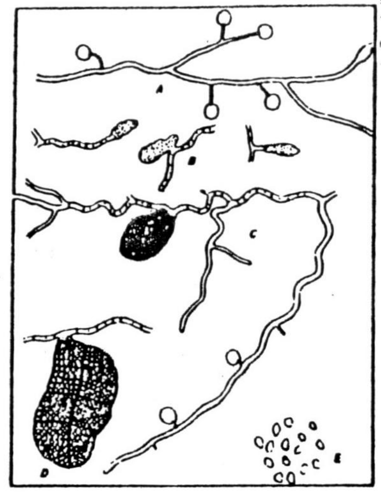
PROSPECTS AND PROBLEMS OF NITROGEN MANAGEMENT USING SYMBIOTIC NITROGEN FIXERS



K. Cromack, Jr.,[1] C. C. Delwiche,[2] and D. H. McNabb[3]
[1]Department of Forest Science
Oregon State University
Corvallis, OR 97331
[2]Department of Land, Air & Water Resources
University of California
Davis, CA 95616
[3]Department of Forest Engineering
Oregon State University
Corvallis, OR 97331

ABSTRACT

Establishment of N fixing species, degree of nodulation, and rates of N fixation are affected by basic life history of the species concerned, by physical and chemical site factors and by interactions with other plant species. The role of N fixing species in nutrient cycling can be assessed by direct measurement of N fixation rates utilizing acetylene reduction or ^{15}N labeling techniques. Alternatively, total ecosystem N accretion rates, including the soil organic matter and above and below-ground biomass, have been obtained in a number of different studies. Recycling of N by N fixing species is dependent upon rates of decomposition of litter components; data from several such species suggest that both C and N substrate quality in N fixing species generally is higher than for non-N fixing species on the same sites. Prospects and problems of N management are viewed in the overall context of site preparation for N fixation, coupled with management of high quality N litter residue. A new technique of screening for potential new N fixers in mixed plant communities is discussed.

INTRODUCTION

Replacement of N by both biological and non-biological sources is essential if sustained productivity is to be maintained in both agricultural and forest ecosystems. Future intense forest management, with consequent shorter rotation time, will necessitate replacement of N capital at a greater rate than currently occurs in secondary succession leading to old-growth forests. Due to a combination of factors including priority allocation of energy resources, maintenance of long-term productivity of forest lands without significantly accelerating rates of soil erosion and nutrient depletion, and increased use of trees genetically selected for increased yield, it is important now to assess the current potential for biological N fixation in future forest management. Intercropping of legumes with other agricultural crops has been demonstrated to be effective under a number of circumstances, particularly in tropical climates with heavy rainfall and for range crops in temperate climates (Sanchez 1976).

The USFS, Pacific Northwest Forest and Range Experiment Station, Project 1653 and the National Science Foundation Ecosystems Studies grant no. DEB-77-06075 are acknowledged for their support.

INTEGRATIVE OBSERVATIONS ON NITROGEN ACCRUAL AND LOSS

Estimates of typical rates of N turnover in native ecosystems can be made from existing data on long-term N balance studies in diverse systems. Data from both agricultural and forest systems show annual N inputs leading to substantial accretion over long time periods (Jenkinson 1976; Newton, El Hassan and Zavitkovski 1968; Youngberg and Wollum 1976; Tarrant and Miller 1963). Such data provide only an integrated measure of accrual or loss but at least they provide a minimum figure for N fixation in the case of accrual and mineralization with accompanying harvest, leaching or dentrification in the case of net N loss.

The Broadbalk "wilderness" study

Beginning with the early studies by Lawes, Gilbert and Warington at the Rothamsted Experiment Station, careful account has been kept on plots which had drainage tile installed in 1849 and detailed information has been accumulated on N gains and losses including the analysis of the soil and harvested crops.

