Nitrogen Fixation by Scotch Broom (*Cytisus scoparius* L.) and Red Alder (*Alnus rubra* Bong.) Planted Under Precommercially Thinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)

by

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AN ABSTRACT OF THE THESIS OF

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Title: NITROGEN FIXATION BY SCOTCH BROOM (CYTISUS SCOPARIUS L.) AND RED ALDER (ALNUS RUBRA BONG.) PLANTED UNDER PRECOMMERCIALLY THINNED DOUGLAS-FIR (PSEUDOTSUGA MENZIESII (MIRB.) FRANCO)

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Red alder (Alnus rubra Bong.), scotch broom (Cytisus scoparius L.) and snowbrush (Ceanothus velutinus Dougl.) were planted under precommercially thinned Douglas-fir (Pseudotsuga menziesii Mirb. Franco) in the central Oregon Cascades. Plug grown red alder had significantly greater survival than all wildling propagules except for the second broom planting. Browsing was strongly positively correlated with mortality for snowbrush. Survival was somewhat correlated with Douglas-fir basal area (BA) and cover but not with available light.

Nitrogen fixation in underplanted alder and broom and naturally occurring alder, broom and snowbrush was measured by acetylene reduction. Plant moisture stress (PMS) appeared to exert a stronger control on nitrogen fixation through the season than soil temperature. Nitrogen fixation did not appear to be related to available light or Douglas-fir BA or cover. On single dates neither PMS nor soil temperature appeared to be related to nitrogen fixation.

Averaged over the season, broom had significantly greater nitrogen fixation per unit nodule weight than alder but on a per plant basis the species were nearly equal. For underplanted alder, leaf area may have a higher immediate priority for photosynthate than nitrogen fixation as indicated by negative correlations between percent foliar nitrogen and leaf/top and leaf/nodule dry weight ratios. Nitrogen fixation ability keeps apace with leaf development as seen by the positive correlations between leaf and stem total nitrogen values with nodule weights; leaf and nodule dry weights; and leaf weights and nitrogen fixation. For all species, total foliar nitrogen (leaf dry weight x percent nitrogen) was better correlated to nitrogen fixation than percent foliar nitrogen. A greater leaf/nodule ratio for underplanted alder compared to naturally occurring may have resulted from lowered light levels in the thinned stands. In late February, all broom had strong nitrogenase activity compared to sporadic weak activity for alder and no activity for snowbrush. This may suggest that fixation on broom is much less controlled by dormancy. Red alder plugs offer the best potential for nitrogen fixation because of their higher survival, potentially greater growth and fixation, ease of planting, and lesser weed potential.

Given seasonal estimates of nodule fixation rates and the proportion of alder mass as active nodules, nitrogen fixation for alder can be estimated over time from its expected growth under the Douglas-fir. The termination of alder growth is likely set by crown closure of the Douglas-fir. This in turn depends on the number of Douglas-fir left after precommercial thinning and the radial growth rate of their crowns.

A probability tree can organize and display the uncertainties of future growth and nitrogen fixation from underplanted alder. It displays possible paths of growth that individual alder may follow and allows calculation of an expected or mean value for cumulative nitrogen fixation. For an example 15 year period, the expected cumulative fixation for an individual underplanted alder is about 0.668 kg. For comparison, a fully stocked alder stand with this rate of accretion averages 121 kg $ha^{-1}yr^{-1}$ of nitrogen. The initial cost of 224 kg N ha^{-1} from underplanted alder accrued over a 15 year period is about double the current cost of applying an equivalent amount of urea. The longer recovery period for the underplanting costs further magnify the difference.

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I. Initial Survival and Nitrogen Fixation

NITROGEN AND SILVICULTURE

Present Use and Future Uncertainty

Nitrogen fertilization, an accepted means of increasing Douglas-fir growth in the Pacific Northwest, faces an increasingly uncertain future as industrial ammonia production shifts from the U.S. to countries with more abundant natural gas and centrally planned economies (Bengtson, 1979). Urea derived from ammonia is the most common form of nitrogen fertilization in Pacific Northwest forests. Despite large increases in the price of urea, nitrogen application has continued, however, to be attractive because of even larger increases in the value of Douglas-fir stumpage (Miller and Fight, 1979).

Although the energy cost of fixing atmospheric N_2 also has decreased more than 10 fold between 1930 and 1970 (Evans, 1980), global politics or a shortage of natural gas - the present primary feed stock for industrial ammonia production - could cause excessively large increases in the price of urea, or shortages or both. Gordon *et al.* (1979) state "short term realities suggest that competition for chemically fixed nitrogen will become increasingly keen and that forestry needs will be allocated at a lower priority than agriculture."

If such conditions should occur, the use of symbiotic nitrogen fixing plants may prove a practical alternative to urea. Symbiotic nitrogen fixers use solar energy to reduce atmospheric nitrogen to ammonia thus utilizing a nearly unbounded but diffuse source of energy. Establishing an adequate number of nitrogen fixing plants on a site will still, however, very likely require the use of petroleum, a non-renewable but nicely concentrated source of energy.

Symbiotic Nitrogen Fixers

The pool of potential silviculturally beneficial N-fixing plants is large. A variety of terrestrial plants growing in diverse habitats have the ability to reduce or fix atmospheric nitrogen in concert with symbiotic nodule forming endophytes. The legumes (*Fabaceae*), the largest and most diverse single group, are the best known because of their agricultural importance, although most nitrogen fixing legumes are not agricultural cultivars.

Most legumes are tropical, although several species are important agricultural cultivars in the temperate zones and woody species such as scotch broom (*Cytisus scoparius*, L.) , locust (*Robinia* spp.) and gorse (*Ulex europaeus* L.) are native to the north temperate zone. Legume species are variously woody or non-woody, annual or perennial, with all nitrogen fixers, however, being capable of forming root nodule symbioses with *Rhizobium* spp. bacteria.

The actinorhizal nitrogen fixers, or those with *Alnus* type nodules, consist of about 180 mostly temperate zone species belonging to 15 genera from 7 families (Lechevalier and Lechevalier, 1979). Their root nodule forming endophytes are actinomycetes (*Frankia* spp.) (Lechevalier and Lechevalier, 1979) presumably similar to those isolated for *Comptonia peregrina* (Baker and Torrey, 1979) which can also infect *Alnus glutinosa* (Lalonde and Calvert, 1979).

Implementation and Silviculture

In most forest ecosystems, the site resources that control productivity - light, water availability, and nutrient availability - do not vary greatly over time barring major disturbances. Thus available site resources constitute constraints on productivity. Where nitrogen limits yield, these site resources can sometimes be re-allocated between the main crop species and the nitrogen-fixer to enhance overall site productivity, with the gains expressed in the greater yields (Tarrant and Trappe, 1967; Gordon and Dawson, 1979).

Past studies (Table I) have indicated that symbiotic nitrogen fixers can increase site productivity for non-nitrogen fixing species, with the nitrogen fixer being either grown in rotation or concurrently with the other. On light-limited Douglas-fir sites, low in nitrogen, re-allocation of site resources to red alder (*Alnus rubra*, Bong.) enhanced the yield of Douglas-fir (Miller and Murray, 1978), European black alder (*Alnus glutinosa* L.) increased the foliar nitrogen content and growth of associated hardwoods and pines growing on coal spoil (Plass, 1977), and lupine (*Lupinus arboreus* L.) enhanced pine growth in New Zealand (Gadgil, 1971 and 1976). Growth increases in the target species may not, however, always result solely from nitrogen addition. Weed control (Haines et al., 1978), elimination of

TABLE I. SOME STUDIES OF NITROGEN FIXING PLANTS IN SILVICULTURE.

