W. Atkinson, editors. Utilization and management of alder. United States Forest Service General Technical Report PNW-70.
- Miller, R., and M. Murray. 1979. Fertilizer versus red alder for adding nitrogen to Douglas-fir forests of the Pacific Northwest. Pages 356–373 in J. Gordon, C. Wheeler, and D. Perry, editors. Symbiotic nitrogen fixation in the management of temperate forests. Proceedings of a workshop 2–5 April 1979. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Miller, R., and R. Tarrant. 1983. Long-term growth re-

- sponse of Douglas-fir to ammonium nitrate fertilizers. *Forest Science* **29**:127-137.
- Newton, M., B. A. El Hassan, and J. Zavitkovski. 1968. Role of red alder in western Oregon forest succession. Pages 73-84 in J. Trappe, J. Franklin, R. Tarrant, and G. Hansen, editors. *Biology of alder*. United States Forest Service, Portland, Oregon, USA.
- Radulovich, R., and P. Sollins. 1987. Improved performance of zero-tension lysimeters. *Soil Science Society of America Journal* **51**:1386-1388.
- Reid, P. 1983. Assessing the influence of silvicultural practices on Douglas-fir nutrition and stemwood production. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Robertson, G. P., and J. Tiedje. 1984. Denitrification in successional and old-growth Michigan forests. *Soil Science Society of America Journal* **48**:383-389.
- Sachs, D. 1983. Management effects on nitrogen nutrition and long-term productivity of western hemlock stands: an exercise in simulation with FORCYTE. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Schubert, K. 1982. The energetics of biological nitrogen fixation. *American Society of Plant Physiologists*, Rockville, Maryland, USA.
- Sollins, P., S. P. Cline, T. Verhoeven, D. Sachs, and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* **12**:1585-1595.
- Strickland, T. C., P. Sollins, D. S. Schimel, and E. A. Kerle. 1988. Aggregation and aggregate stability in forest and range soils. *Soil Science Society of America Journal* **52**:829-833.
- Struwe, S., and A. Kjoller. 1991. Denitrification in forest ecosystems. *Forest Ecology and Management* (special issue) **44**:1-92.
- Tarrant, R. F. 1961. Stand development and soil fertility in a Douglas-fir-red alder plantation. *Forest Science* **7**:238-246.
- . 1978. Attitudes toward red alder in the Douglas-fir region. Pages 1-8 in D. Briggs, D. DeBell, and W. Atkinson, editors. *Utilization and management of alder*. United States Forest Service General Technical Report **PNW-70**.
- Tarrant, R. F., K. C. Lu, W. Bollen, and J. Franklin. 1969. Nitrogen enrichment of two forest ecosystems by red alder. United States Forest Service Research Paper **PNW-76**.
- Tarrant, R. F., and R. Miller. 1963. Soil nitrogen accumulation beneath a red alder-Douglas-fir plantation. *Soil Science Society of America Proceedings* **37**:231-234.
- Tarrant, R. F., and J. Trappe. 1971. The role of *Alnus* in improving the forest environment. *Plant and Soil* (special volume) **1971**:335-348.
- Van Miegroet, H. 1986. Role of N status and N transformations in H⁺ budget, cation loss and S retention mechanisms in adjacent Douglas-fir and red alder forests. Dissertation. University of Washington, Seattle, Washington, USA.
- Van Miegroet, H., D. Cole, D. Binkley, and P. Sollins. 1989a. The effect of nitrogen accumulation on soil chemical properties in alder forests. Pages 515-528 in R. Olson and A. LeFohn, editors. *Effects of air pollution on western forests*. Air and Waste Management Association, Pittsburgh, Pennsylvania, USA.
- Van Miegroet, H., D. Cole, and P. Homann. 1989b. The effect of alder forest cover and alder forest conversion on site fertility and productivity. *Proceedings of the 7th North American Forest Soils Conference*, Vancouver, British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada.
- Wells, C., A. Jones, and J. Craig. 1989. Denitrification in Southern Appalachian spruce-fir forests. Pages 117-121 in G. Hertel, editor. *Effects of air pollution on the spruce-fir forests of the Eastern United States and the Federal Republic of Germany*. United States Forest Service General Technical Report **NE-120**.