A plot which previously had been cropped with wheat (with no fertilization) was allowed to revert to "wilderness" beginning in 1883. Total N in the top 23 cm of soil rose from approximately 3,000 kg/ha in 1883 to over 7,000 kg/ha in 1967 in a portion of the plot which had been "stubbed" (i.e., saplings removed) periodically and was populated largely by herbaceous plants (Jenkinson 1976). The remainder of the plot, now in deciduous forest, also gained N "steadily" since 1883 but figures are not given. This N accrual of about 49 kg/ha/yr, largely from biological N fixation presumably, was comparable with that of the cultivated soil which had been fertilized annually with 35 short tons of farm yard manure. Losses by leaching and denitrification were not estimated on this plot so the conclusion is implied that biological N fixation was in excess of 34 kg/ha/yr by the amount of these unestimated losses.

Sand dune colonization

Observing the colonization of sand dunes on the southern shore of Lake Michigan, Olson (1958) reported N accretion rates (in the top 10 cm) during the period of maximum increase in total soil N of only 4 kg/ha/yr. This was of the order of annual input by rainfall. The initial population was largely herbaceous with scattered legumes and pioneering grasses through a variety of shrubs to a mixed deciduous hardwood association and some pines. The light sandy soil is particularly susceptible to leaching loss and it is probable that nutrients other than N were limiting so that the comparatively low N status (approximately 0.1% N) is not surprising. Similar observations were made by Salisbury (1925) on dune sands. This contrast with the high rates of N gain in the Broadbalk "wilderness" probably results from differences in climate and soil and emphasizes the hazard in generalization regarding N fixation rates in native ecosystems.

Conversion of a native grassland to agriculture results in a loss of N (Jenny 1941) emphasizing that the N status of an ecosystem is characteristic of its management, an argument applicable to forest soils.

FACTORS AFFECTING N FIXATION

Climate and soil set general limits upon ecosystem productivity, including N fixation. Seasonal water balance of sites expressed physiologically as plant moisture stress, can override other factors such as favorable soil temperature. McNabb, Youngberg and Geist (1977) found plant moisture stress to be a significant factor limiting N fixation by Ceanothus velutinus in eastern Oregon. Soil temperature was found to be significantly related to N fixation by C. velutinus var. velutinus in a mid-elevation site in the western Cascades of Oregon (McNabb and Cromack, unpub. data).

Edaphic factors such as available cations affect nodulation rate of symbiotic N fixing plants such as C. velutinus Dougl. (Scott 1973). Specific cations such as Ca can affect nodulation rate and N concentration in all plant parts (Banath, Greenwood and Loneragan 1966; Scott 1973). Total soil N can influence both the number and size of nodules in red alder (Alnus rubra) (Zavitkovski and Newton 1968).

Manipulation of physical factors such as light, through thinning of overstory trees enabled red alder to become established in the understory of a 62 year old Douglas-fir (Pseudotsuga menziesii) stand in western Oregon (Berg and Doerksen 1975). Nodulation of Lupinus arboreus was reduced by shading and almost totally inhibited by defoliation (Gadgil 1971).

Other site factors such as distribution of coarse woody debris following clear-cutting and burning may influence the number of nodules per unit of soil in N fixing species such as red alder and snowbrush (Ceanothus velutinus) (B. Bormann, pers. commun.; McNabb and Cromack, unpub. data). Harvey, Larsen and Jurgensen (1976) found both decaying wood and charcoal to influence distribution of ectomycorrhizae in a mature Douglas-fir/larch (Larix occidentalis) forest soil in western Montana. Decaying logs also appear to have a stimulating influence upon nodulation of red alder and snowbrush.

INTERCROPPING SYSTEMS

Forest vs. herbaceous crops

Considering only economic factors there are even stronger arguments which favor the use of biological N fixation for forest crops than the commonly recognized values of N fixers in herbaceous agriculture crops. The period of time between fertilizer application to a forest and the realization of economic gain from the application may be as long as a decade or more. Thus, the increased yield necessary to justify the long-term capital investment would have to be considerably greater than that necessary to justify the use of a fertilizer for an annual crop. For this reason only with comparatively short-term forest crops (Christmas trees or trees harvested at a young age for fiber) is the extensive use of fertilizers likely to be profitable.

Intercropping of legumes with other agricultural crops has been demonstrated to be effective under a number of circumstances, particularly in tropical climates with heavy rainfall and for range crops in temperate climates (Sanchez 1976).