Reference	Site	Results
Berg and Doerksen (1975)	Oregon, Coast Range, USA Second growth Douglas-fir	Naturally occurring red alder followed commercial thinning of Douglas-fir; increased soil N.
Miller and Murray (1978)	Wind River Forest Western Washington, USA Douglas-fir/red alder mixed stands	Mixed stands have greater total volume, increased N and decreased bulk density compared to adjacent, same aged, pure Douglas-fir
Plass (1977)	Kentucky, USA Planting trials on coal spoil	Increased foliar N height and diameter growth for hardwoods and pine grown with *Alnus glutinosa*
Richards and Bevege (1967)	Australia, pine plantation on lateritic, podzolic soils	Legume covers depressed growth of exotics in first year; enhanced natives for 3-5 years
Haines *et al.* (1978)	Northern Alabama, USA *Platanus occidentalis* plantation	Legumes increased height, volume increment and foliar N; main effect concluded to be weed control during growing season
Wetherell (1957)	Northern England, heathland plantations of *Picea sitchensis*	Scotch broom most effective nurse species in suppression *Calluna* heath; hand release of young spruce from broom was necessary
Gadgil (1971 and 1976)	New Zealand, coastal sand dunes *Pinus radiata* plantations	Naturally occurring *Lupinus arboreus* added N under thinned stands increasing pine growth
Sprent and Sylvester (1973)	New Zealand, *Pinus radiata* plantations on coastal and sand dunes	Thinning at 10-12 and 18-22 years stimulated extensive germination of *L. arboreus*; N fixation dependent on light transmission through trees

allelopathic competition (Wetherell, 1957), and improved soil moisture and temperature (Youngberg *et al.*, 1979) are additional reasons stated for the increased yield of the target species.

Competition from nitrogen fixers can also decrease yield. The rapid juvenile growth rate of nitrogen-fixers such as red alder, can cause excessive suppression and mortality in a crop species such as Douglas-fir on light limited sites (Newton *et al.* 1968). Sitka spruce (*Picea sitchensis* (Bong.) Carr) needed hand release from scotch broom planted as a heath suppressing nurse species (Wetherell, 1957). On water limited sites, water competition by the nitrogen-fixer may suppress young conifer growth in the Oregon Cascades by *Ceanothus velutinus* Dougl. (Petersen, 1980).

From another perspective, the problem of allocating site resources between the nitrogen fixer and crop species to enhance overall site productivity is analogous to the use of a supercharger to increase power output from a Diesel or gasoline engine. Power is required to turn the supercharger, but the net power output of the system is increased. This analogy also applies to individual nitrogen fixing plants. The plant respires photosynthate during nitrogen fixation, which could be used elsewhere. The increased availability of nitrogen, however, presumably enhances photosynthesis enough to result in a net increase in photoassimilation. Thus a photosynthesis-nitrogen fixation positive feedback loop may exist. The environments under which the feedback loop becomes positive - either for individual plants or mixed stands - need, however, to be better defined.

Thus among the questions that must thus be answered to beneficially apply nitrogen fixers in silviculture are, 1) can a given site support a positive photosynthesis-nitrogen fixation feedback loop; thus re-allocating site resources to enhance overall site productivity, and 2) if so, what is the optimal mix of nitrogen fixers and crop species for a given site?

To increase site productivity, the nitrogen-fixer must add enough nitrogen or change the site in other ways to increase the yield of the main crop species. This increase, plus any yield from the nitrogen-fixer, must outweigh the growth lost by the main crop species caused by its incomplete site utilization in either space or time. To be economically feasible, the increased yield must result in greater profits or lowered costs as compared to either conventional or no fertilization.

An intuitively logical way to minimize competition effects on the crop species is to introduce the nitrogen fixer after the main species is established at an acceptable stocking level, but before it fully occupies the site. Site resources are thus potentially available for nitrogen fixation and site improvement that either would be unused or utilized by less productive species. These conditions can be provided by precommercial and commercial thinning (Berg and Doerksen, 1975; Miller *et al.*, 1975; Gadgil, 1971 and 1976; Sprent and Sylvester, 1973).

OBJECTIVES

The primary objective of this study was to test whether red alder and scotch broom could survive and fix nitrogen when planted under precommercially thinned Douglas-fir in the Oregon Cascades. Secondary objectives were to assess the effects of the surrounding environment on survival and nitrogen fixation of these two species, and to assess survival of two trefoil varieties and wildling snowbrush that were also underplanted. This is the first replicated study of survival and nitrogen fixation by dissimilar nitrogen fixing species planted under precommercially thinned Douglas-fir in the Pacific Northwest.

METHODS

Experimental Design

The underplanting sites were within the H. J. Andrews Experimental Forest, located 50 miles east of Eugene, Oregon in the Cascade Mountains. In the spring of 1978, six stands of 18 to 20 year old Douglas-fir were underplanted with red alder and scotch broom and two varieties of trefoil (*Lotus pedunculatus* L. and *L. corniculatus*, L.) in a randomized block design, using stands as replicates. The replicates ranged across site classes III and IV, north and south aspects, and ranged in elevation from 546 to 1,080 m (Table II). Adjacent treatment plots in a replicate stand were about 31 m by 62 m (100 by 200 ft) with the short side along the contour and the long dimension on the grade. Two replicates had been thinned in 1977 and the others were thinned two months after underplanting in the summer of 1978.

The broom and alder propagules were one to three year old wildlings about one half meter tall from the Oregon Coast Range, the alder coming from near Falls City, and the broom from Kings Valley. The alders were stored for about 10 weeks and the broom four weeks at 1-2°C before planting. Both were planted in late March during wet cold weather at about 200 plants per plot at 3 m by 3 m (10 x 10 ft) by an inexperienced crew. The trefoil varieties, "Birdsfoot" and "kalo Dwarf English," were obtained from the U.S. Soil Conservation Service, Corvallis, OR, and were seeded at 5.61 kg/ha (5 lbs/ac) after inoculation with "Nitragen" brand *Rhizobium* inoculum.

TABLE II. SUMMARY DATA FOR REPLICATES.

Replicate (USFS management unit)	Site class	Elevation meters	Slope %	Aspect	Year established	Year thinned	Leave trees per acre	Replicate (USFS management unit)	Douglas-fir basal area m^2 ha^{-1} $\bar{x}$ (S.E.)	Douglas-fir percent canopy cover $\bar{x}$ (S.E.)	Percent full sunlight $\bar{x}$ (S.E.)
B 132	III	546	70	SE	1963	1978	250	B 132	7.02 (0.51)	25% (10%)	10.0 (1.68)
L 404U	III	721	40	SE	1957	1977	250	L 404U	5.37 (0.64)	15% (9%)	14.6 (2.73)
L 404L	III	661	20	SE	1957	1977	250	L 404L	2.07 (0.64)	2% (3%)	18.5 (5.27)
L 202	IV	871	40	NE	1960	1978	250	L 202	8.05 (1.28)	21% (7%)	4.60 (0.60)
L 205	IV	1,080	50	N	1960	1978	313	L205	5.02 (0.75)	14% (11%)	3.25 (0.48)
L 206	IV	991	75	N	1960	1978	283	L 206	3.64 (0.60)	11% (6%)	4.74 (0.48)

In 1979, snowbrush (*Ceanothus velutinus* Dougl.) wildlings, red alder plugs and wildlings, and broom wildlings were planted by an experienced crew in April during warm, clear and windy weather. The snowbrush and alder wildlings were one to three years old from 1,200 meter (3,000 ft) elevation sites about 16 km (10 miles) east of the Andrews. The broom again came from the Kings Valley source, and the 66 cc (4 cubic inch) alder plugs were 1-0 seedlings grown by the IFA nursery at Nisqually, WA, from a low elevation Washington seed source.

Acetylene Reduction Assay

The broom and alder were assayed for nitrogenase activity on six dates between April and November, by the acetylene reduction (AR) assay following the methods of McNabb and Geist (1979). Nodules were excised from sample plants keeping the root systems as intact as possible, and incubated for 40 minutes in about 10% acetylene by volume. Soil temperature adjacent to the nodules, gas temperature and barometric pressure were recorded. At the end of incubation, gas samples were drawn into partially evacuated 13 ml glass tubes (Vacutainer, T.M.).

For each sample, a Hewlett-Packard gas chromatograph fitted with an electronic integrator automatically calculated the ratio of moles of ethylene to the sum of moles of acetylene plus moles of ethylene. This gave the proportion of acetylene reduced by the nodules. The original molar amount of acetylene in the incubation vessel - derived from the volume injected, its temperature and the barometric pressure

- multiplied by the proportion reduced to ethylene gave the molar amount of acetylene reduced by the nodules.