Aside from the contribution of N which an intercropping system can provide in forest management, there are the additional advantages of shade which a nurse crop can furnish, the control of erosion and the more effective use of photosynthetic area, assuming that the crop is one of economic value (American Society of Agronomy 1976). Annuals or other herbaceous plants have the advantage that they are unlikely to overtop a forest planting, but properly selected woody plants also can be used effectively.

Forest associations

Although there are no fundamental limitations restricting N fixing plants which are potentially useful for forest intercropping, one of the more likely starting points would be with the management of existing associations, including possible genetic modification of component plants. Typical N fixers in temperate forest associations include (in addition to numerous herbaceous plants) the woody genera *Myrica*, *Alnus*, *Ceanothus*, *Purshia* and others.

Nitrogen fixation rates for a variety of Pacific Northwest forest ecosystems are given in Table 1. Red alder generally has the highest rate of N fixation. Snowbrush is second when compared to red alder; snowbrush values are in line with the original estimates by Delwiche *et al*. (1965). Species such as lupines and Scotch broom fix somewhat less N, but potentially significant N accretion rates may occur on sites where these species sustain their N fixation rates for at least 5-10 years.

An older snowbrush stand in the western Cascades of Oregon yielded biomass and N capital values of 42,680 kg/ha and 225.0 kg/ha, respectively (Table 2). This stand had a total biomass similar to that of eastern Oregon snowbrush stands (Youngberg and Wollum 1976). A one-year cycle of N fixation in this stand (Figure 1) gave an estimate of 80 kg/ha N fixed, based upon a nodule biomass of 750 kg/ha (McNabb and Cromack, unpub. data).

Comparison of short-term vs. long-term N fixation rates (Table 3) reveal that precipitation inputs and other sources of N fixation, both free-living and symbiotic, add appreciable N capital to sites in areas such as western Oregon when viewed in the time perspective of 500 years. Precipitation inputs of N are approximately balanced by leaching losses, as measured by input-output data from watershed studies (Fredriksen 1975). Processes such as soil N fixation and denitrification remain to be evaluated more fully (Mitchell, Waide and Todd 1975).

Nitrogen recycling function

Decomposition of litter components and mineralization of N is the ecosystem mechanism whereby N recycling is accomplished. Traditional means of evaluating potential decomposibility such as the C/N ratio, indicate that plant components of N fixers will decompose at a greater rate than similar components of trees such as Douglas-fir, from later stages of succession (Table 4). Newer methods of assessing C substrate quality (Van Soest 1963) show that N fixing species generally have a lower lignin content and higher concentration of acid detergent soluble extract (labile C) than species such as Douglas-fir (Table 4). Foliage and small stems of N fixing species such as red alder, snowbrush, redstem *Ceanothus*, Scotch broom and bitterbrush are edible by ruminants and other herbivores (E. Harshman, pers. commun.). Radwan, Ellis and Crouch (1978) have published similar C substrate quality data for red alder. Therefore, an important ecosystem function of N fixing species is to add high quality grazing or browsing foods to secondary succession. This could be an important function also in helping regulate animal damage to commercial species by positive management for alternative foods of greater palatability.

Initial substrate quality data and annual decomposition rate data from 10 species including leaf litter of Douglas-fir, fireweed (*Epilobium angustifolium*), red alder, snowbrush, vine maple (*Acer circinatum*), golden chinkapin (*Castanopsis*

TABLE 1. SYMBIOTIC N FIXATION IN THE PACIFIC NORTHWEST

Species	Location	Duration of N fixation (yrs)	Annual N fixation (kg/ha/yr)	Total N fixation (kg/ha)	Reference
Red Alder	Oregon, Coast Range	15	320	4800	Newton *et al.* (1968)
Red Alder	Oregon, Coast Range	17	11.8-45.9	200-780	Berg & Doerksen (1975)
Red Alder	Wash., Western Cascades	25	40	1000	Tarrant & Miller (1963)
Red Alder	Wash., Cedar River	38	85	3240	Cole *et al.* (1978)
Snowbrush	Oregon, Western Cascades	10	108	1076	Youngberg & Wollum (1976)
Snowbrush	Oregon, Western Cascades	10	80	800	McNabb & Cromack (unpub.)
Snowbrush	Eastern Oregon	10	70	705	Youngberg & Wollum (1976)
Snowbrush	Eastern Oregon	10	32.2	322	McNabb *et al.* (1977)
Scotch Broom	Oregon, Coast Range	5	33	160	Helgerson *et al.* (1979)
Lupine (*L. sericeus*)	Eastern Oregon	15	7.2	108	McNabb *et al.* (1976)
Lupine (*L. leucophyllus*)	Eastern Oregon	11	10.5	115	McNabb *et al.* (1976)
Russet buffaloberry	Eastern Oregon	42	0.35	14.7	McNabb *et al.* (1976)

TABLE 2. BIOMASS AND N CAPITAL OF AN H. J. ANDREWS EXPERIMENTAL ECOLOGICAL RESERVE STAND OF *CEANOTHUS VELUTINUS* VAR. *VELUTINUS*. ELEVATION 1125 M. STAND AGE 17 YEARS.

C. velutinus component	Biomass kg/ha ($\bar{X}$ ± SE)	Nitrogen %	Nitrogen kg/ha ($\bar{X}$ ± SE)
Leaves	3,551 ± 945	1.78	63.4 ± 16.8
Stems	30,339 ± 2,880	0.36	109.2 ± 10.4
Roots	8,040 ± 2,280	0.43	34.6 ± 9.8
Nodules	750 ± 350	2.37	17.8 ± 8.3
Totals	42,680		225.0