The sampling sequence for replicates on a specific date followed a six by six Latin square design, with dates and sequence within dates as rows and columns, and with the six replicates as cells. Additional assays were periodically run on alder, broom and snowbrush of similar sizes and ages occurring naturally on the Andrews Forest to provide a comparison with the underplanted stock. The naturally occurring plants less than three years old, were located on landings, clearcuts, skid roads and road side areas. Underplanted and naturally occurring plants were again assayed on February 20 and 21, 1980, for wintertime activity. Because moisture stress strongly affects nitrogen fixation (Sprent, 1972) daytime plant moisture stress (PMS) was measured with a pressure bomb (Scholander *et al.*, 1965) at the time of assay for most plants.

Mortality and Other Environmental Variables

The plots were surveyed for mortality in late July and September, 1978, and in early August and October, 1979. Each plot was covered until a minimum of 30 alive and dead plants were tallied. Browsing was also assessed in 1979. Nitrogen contents of leaves and stems from sampled plants were measured by micro-Kjehldahl digestion.

Douglas-fir basal area (BA), canopy cover and available light in the treatment plots and unthinned controls were measured in September, 1979 at six randomly selected points in each plot. BA was measured with a 10 factor prism. Projected canopy cover was measured over a square meter quadrat. Available light as a percent of full sunlight was measured by pads of "Ozalid" T.M. paper exposed at ground level next to sample plants and compared to pads exposed in the open (Friend, 1960).

Intensive Alder Sampling

Underplanted alders were intensively sampled to better define the effects of Douglas-fir on AR and plant size for underplanted alder on single dates, and to better define the relationships between nodule weight and the weight of other plant organs. On June 20, and July 5, 1980, AR, PMS, available light, and the basal area of surrounding Douglas-fir of individual underplanted alders were measured on one replicate (Unit 206). This replicate was chosen because it contained adequate numbers of surviving alder.

Thirty alders were assayed June 20, with 14 wildlings measured in the morning and 16 plugs in the afternoon. On July 5, 24 plants were assayed with plug and wildling types about equally represented but mixed through the day. Available light as percent of total sunlight was again measured with pads of "Ozalid" paper exposed next to individual plants. Basal area was measured with a 10 factor prism using sample plants as center points. PMS was measured as before.

RESULTS AND DISCUSSION

The primary objective was met. Scotch broom and red alder were able to survive and fix nitrogen beneath precommercially thinned Douglas-fir. Survival and AR rates varied greatly, but can be partially explained by environmental and plant variables.

Survival

Propagule and Planting Quality

Planting stock vigor, planting weather and the type of crew all affect initial survival of outplanted stock. The 1978 plantings had long storage time, cold wet planting weather and an inexperienced crew. In comparison, the 1979 plantings had short storage times (except for the plug alder), warm windy planting weather and an experienced crew.

For broom, the significantly greater survival after one year for the 1979 plantings (Table III) suggests that shorter storage times or an experienced planting crew or both are more important than planting weather for broom survival.

The significantly greater survival of the 1979 alder plugs compared to the other alder propagules (Table III) suggests that despite their smaller size and longer storage times the plugs are more vigorous than the wildling transplants. This may likely be related to the wildlings' often severe root damage. Root damage and transplant shock may have also caused much mortality of the unbrowsed snowbrush.

TABLE III. PERCENT SURVIVAL OF UNDERPLANTED NITROGEN FIXERS AND STANDARD ERROR OF THE MEAN FOR ALL UNDERPLANTINGS FOR FOUR SAMPLING DATES.[1]

		Survival %							
		1978				1979			
		July		September		August		October	
Planting	Source	Avg.	S.E.	Avg.	S.E.	Avg.	S.E.	Avg.	S.E.
1978 Alder	Coast Range Wildling	84	2	37	8	20	6	20	8
1978 Broom	Coast Range Wildling	48	12	35	11	20	9	23	13
1979 Plug* Alder	IFA Nursery Low Elev. Source					64	12	62	11
1979 Alder	3000' Cascade Wildling					50	12[1]	24	12[1]
1979 Broom*	Coast Range Wildling					71	4[1]	65	9[1]
1979 Snowbrush	3000' Cascade					41	10	20	11

[1]Based on five replicates.

*The 1979 plug alder and 1979 broom had significantly greater survival than the other propagules ($p = 0.05$) in October, 1979, and September, 1978 as based on the arc sin $\sqrt{\%}$ survival.

The lack of mortality between the two 1979 sampling dates for the 1978 plantings suggests that survival may stabilize during the second growing season.

Browsing and Survival

Browsing appears very strongly associated with mortality for snowbrush (Figure 1). This is suggested by the browsing of all live plants, and most dead plants, and the clipping at ground level of a majority of dead plants. The clean clipping suggests that rodents rather than ungulates were responsible.

Broom survival appears unaffected by browsing, as suggested by the large number of live plants nearly all of which were browsed. Browsing was probably primarily by ungulates as indicated by the greater distance from the ground and the rough browse marks.

Environment and Survival

The partially significant correlations of survival with Douglas-fir BA and cover compared to the very weak associations with percent light (Table IV) suggest that water competition may affect survival more strongly than light competition. This is consistent with the correlation of PMS and plant AR over the season (discussed later). The inconsistently significant correlations of survival with Douglas-fir BA and cover suggest that understory brush may also possibly be affecting survival. The plot of individual AR rates *versus* Douglas-fir BA for the intensively sampled alder suggest, also, that something, perhaps

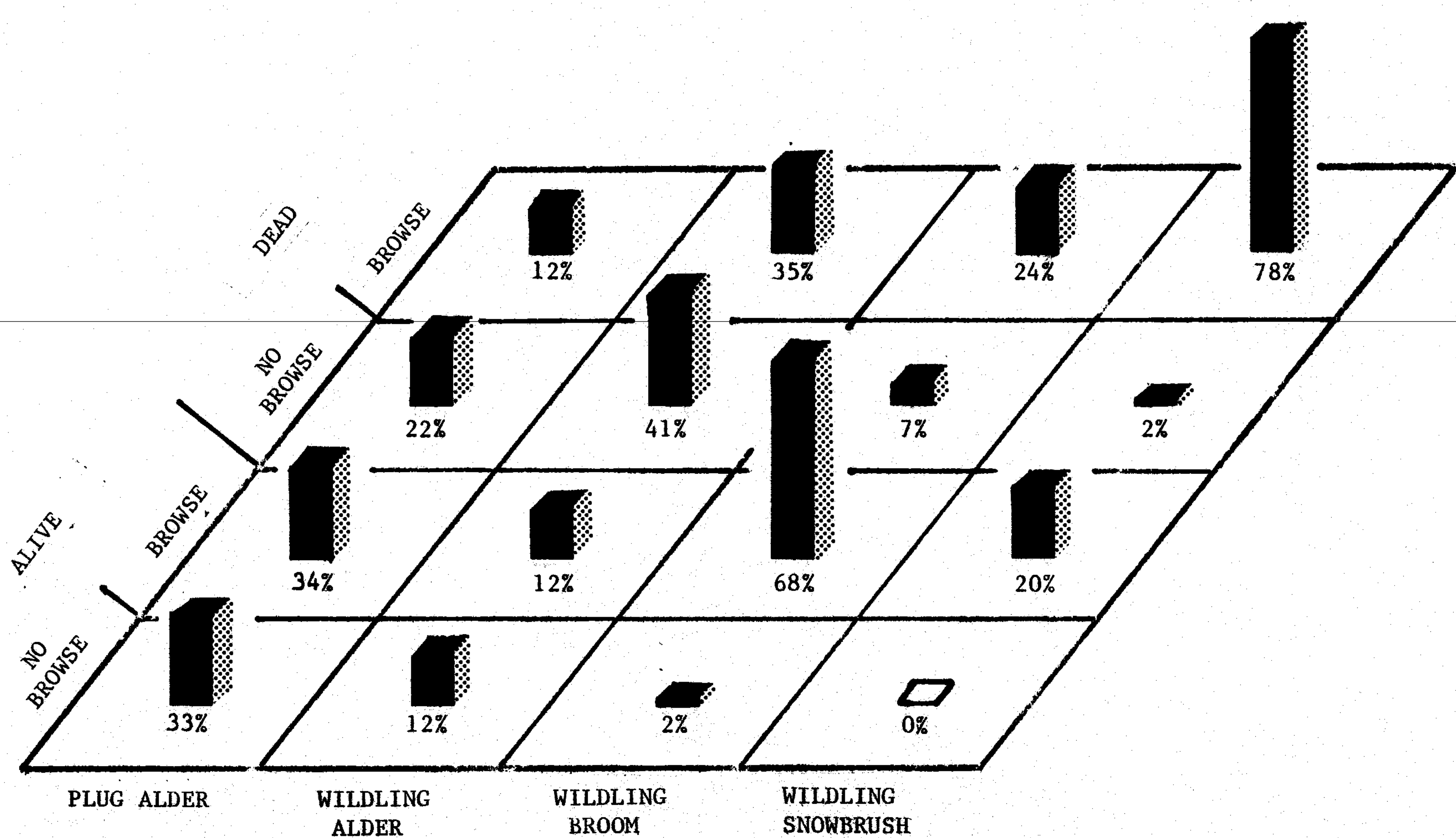

Figure 1. Average percent values for alive and dead by browsed and unbrowsed after one season's growth for plug alder, wildling alder, wildling broom and wildling snowbrush planted in 1979.