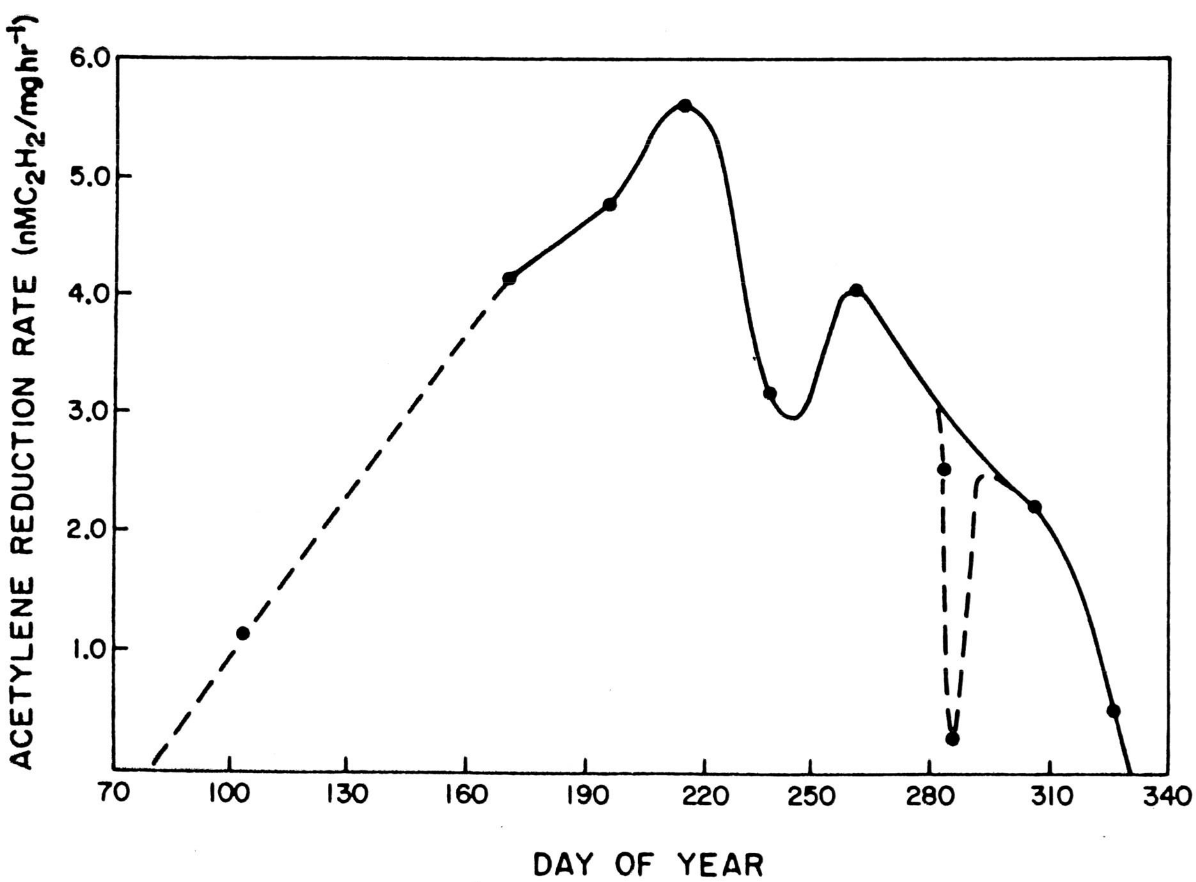


Figure 1. Seasonal variation in C_2H_2 reduction rate in a 17-year-old snowbrush stand.

TABLE 3. COMPARISON OF SHORT AND LONG-TERM N ACCRETION IN PACIFIC NORTHWEST FOREST ECOSYSTEMS (UNITS ARE IN KG/HA)

	Short-term		Long-term	
	Annual	15 yrs	Annual	500 yrs
Rainfall*	1.5	22.5	1.5	750
Dust*	0.6	9.0	0.6	300
N fixation				
Vegetation†	32-320	480-4800	-	480-4800
Logs+ (50-250 mT/ha)	0.5	7.5	2.6	775
Lichens§	-	-	5.0	1250

* Fredriksen (1975).

† Youngberg & Wollum (1976), McNabb *et al*. (1977), Newton *et al*. (1968).

\+ Based upon rates published by Larsen *et al*. (1978). Log biomass based upon Grier and Logan (1977) and MacMillan *et al*. (1977). Assume 50 mT/ha of logs for first 250 years and 250 mT/ha for remaining 250 years.

§ W. C. Denison and B. Caldwell (pers. commun.).

TABLE 4. C AND N SUBSTRATE QUALITY INDICES FOR N FIXING SPECIES AND DOUGLAS-FIR IN THE PACIFIC NORTHWEST

Species	Component	%N	C/N*	% Lignin**	% Acid detergent soluble fraction**
Douglas-fir	Senescent needles[++]	0.50	100	24.1	59.5
Douglas-fir	Twigs (10 mm)[+]	0.15	333	43.4	26.7
Douglas-fir	Roots (2-3 mm)[Δ]	0.28	178	25.7	52.6
Red Alder	Senescent leaves[ΔΔ]	2.10	24	9.5	80.6
Red Alder	Bolewood[†]	0.17	294	19.4	29.5
Red Alder	Roots (2-5 mm)[++]	0.75	67	17.4	48.0
Snowbrush	Senescent leaves[ΔΔ]	0.81	62	10.0	78.3
Snowbrush	Stemwood <5 mm[††]	0.75	67	17.7	54.8
Snowbrush	Roots <5 mm[††]	0.82	61	18.0	53.7
Snowbrush	Nodules[††]	2.40	21	24.7	67.7
Redstem *Ceanothus*	Green leaves[§]	1.2	42	2.9	88.7
Scotch Broom	Green leaves[§]	4.7	11	3.7	86.1
Bitterbrush	Green leaves[§]	3.1	16	4.5	83.1
Alfalfa	Green leaves*	3.0	17	5.3	77.7

* Assumes C content approximately 50%.

** Van Soest (1963).

[+] Fogel and Cromack (1977).

[++] Fogel and Cromack (unpub. data).

[Δ] Sollins, Cromack, Fogel and Li (in press).

[ΔΔ] Cromack and Monk (1975).

[†] L. Roberts (pers. commun.).

[††] McNabb and Cromack (unpub. data).

[§] Cromack (unpub. data).

chrysophylla), and woody litter components of Douglas-fir show a significant ($p < 0.01$) correlation (Cromack and Fogel, unpub. data):

$$y = 59.2 - 1.1x \quad (1)$$

where y = % weight lost
x = % initial lignin concentration
$n = 10$
$r^2 = 0.86$

Observed vs. calculated decomposition rates show clearly that litter components of N fixing species will decompose relatively rapidly, on the order of 4.3-7.9 yrs (Table 5). Similar Douglas-fir litter components take from 10.7-33.3 yrs to decompose (for senescent needles and twigs, respectively).

Rapid decomposition of litter components from N fixing species makes such residues potentially valuable by adding litter from which N would be readily available, to recent organic matter of low C/N ratio (Young and Spycher 1979; Spycher and Young 1979). If possible, brush residues should be left to decompose in place where mechanical or chemical clearing operations are carried out. In a recent study of a second-growth Douglas-fir ecosystem Fogel and Hunt (1979) found that the major proportion of C input occurs belowground via turnover of mycorrhizae and other soil fungal components. Though belowground dynamics of N fixing species remain to be investigated in detail, soil accretion data of Youngberg and Wollum (1976) indicate that as much as half of the accrued N, and presumably C as well, are added from belowground turnover of snowbrush components.

Other potential benefits of N fixing species should be evaluated in a total ecosystem context. For example, the role of brush species, including N fixing species, in retarding erosion in both upland and riparian zones needs to be considered (Youngberg 1966; F. Swanson, pers. commun.). Alder species as specialized colonizers of riparian zones may add considerable fixed N, as well as supplying the stream or swamp with high substrate quality allochthonous litter components (Fleschner, Delwiche and Goldman 1976; S. Cline, pers. commun.; Triska and Sedell 1976). Seeding of red-stem *Ceanothus* and other *Ceanothus* species can be enhanced by using properly heat-treated seed on bare sites to control erosion and at the same time provide shade for other tree seedlings such as Douglas-fir (Gratkowski 1973).

FIELD EVALUATION

Estimation of accrual rates of N

Long-term observations of the N status of ecosystems such as those described above are perhaps the most reliable but are not possible under many circumstances and provide useful information only after an extended period. A more direct and immediate estimation of N fixation would be of use in the selection of an association for intercropping and other management planning.

The acetylene reduction technique

Direct field application of the acetylene reduction technique has seen some success with agricultural crops (National Science Foundation 1975; Hardy *et al*. 1968). The advantages of the technique include the comparative ease with which it can be

TABLE 5. DECOMPOSITION PARAMETERS FOR LITTER COMPONENTS OF DOUGLAS-FIR, RED ALDER AND SNOWBRUSH

Observed rates	Annual weight loss (%)	Annual decay rate (k)*	Yrs for 50% decomp. (0.69/k)*	Yrs for 95% decomp. (3/k)*
Douglas-fir green needles#	25.0	0.28	2.5	10.7
Snowbrush senescent leaves+	48.0	0.64	1.1	4.7
Red Alder senescent leaves+	51.0	0.71	1.0	4.3
Douglas-fir twigs+	9.0	0.09	7.7	33.3
Calculated rates				
Red Alder roots 2-5 mm	37.6	0.50	1.4	6.0
Snowbrush stemwood <5 mm	39.5	0.50	1.4	6.0
Snowbrush roots <5 mm	39.2	0.50	1.4	6.0
Snowbrush nodules	31.8	0.38	1.8	7.9

* Decomposition rate (k) based upon negative exponential method of Olson (1963) and Jenny, Gessel and Bingham (1949).

Decay rates cited from Fogel and Cromack (1977).

+ Fogel and Cromack (unpub. data).

applied in the field making possible a large number of determinations under conditions approximately those of the unaltered nodule system (for nodulated plants). The technique still is subject to error and difficulties in sampling as well as natural variability in time and space. As a result estimates are still uncertain when translated into quantities of N fixed annually. The method still has many advantages of flexibility and cost over direct isotopic tracer methods.

Natural isotope abundance studies

Because soil N is slightly enriched in ^{15}N over atmospheric N, the natural isotope abundance of plant material compared with that of the soil affords a possibility of screening individual species of a mixed association for the ability to fix N. The technique has received limited evaluation (Delwiche *et al*. 1979) and appears to be potentially useful when properly applied. Aside from the technical difficulties in getting accurate measurements of small differences in isotopic composition, the principal limitations appear to be in the variability of N isotope distribution in the soil profile and among different nitrogenous materials at a given point in the profile.