TABLE IV. SIMPLE LINEAR CORRELATIONS (r) OF SURVIVAL WITH DOUGLAS-FIR BA AND COVER WITH ASSOCIATED PROBABILITIES (p) OF A GREATER r VALUE.

Planting	End of year	BA		Cover		arc sin $\sqrt{\text{light}}$	
		r	P	r	P	r	P
<u>1978</u>							
Alder	1978	-0.86	0.03	-0.58	0.23	0.09	0.71
	1979	-0.53	0.28	-0.39	0.44	0.13	0.65
Broom	1978	-0.69	0.13	-0.68	0.20	0.76	0.13
	1979	-0.61	0.19	-0.20	0.76	0.83	0.04
<u>1979</u>							
Alder wildlings	1979	-0.61	0.20	-0.78	0.12	0.12	0.80
Alder plugs	1979	-0.77	0.13	-0.50	0.40	0.40	0.50
Broom	1979	-0.71	0.24	N.A.	N.A.[1]	0.53	0.40
Snowbrush	1979	-0.49	0.32	-0.76	0.13	0.52	0.40

[1]Not available.

understory competition in the absence of Douglas-fir may limit the numbers of underplanted alder at lower basal areas (Figure 2).

Trefoil Survival

The complete absence of survival, except where the seed was incorporated into mineral soil, suggests that trefoil seed cannot compete under precommercially thinned Douglas-fir.

Nitrogen Fixation

The operational environment appeared to partially control nitrogen fixation over the growing season. On individual days, however, no environmental variable appeared related to AR. A tight relationship between growth and nitrogen fixation was indicated by the correlations between allometric variables, nitrogen contents and AR (Tables VII, VIII, XI, and XII).

Environmental Effects

No discernable seasonal patterns were observed for either nodule or plant AR. Soil temperature and PMS appeared partially related, however, to nitrogen fixation over the growing season. Plots of AR, soil temperature and PMS over the season are in the Appendix.

Soil Temperature and PMS. Past research has indicated that individually PMS and nodule temperature have strong effects on AR with actinorhizal plants and legumes differing significantly in their response to temperature (Waughman, 1977). More specifically, alder and broom nitrogenase activities have exhibited different temperature

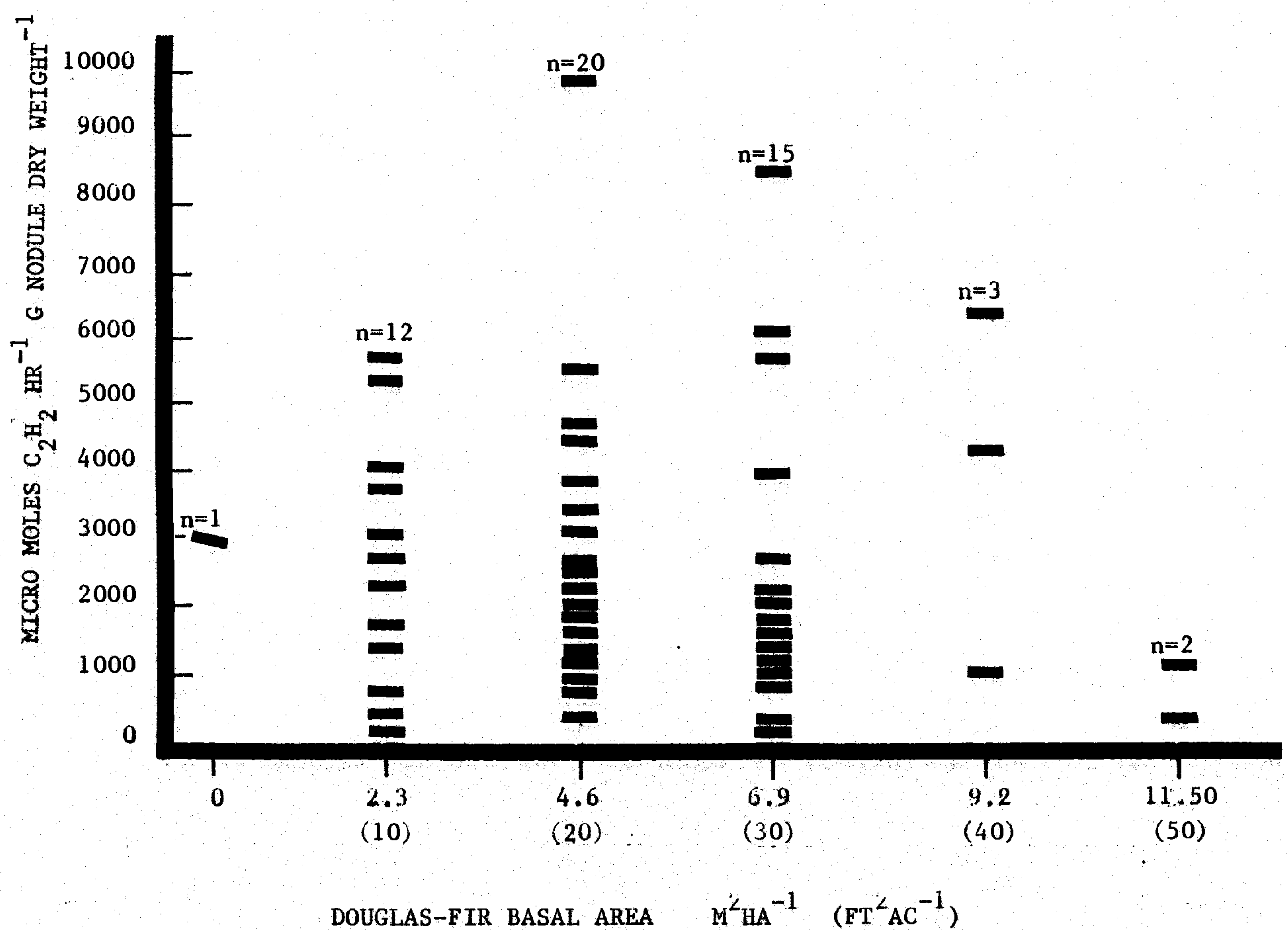

Figure 2. Plant AR versus basal area of surrounding Douglas-fir for intensively sampled alder.

response curves with alder reaching a maximum at a greater temperature and being attenuated more rapidly by lower temperatures than broom (Wheeler et al., 1979). PMS has also demonstrated a strong control over nitrogen fixation, with increasing severity of stress (decreasing water tensions) associated with lowered fixation rates (Sprent, 1972; McNabb et al., 1979; Perry et al., 1979).

For the seasonally sampled underplantings and naturally occurring species, PMS appeared to exert a stronger control over AR than did soil temperature through the growing season. This is supported by the large number of significant correlations between PMS and AR compared to soil temperature (Table V, Appendix).

Furthermore, the underplanted and naturally occurring species differ tantalizingly in the way that their nodule and plant AR rates are correlated with PMS. The underplantings strong negative correlation with PMS (AR decreases as PMS becomes more severe) suggests that through the season under precommercially thinned Douglas-fir, nitrogen fixation is limited by daytime water availability. The log correlations suggest that the attenuation is rapid. This is likely explained again by the damaged roots of the underplantings not being able to adequately supply the rest of the plant with water, as well as increased water use from the surrounding Douglas-fir stand and understory.

Conversely, the positive correlation of AR with PMS (AR increases as PMS becomes more severe) for the naturally occurring broom and snowbrush suggests that for the more open grown naturally occurring species, PMS may enhance nitrogen fixation. If the open grown plants

TABLE V. LINEAR CORRELATIONS (r) OF PMS AND SOIL TEMPERATURE WITH AR FOR POOLED SAMPLING DATES. PROBABILITY (p) OF A LARGER (r) VALUE GIVEN BELOW.