LITERATURE CITED

American Society of Agronomy. 1976. Special Publication No. 27. Multiple cropping, M. Stelly, (Ed.) American Society of Agronomy, Madison, Wisc.

Banath, C. L., E. A. N. Greenwood and J. F. Loneragan. 1966. Effect of calcium deficiency on symbiotic nitrogen fixation. Plant Physiol. 41:760-763.

Berg, A. and A. Doerksen. 1975. Natural fertilization of a heavily thinned Douglas-fir stand by understory red alder. Res. Note No. 56, School of Forestry, Forest Res. Lab., Oreg. State Univ., Corvallis, Ore. 3 p.

Cole, D. W., S. P. Gessel and J. Turner. 1978. Comparative mineral cycling in red alder and Douglas-fir. *In*: Utilization and Management of Alder. D. G. Briggs, D. S. DeBell and W. A. Atkinson (Eds.) USDA FS Gen. Tech. Rpt. PNW-70. Pacific Northwest For. and Range Expt. Sta., For. Serv., Portland, Ore. p. 327-336.

Cromack, K. Jr. and C. D. Monk. 1975. Litter production, decomposition and nutrient cycling in a mixed hardwood watershed and a white pine watershed. *In*: F. G. Howell, J. B. Gentry and M. H. Smith (Eds.), Mineral Cycling in Southeastern Ecosystems, ERDA Symposium Series (CONF-740513). p. 609-624.

Delwiche, C. C., P. J. Zinke and C. M. Johnson. 1965. Nitrogen fixation by *Ceanothus*. Pl. Physiol. 40:1045-1047.

Delwiche, C. C., P. J. Zinke, C. M. Johnson and R. A. Virginia. 1979. Nitrogen isotope distribution as a presumptive indicator of nitrogen fixation. Bot. Gaz. 140(15): in press.

Fleschner, M. D., C. C. Delwiche and C. R. Goldman. 1976. Measuring rates of symbiotic nitrogen fixation by *Alnus tenuifolia*. Amer. J. Bot. 63:945-950.

Fogel, R. and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Canad. J. Bot. 55:1632-1640.

Fogel, R. and G. Hunt. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Canad. J. For. Res. (in press).

Fredriksen, R. L. 1975. Nitrogen, phosphorus and particulate matter budgets of five coniferous forest ecosystems in the western Cascades Range, Oregon. Ph.D. thesis, Oregon State Univ., Corvallis. 127 p.

Gadgil, R. L. 1971. The nutritional role of Lupinus arboreus in coastal sand dune forestry. II. The potential influence of damaged lupine plants on nitrogen uptake by Pinus radiata. Plant Soil 34:573-575.

Gratkowski, H. 1973. Pregermination treatments for redstem Ceanothus seeds. USDA For. Serv. Res. Paper PNW-156. Pacific Northwest For. and Range Expt. Sta. USDA For. Serv., Portland, Ore. 10 p.

Grier, C. C. and R. S. Logan. 1977. Old-growth Douglas-fir communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47:373-400.

Hardy, R. W. F., R. O. Holsten, E. K. Jackson and R. C. Burns. 1968. The acetylene assay for nitrogen fixation: laboratory and field evaluation. Pl. Physiol. 43:1185-1207.

Harvey, A. E., M. J. Larsen and M. J. Jurgensen. 1976. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. 22:393-398.

Helgerson, O., C. T. Wheeler, D. A. Perry and J. C. Gordon. 1979. Annual nitrogen fixation in Scotch broom (Cytisus scoparius L.) In: Symbiotic Nitrogen Fixation in the Management of Temperate Forests, J. C. Gordon, C. T. Wheeler and D. A. Perry (Eds.) (in press).

Jenkinson, D. S. 1976. The nitrogen economy of the Broadbalk experiments. I. Nitrogen balance in the experiments. Rothamsted Experimental Sta. Rep., Part 2: 103-109.