	Underplanted		Naturally Occurring		
	Alder	Broom	Alder	Broom	Snowbrush
PMS With					
Nodule AR	N.S.*	N.S.	N.S.	0.36 0.07	N.S.
Log nodule AR	-0.59 0.001	-0.31 0.11	N.S.	N.S.	0.38 0.03
Plant AR	N.S.	N.S.	N.S.	0.35 0.08	N.S.
Log plant AR	-0.64 0.0002	-0.56 0.002	N.S.	N.S.	0.35 0.04
Soil Temperature With					
Log nodule AR	N.S.	N.S.	N.S.	N.S.	0.38 0.03
Plant AR	N.S.	-0.33 0.03	N.S.	N.S.	N.S.
Log plant AR	N.S.	N.S.	N.S.	N.S.	0.27 0.13

*Significance level set at 0.15 for inclusion in table.

had larger stores of photoassimilate, water stress could reduce top expansion thus making carbohydrate available for nitrogen fixation. The larger and healthier root systems of the naturally occurring plants could also have kept their nodules under less negative moisture stress as indicated by their slightly less negative seasonal PMS means (Table VI).

The lack of any correlation between PMS and AR for the naturally occurring alder, however, suggests that snowbrush and broom may differ significantly from alder in their response to moisture stress when grown in the open. Broom and snowbrush are found typically on drier sites than red alder. Although snowbrush nodule AR has been observed to be negatively correlated with PMS on individual days (McNabb *et al.*, 1979) the positive correlation over the season may indicate that broom and snowbrush have an adaptive competitive advantage if they can fix and accumulate nitrogen during the drier parts of the year when other nitrogen fixers cannot.

Available Light. The lack of any correlation between available light and BA in the thinned plots is inconsistent with past studies that show a relationship between stocking and light transmission (Kittredge, 1948; Del Rio and Berg, 1979). Average light values in the thinned stands correspond approximately to basal areas between 26.5 and 33.5 m^2ha^{-1} (115 and 146 ft^2ac^{-1}) (Del Rio and Berg, 1979). The underplanted stands, however, averaged only 5.53 m^2ha^{-1} (24 ft^2ac^{-1}) suggesting that something other than the Douglas-fir canopy, perhaps understory vegetation, was intercepting light.

TABLE VI. MEAN SEASONAL NODULE AND PLANT AR RATES, SOIL TEMPERATURES AND PMS VALUES WITH ASSOCIATED AND STANDARD ERRORS FOR POOLED SEASONAL DATA AND INTENSIVELY SAMPLED ALDER.

Plant Type	Nodule AR µ moles C_2H_4 g nod. d.w.$^{-1}$ hr^{-1} $\bar{X}$	(S.E.)	Plant AR µ moles C_2H_4 plant^{-1} hr^{-1} $\bar{X}$	(S.E.)	Plant AR/leaf dry weight µ moles C_2H_4 plant^{-1} hr^{-1} g leaf d.w.$^{-1}$	Soil Temperature °C $\bar{X}$ (S.E.)	PMS 10^6 Pa $\bar{X}$ (S.E.)
Pooled Seasonal Dates							
Underplanted							
Red alder	51	(32)	4.12	(2.27)	0.54	13.65 (0.73)	- 9.82 (1.54)
Broom	190	(65)	4.81	(3.87)	21.86	14.54 (0.7.)	-13.36 (1.62)
Significance level	0.06		N.S.				
Naturally Occurring							
Red alder	30	(8)	6.37	(2.89)	1.24	15.40 (1.91)	- 8.40 (1.22)
Broom	236	(117)	9.78	(5.42)	8.15	17.21 (1.48)	-11.5 (1.52)
Snowbrush	10	(4)	1.49	(0.61)	0.18	15.40 (1.15)	-10.51 (1.16)
Intensively Sampled Alder							
Wildlings	24	(4)	5.91	(1.75)	3.65	13.35 (0.43)	- 8.41 (0.37)
Plugs	27	4	6.36	2.05	3.52	11.83 (0.23)	- 6.31 (0.33)

Douglas-fir Basal Area. The basal area of the surrounding Douglas-fir may, however, define maximum rates of nitrogen fixation for the underplanted alder. This is suggested by the plot of plant AR versus BA for the intensively sampled alder (Figure 2) that shows an apparent maximum around 4.60 m^2ha^{-1} (20 ft^2acre^{-1}).

Because the trees are the largest plants in the ecosystem, however, they logically should exert the greatest influence on anything planted in the understory and hence could limit maximal AR rates at higher basal areas. If the lower basal areas represent areas that were not thinned because they were already open, they thus may have had an already large presence of brush, explaining the lowered numbers of alders and AR rates.

An alternative explanation is, that the frequency relationships with BA may reflect the predilictions of the planters. Although instructed to plant without regard to existing plant competition, human nature suggests that they would have tended to avoid either brushy or dense areas.

A contrary fact is, however, that if understory species were responsible for the variation in AR rates in a given BA class by attenuating light then this should have been reflected by a significant correlation between available light and AR for the intensively sampled alder. The Ozalid pads were placed on the ground adjacent to the plants that were assayed and thus should have been influenced by shading from the adjacent understory. Neither plant nor nodule AR were, however, related to available light. This further suggests the greater importance of PMS over the growing season as a controlling factor for fixation under Douglas-fir.

Individual Sampling Dates. On single dates, either for the seasonally sampled species or for the intensively sampled alder, neither PMS nor soil temperature were significantly related to either nodule or plant AR. This contradicts the previously cited studies which indicate that PMS and nodule temperature significantly affect nitrogen fixation. The small number of plants and the large variation in AR between plants on individual dates during the season may have prevented the definition of these relationships. Plant numbers appeared, however, more than adequate for the intensively sampled alder.

A possible explanation is that the PMS and soil temperature values recorded in the field are not within the ranges over which they control AR or do not vary enough. The mean temperatures recorded (see Appendix) are, however, well within the lower ranges of the response curves (2°C to 35°C) established by past studies. The actinorhizal species in particular should have shown a response because of their exponential response to temperature (Waughman, 1977). The PMS values are also within the range (-4.8 to $-8.6 \ 10^5$ Pa) that reduced nodule AR threefold and reduce nodule weight nearly 20% for *L. arboreus* (Sprent, 1973) and which reduced nodule AR about five fold for snowbrush (McNabb and Geist, 1979).

Photosynthate availability has been strongly associated with nitrogen fixation by Wheeler (1971) in explaining diurnal fluctuations in AR for *A. glutinosa*, and Gordon and Wheeler (1978) demonstrated a strong link between photosynthesis and nitrogen fixation. Air temperature, soil temperature, insolation and PMS all affect photosynthesis and thus indirectly, nitrogen fixation. Hysteresis between the onset of environmental controls over photosynthesis and its concomitant effect on nitrogen fixation could partially explain the lack of correlation between PMS and AR for the intensively sampled alder. The effects of severe PMS as reduced photoassimilate could plausibly not reach the nodules until the evening.

Allometry and AR

Plant and Nodule AR. The most striking result was the closeness of plant AR for the underplanted broom and alder, despite significant differences in nodule AR rates (Table VI). Lower nodule AR rates in alder were compensated by greater per plant nodule mass, compared to broom which had much greater nodule AR rates but much lower per plant nodule weights. This tendency toward equal per plant rates was also observed between the naturally occurring broom and the actinorhizal alder and snowbrush. This phenomena has also been observed between red alder and Sitka alder by Carpenter *et al.* (1979).

This could imply that for plants of equal size, legumes and actinorhizal species may expend about the same amount of metabolic energy to fix nitrogen despite differences in endophytes, nodule proportions and fixation rates.

Also striking was the complete lack of correlation between nodule AR or its log and plant organs for any species at any time compared to the relatively good correlations between plant AR and organ dry weights (Tables VII and VIII). Although the latter are undoubtedly caused partially by the tight allometric correlations between nodule dry weights with other organs, it also implies that nitrogen fixation per plant keeps apace with plant size.

Leaves, Stems and Nodules. Leaves may be less important than stems for nitrogen fixation in broom. This is suggested by higher correlations for stems with nodules and plant AR than for leaves (Tables IX, VII), and is consistent with brooms leaf habit. Its trifoliate leaves are very small and its leaf/top ratio is much less than alders' (Table X). The importance of broom stems as photosynthetic organs is also suggested by broom's very high AR rates during a brief warm period in February when it had no leaves. The importance of broom stems fits with the report by Wheeler *et al*. (1979) of a cessation of nodule activity for broom when its young green stems are killed by winter frost.

For underplanted alder; the high correlations between leaf and nodule dry weights for seasonally and intensively sampled plants, and the tight correlation between leaf dry weight and plant AR for the intensively sampled alder suggest that photosynthetic capacity and nitrogen fixation are tightly linked. Although no direct measurements of photosynthesis were made, the relationships between leaf weights, nodule weights and nitrogen fixation are consistent with studies linking leaf weight with nodule weight and AR in *A. glutinosa* (Dawson, and Gordon, 1979) and net photosynthesis with plant AR and nodule fresh weight among 12 clones of *A. glutinosa* (Gordon and Wheeler, 1978).

TABLE VII. LINEAR CORRELATIONS (r) BETWEEN LOG PLANT AR AND PLANT ORGANS FOR POOLED SEASONAL SAMPLING. PROBABILITIES (p) OF A GREATER r VALUE ARE BELOW.

	Underplanted		Naturally Occurring		
Log Plant AR With	Alder	Broom	Alder	Broom	Snowbrush
Stem dry weight	N.S.*	0.51 0.005	N.S.	0.41 0.04	N.S.
Leaf dry weight	0.33 0.08	N.S.	0.33[1] 0.12	N.S.	N.S.
Nodule dry weight	0.36 0.04	0.55 0.001	0.45 0.05	0.60 0.002	0.26 0.13

[1]Correlation with plant AR, not log plant AR.

*Significance level for inclusion in table set at 0.15.

TABLE VIII. LINEAR CORRELATIONS (r) FOR INTENSIVELY SAMPLED ALDER BETWEEN PLANT ORGAN DRY WEIGHTS AND PLANT AR. PROBABILITY (p) of A GREATER VALUE ARE GIVEN BELOW.

	Leaf d.w.	Nodule d.w.	Stem d.w.	Root d.w.
Nodule d.w.	0.92 0.0001			
Stem d.w.	0.78 0.0001	0.71 0.0001		
Root d.w.	0.64 0.0001	0.74 0.0001	0.75 0.0001	
Top d.w.	0.89 0.0001	0.81 0.0001	0.98 0.0001	0.75 0.0001
Plant d.w.	0.86 0.0001	0.84 0.0001	0.95 0.0001	0.88 0.0001
Plant AR	0.90 0.0001	0.87 0.0001	0.63 0.001	0.55 0.001
Nodule AR	0.38 0.005	0.21 0.13	0.26 0.06	0.11 0.43

The naturally occurring broom and alder do not, however, show significant correlation between leaf and nodule dry weights (Table IX). Correlations with the log plant AR are, however, very similar to the underplantings (Table VII).

The naturally occurring snowbrush is, however, more problematical. Of its organs, only nodule dry weight was related to plant AR, and nodule dry weights were not correlated to other organs contrary to naturally occurring broom and alder. This may indicate that for young snowbrush, nitrogen fixation is not limited by photosynthetic capacity but is constrained by the amount of nodules per plant. All broom and alder plants were nodulated, but finding nodulated snowbrush plants was often difficult. Thus for young snowbrush, per plant nitrogen fixation may be controlled more by the degree of nodule formation than photosynthate production or allocation. This may be related to the difficulty in nodulation caused by reduced endophyte populations (Youngberg _et al_., 1979).

Nitrogen Contents, Allometry and AR. The lack of significant correlations for percent foliar nitrogen with allometric and AR variables (Tables XI, XII) compared to the much better correlations obtained for total foliar nitrogen (Tables XII, XIII) suggests that total foliar nitrogen is the better measure of plant nitrogen fixation. Autocorrelation, however, very likely explains the very high correlations between the variable pairs of total leaf nitrogen and leaf weight, and total stem nitrogen and stem weight. Auto and proxy correlation must similarly explain part of the high correlation between

TABLE IX. LINEAR CORRELATIONS (r) OF PLANT ORGANS FOR POOLED SEASONAL DATES. ASSOCIATED PROBABILITIES (p) OF A LARGER r ARE BELOW.

Variable Pair	Underplanted		Naturally Occurring		
	Alder	Broom	Alder	Broom	Snowbrush
Leaf d.w. * top d.w.	0.30 0.08	0.66 0.0001	0.79 0.0001	0.54 0.004	0.91 0.0001
Leaf d.w. * stem d.w.	0.27 0.10	0.86 0.0001	0.49 0.02	N.S.	0.77 0.0001
Leaf d.w. * nod. d.w.	0.72 0.0001	0.36 0.03	N.S.	N.S.	N.S.
Stem d.w. * nod. d.w.	N.S.	0.87 0.0001	0.49 0.02	0.49 0.008	N.S.
Top d.w. * nod. d.w.	0.26 0.13	0.86 0.0001	0.39 0.06	0.48 0.01	N.S.

TABLE X. MEAN DRY WEIGHTS, ALLOMETRIC RATIOS AND LEAF N FOR UNDERPLANTED ALDER AND BROOM AND NATURALLY OCCURRING ALDER, BROOM AND SNOWBRUSH POOLED OVER SAMPLING DATES.

	Leaf d.w.g	Stem d.w.g	Top d.w.g	Nod. d.w.g	Nod. % (Nod. d.w. /Top d.w.	Leaf % (Leaf d.w. /Top d.w.)	Leaf d.w./ Nod. d.w.	Leaf N content (percent weight)	Stem N content (percent weight)
<u>Underplanted</u>									
Red alder	1.08	6.84	7.50	0.17	3.37	14	6.35	2.42	0.94
Broom	0.23	4.94	5.16	0.02	0.65	4	11.0	2.64	1.66
Probability of a greater t statistic given H_0: $\bar{X}_1 = \bar{X}_2$	0.01	0.18	0.12	0.0001	0.0001	0.002	0.01	0.50	0.004
Intensively sampled alder	1.71	3.87	5.57	0.20	6.01	31	8.55	2.70	N.A.
<u>Naturally Occurring</u>									
Red alder	5.12	8.81	13.93	0.23	2.71	37	22.26	2.53	1.11
Broom	1.20	6.01	7.21	0.03	0.52	17	40.00	3.27	1.81
Snowbrush	8.39	9.05	17.44	0.22	2.12	48	38.14	1.93	0.81

TABLE XI. LINEAR CORRELATIONS (r) BETWEEN PERCENT LEAF N AND AR FOR POOLED SEASONAL SAMPLING. PROBABILITIES (p) OF A GREATER r VALUE ARE BELOW.

Percent foliar N with	Underplanted		Wild		
	Alder	Broom	Alder	Broom	Snowbrush
Log plant AR	N.S.*	0.59 0.01	N.S.	N.S.	N.S.
Nodule AR	N.S.	N.S.	N.S.	N.S.	0.36 0.07
Log nodule AR	0.36 0.12	0.47 0.06	N.S.	N.S.	N.S.

*Significance of level of 0.15 needed for inclusion in table.

TABLE XII. CORRELATIONS FOR INTENSIVELY SAMPLED ALDER OF PERCENT FOLIAR NITROGEN AND TOTAL FOLIAR NITROGEN WITH ALLOMETRIC VARIABLES AND AR WITH PROBABILITIES (p) OF A GREATER r VALUE BELOW.

	Leaf dry weight	Nodule dry weight	Stem dry weight	Root weight	Plant dry weight	BA	Percent light	Nodule/ top ratio	Leaf/ top ratio	Leaf/ nodule ratio	Nodule AR	Plant AR
Percent foliar nitrogen	N.S.*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	−0.38 0.005	−0.35 0.01	N.S.	N.S.
Total foliar nitrogen	0.99 0.0001	0.91 0.0001	0.76 0.0001	0.62 0.0001	0.84 0.0001	N.S.	N.S.	−0.30 0.03	N.S.	0.23 0.09	0.40 0.003	0.91 0.0001

*Significance level of 0.15 needed for inclusion in table.