Jenny, H. 1941. Factors of Soil Formation. McGraw-Hill, New York.

Jenny, H., S. P. Gessel and F. T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68: 419-432.

Larsen, M. J., M. F. Jurgensen and A. E. Harvey. 1978. N_2 fixation associated with wood decayed by some common fungi in western Montana. Canad. J. For. Res. 8:341-345.

MacMillan, P., J. Means, G. M. Hawk, K. Cromack, Jr. and R. Fogel. 1977. Log decomposition in an old-growth Douglas-fir forest. Northwest Sci. 1977:13. (meeting abstracts).

McNabb, D. H., C. T. Youngberg and J. M. Geist. 1976. N_2 fixation by plants in forest and range ecosystems of northwest Oregon. Completion Rept. Cooperative Aid Agreement, Oregon State Univ. Suppl. No. 86. 110 p.

McNabb, D. H., J. M. Geist and C. T. Youngberg. 1977. Nitrogen fixation by _Ceanothus_ _velutinus_ in northeastern Oregon. _In_: Agronomy Abstracts. p. 127-128.

Mitchell, J. E., J. B. Waide and R. L. Todd. 1975. A preliminary model for nitrogen cycling in the Southeast. _In_: Mineral Cycling in Southeastern Ecosystems. F. G. Howell, J. B. Gentry and M. N. Smith (Eds.), ERDA CONF-740513, Nat. Tech. Inf. Serv., Springfield, Va. p. 41-57.

National Science Foundation. 1975. Enhancing Biological Nitrogen Fixation. H. Evans (Ed.) Division of Biological and Medical Sciences, Nat. Sci. Found., Wash., D.C.

Newton, M., B. A. El-Hassan and J. Zavitkovski. 1968. Role of red alder in western Oregon forest succession. _In_: Biology of Alder. J. M. Trappe, J. F. Franklin, R. F. Tarrant and G. H. Hansen (Eds.) Pacific Northwest For. and Range Exp. Sta., Portland, Ore. p. 73-84.

Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. 119:125-170.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322-331.

Radwan, M. A., W. D. Ellis and G. L. Crouch. 1978. Chemical composition and deer browsing of red alder foliage. Pacific Northwest For. and Range Exp. Sta. Res. Paper PNW-246. Forest Serv., Portland, Ore. 6 p.

Salisbury, E. J. 1925. Note on the edaphic succession in some dune soils with special reference to the time factor. J. Ecol. 13:322-328.

Sanchez, P. 1976. Properties and Management of Soils in Tropics. Wiley Interscience, New York.

Scott, W. 1973. Some Soil Factors Affecting Snowbrush Nodulation. Ph.D. thesis, Oregon State Univ., Corvallis. 103 p.

Sollins, P., K. Cromack, Jr., R. Fogel and C. Y. Li. 1980. Role of low molecular weight organic acids in the inorganic nutrition of fungi and higher plants. _In_: Fungal Ecology. D. T. Wicklow and G. C. Carroll (Eds.) Marcel Dekker, New York. (in press).

Spycher, G. and J. L. Young. 1979. Water-dispersible soil organic-mineral particles: II. Inorganic amorphous and crystalline phases in density fractions of clay-size particles. Soil Sci. Soc. Amer. J. (in press).

Tarrant, R. F. and R. E. Miller. 1963. Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas-fir. Soil Sci. Soc. Amer. Proc. 27:231-234.

Triska, F. J. and J. R. Sedell. 1976. Decomposition of four species of leaf material in three replicate streams with different nitrate input. Ecology 57(4):783-792.

Van Soest, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Official Agric. Chem. 46:829-835.

Young, J. L. and G. Spycher. 1979. Water-dispersible soil organic-mineral particles: I. Carbon and nitrogen distribution. Soil Sci. Soc. Amer. J. (in press).

Youngberg, C. T. 1966. The silvicultural benefits of brush. Soc. Amer. For. Proc., p. 55-59.

Youngberg, C. T. and A. G. Wollum. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. Soil Sci. Soc. Amer. J. 40:109-112.

Zavitkovski, J. and M. Newton. 1968. Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. Ecology 49:1134-1145.