TABLE XIII. CORRELATIONS (r) OF TOTAL NITROGEN IN LEAVES AND STEMS WITH ALLOMETRIC AND AR VARIABLES WITH PROBABILITIES (p) OF A GREATER r BELOW.

Total Nitrogen from	Leaf Dry Weight	Nodule Dry Weight	Stem Dry Weight	Leaf/Top Ratio	Leaf/ Nodule Ratio	Log Nodule AR	Plant AR
Underplantings							
Alder leaves	0.99 0.0001	0.79 0.0001	N.S.*	0.79 0.0001	N.S.	N.S.	N.S.
Alder stems	N.S.	0.45 0.008	0.86 0.001	N.S.	N.S.	N.S.	N.S.
Broom leaves	0.95 0.0001	N.S.	N.S.	0.75 0.0002	N.S.	N.S.	N.S.
Broom stems	N.S.	0.84 0.0001	0.77 0.0001	N.S.	N.S.	-0.40 0.05	N.S.
Naturally Occurring							
Alder Leaves	0.99 0.0001	N.S.	0.87 0.0002	N.S.	0.78 0.005	-0.53 0.09	N.S.
Alder Stems	N.S.	N.S.	0.97 0.0001	N.S.	N.S.	N.S.	N.S.
Broom Leaves	0.94 0.0001	N.S.	N.S.	0.60 0.01	N.S.	N.S.	N.S.
Broom Stems	N.S.	0.61 0.009	0.93 0.001	N.S.	N.S.	N.S.	0.47 0.06
Snowbrush leaves	0.89 0.0001	N.S.	0.74 0.0001	N.S.	N.S.	N.S.	N.S.
Snowbrush stems	0.69 0.0001	N.S.	0.96 0.0001	N.S.	N.S.	N.S.	N.S.

*Significance level of 0.15 needed for inclusion in table.

total nitrogen values and other allometric variables for seasonally sampled alder and broom and intensively sampled alder (Tables XII, XIII).

For the pooled seasonal data, correlations of nodule dry weights with total foliar nitrogen for alder and with total stem nitrogen in broom stems, compared to the lack of correlation between their total nitrogen values and AR (Table XIII) suggest, however, that nodule mass may be more limiting than their nitrogen fixation rates on nitrogen accretion over the growing season. The large variability in AR rates over the season (Table VI) compared to the much less variable nodule weights could also, however, explain the lack of correlation with AR.

For the intensively sampled alder, total foliar nitrogen was, however, highly correlated to both nodule and plant AR (Table XII). This suggests, that as should be expected, the total amount of nitrogen in a plant is also a function of the fixation rate of the nodules as well as nodule mass. These significant correlations probably result from sampling a large number of plants near the peak of their growing season. In contrast, the sporadic positive correlations between these variables for individual sampling dates through the season likely resulted from the small number of plants sampled and seasonal variation in nitrogen fixation.

As the leaf/top and leaf/nodule ratios increase, however, the nitrogen available to those leaves may become diluted, decreasing percent foliar nitrogen, although total foliar nitrogen is increasing. This is supported by the negative correlations between percent foliar nitrogen and the leaf/top and leaf/nodule ratios for the intensively sampled alder (Table XII).

Photosynthesis-Nitrogen Fixation Feedback Loop. These correlations could imply that for alder under the Douglas-fir, leaf area has a higher immediate priority for photosynthate than does nitrogen fixation. As the amount of foliage increases, the nitrogen in the leaves is spread more thinly. Nodule formation and fixation, however, keep apace with leaf development as seen by the correlations for the seasonally sampled alder between leaf and stem total nitrogen values with nodule weights (Tables XI, XII), alder leaf weights and AR (Table VIII), and the very tight correlation between leaf and nodule weights for the underplanted alder (Table VIII).

Nodule formation and nitrogen fixation may thus be triggered by some feedback system caused by too little nitrogen in the photosynthetic organs. This could be caused by an initiation of additional root growth to simply increase the number of infection sites or by some other more subtle control over endophyte behavior such as increasing the susceptibility of roots to infection by an increase in available sugars, hormones, antibiotics or other metabolites.

For the naturally occurring broom this is supported by the positive correlation between plant AR and total stem nitrogen. More problematical, however, are the negative correlations between the log of nodule AR and total nitrogen in underplanted broom stems and naturally occurring alder leaves. These may be statistical flukes because neither nodule AR nor its log were significantly correlated to any other variable.

Nodule/Top Ratio. For the intensively sampled alder, the plot of the nodule/top ratio to top weight (Figure 3) suggests that nodule weights in juvenile alder approach a constant proportion of plant mass. The higher proportion of leaves and nodules for small plants may also suggest that development of photosynthetic and nitrogen fixing capacities occurs before stem growth.

Light, Allometry and AR. Severe shade (10% of full sunlight) can reduce nitrogen fixation rates as reported by Sprent (1973) for *Lupinus arboreus* although other studies report nitrogen fixation occurring between 8 and 15 percent of full sunlight for actinorhizal and legume species (Sprent, 1973, 1976; Gibson, 1966; Pate, 1961; Wheeler and Bowes, 1974; Gordon and Wheeler, 1978). The light levels for underplanted broom and alder averaged about 8%, and ranged from 4% to 30% of full sunlight. Nitrogen fixation in the underplanted broom and alder was thus likely affected by reduced insolation. The greater than ten-fold reduction in average available light values between the underplantings and naturally occurring plants may explain differences in organ weights and allometric ratios between the two groups.

A given leaf area in the underplantings would not be able to reduce as much nitrogen as it would in the open with more light and greater photosynthetic efficiency. This is reflected in the large differences in plant AR/leaf dry weight ratios (Table VI). The naturally occurring red alder is reducing about 2.3 times more acetylene per unit leaf weight than the underplanted alder.

The seemingly greater efficiency of broom leaves for nitrogen fixation as compared to the alder, is belied, however, by the

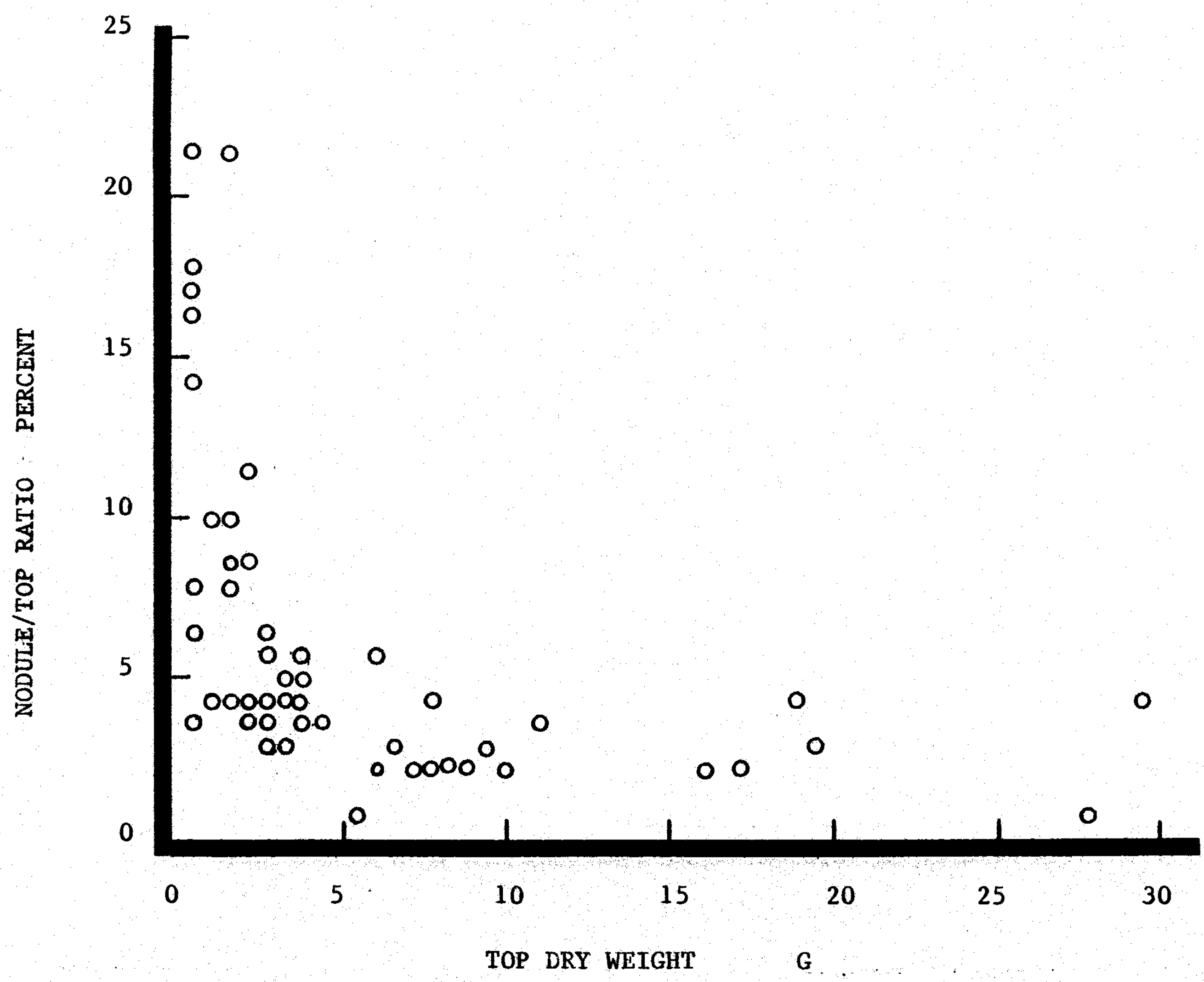

Figure 3. Nodule/top dry weight ratio versus top dry weight for intensively sampled alder.

probable significant role of young green broom stems as photosynthetic organs. The seemingly greater efficiency of underplanted broom leaves compared to the naturally occurring broom - just the opposite of the alder's ranking - likely results from the much lower quantities of foliage (3%) on the underplanted broom compared to 17% for the naturally occurring. With only 3% of top dry weight as foliage, photosynthate production by broom stems is likely even more important for underplanted broom.

For the naturally occurring broom and alder, greater ambient light levels mean fewer leaves are required to power a given plant's nodules to achieve an adequate level of nitrogen fixation. This is belied, however, by the greater leaf/nodule and leaf/top ratios for the naturally occurring species (Table X). These much greater leaf quantities undoubtedly reflect the much greater light availability for the open grown naturally occurring broom and alder.

The much lower leaf/top ratio for the underplanted alder and broom could have been caused by the large amounts of dead stem material in the 1978 transplants. The lower leaf/top ratio may thus have been an artifact of the planting stock.

Winter Nitrogen Fixation. For alder, the lack of foliage combined with its very low or non-existing AR rates suggests that winter AR is powered by stored photosynthate. The lack of nitrogenase activity in about half of the individuals sampled is consistent with Pizelle's observation of sporadic N fixation following leaf fall and dormancy in black alder (cited by Wheeler and McLaughlin (1979)). Although alder

AR is attenuated more by low temperature than broom (Wheeler _et al_., 1979), alders with and without activity were observed over the same range of soil temperatures (5° to 9°C), possibly resulting from genetic differences in response to the environment or differences in stored photosynthate.

The lack of nodule activity for naturally occurring snowbrush, despite the presence of foliage, could have resulted from the poor condition of the leaves, which were partially browned on all plants. The complete absence of activity compared to the leafless alder could in addition be explained by snowbrush having less reserve photosynthate available to its nodules, a stronger dormancy control, or both. Although AR in the actinorhizal snowbrush should be attenuated more by low temperature than broom, the temperatures observed (5° to 11°C) on that sampling date seem low enough to not preclude nitrogenase activity.

The importance of broom stems as photosynthetic organs in powering nitrogen fixation is further supported by broom's very high AR rates during this period when it had no leaves. This also suggests that broom remains able to assimilate carbon and nitrogen during the socalled dormant period if environmental conditions are favorable. Soil temperatures averaged about 10°C for the naturally occurring and about 6°C for the underplanted broom for this time. These results are consistent with the findings by Wheeler _et al_. (1979), for scotch broom in the Coast Range of Oregon. Compared to alder and snowbrush, broom thus appears best able to utilize favorable periods of winter weather for carbon and nitrogen fixation.

SILVICULTURAL IMPLICATIONS

The survival and nitrogen fixation by the underplanted broom and alder indicate that these species have the potential to be used silviculturally to add nitrogen to similar forest ecosystems in the Cascades.

Species and Propagules

Survival, nitrogen fixing ability, weed potential, and fiber production are pertinent criteria for selection of a nitrogen fixer to be introduced under young Douglas-fir.

Survival

Of the propagules tested, the plug alders offer the best potential for survival. Although physically the smallest, and despite a long period of cold storage and warm dry planting weather, they achieved 67% survival - only three percent below the 1979 broom's survival. Survival of wildling alder, in comparison, appears poor regardless of long or short storage times, planting weather or crew quality.

Survival of wildling broom, although very good in 1979, appears contingent upon short storage times, as suggested by the differences in survival after one season between the 1978 and 1979 plantings. Nursery grown broom may also not prove any hardier. This likely would complicate the production and outplanting of broom as compared to alder. Plug alder thus appears to offer the greatest probability for survival success combined with ease of handling. Professional tree planters suggested that the plug alders were twice as easy to plant as the wildlings.

The positive correlations between first year survival and BA suggest that the Douglas-fir be thinned as much as possible to enhance survival. The frequency plot for the intensively sampled alder (Figure 2), and the weakness of the relationships between Douglas-fir stocking and survival, soil temperature, available light, and PMS suggest strongly, however, that survival is also dependent upon understory competition.

Without quantifying data on understory competition, a prudent assumption is that survival will be greater in precommercially thinned stands with less understory competition. Understory brush competes for light and moisture and provides shelter for browsing rodents. Thus to maximize survival and subsequent nitrogen fixation, understory competition should be minimal. This could be achieved by restricting planting to sites with little understory or by herbicide removal of understory competition.

Fixation Potential

Although underplanted broom had a much greater average nodule fixation rate, its per plant rate did not differ significantly from alders. Thus on the basis of one year's performance, the two species appear about equally promising. Future fixation is, however, more difficult to assess.

Because fixation appears to be proportional to plant size, an individual alder should eventually fix more nitrogen than an individual broom. The relationship between growth and nitrogen fixation also suggests that nitrogen inputs can be increased by selecting, propagating and planting fast growing clonal lines of alder as suggested by Dawson and Gordon (1979).

Weed Potential

Both alder and broom flower precociously. Underplanted broom, however, was observed to produce seed the same year it was planted. Broom seeds also have also been observed by the author to germinate and grow in heavy sod. Broom thus has the potential to spread within a stand. Because broom seeds can persist up to 17 years in the litter of a closed Douglas-fir stand following release from overtopping broom (author's observation) broom thus has the potential to rapidly occupy a site following commercial thinning or harvest of the Douglas-fir.

Alder seeds, in comparison, although produced copiously, are thin coated and short lived. They are best adapted to colonizing bare soil and can germinate and grow under reduced (2 to 65% full sunlight) light levels following thinning (Ruth 1968). Alder thus offers the greater probability of staying at a specified stocking level within a stand. The greater mobility of alder seed, however, offers an increased probability of alder moving into adjacent harvested areas. Regrowth of alder following commercial thinning or harvest would only likely occur, however, if living plants were present to provide seed.

Although both species have weed potential, control appears easier with alder. Both species can be killed by herbicides presently registered for forestry use. In the absence of aerial chemical application, however, surviving alders, larger in diameter and more upright than broom, could easily be cut with a powersaw or injected with herbicide.

Fiber Production

Broom offers very little prospect for utilization. It has very small diameter branchy stems, weak wood and its fibers are shorter than alder's. Harvesting broom on steep terrain is simply unfeasible with present or expected technology.

Once regarded solely as a weed, red alder is currently being utilized more intensively as a source of wood and fiber. Its weaker wood and shorter fibers are currently acceptable for furniture and pulp and offers potential use as a flakeboard core for Douglas-fir plywood. As conifer fiber becomes scarcer (Beuter *et al*., 1976), alder will undoubtedly become more valuable despite its smaller size and poorer form. Given its rapid growth rate and an absence of frost and snow damage, merchantable alder could conceivably be available for harvest during a commercial thinning or the final harvest of Douglas-fir. Alder thus has a clearly greater potential for producing useful fiber.

Future Research

More information is needed on a number of aspects to reduce the uncertainty associated with the application of these possible sources of nitrogen fertilization.

Survival

Although survival appears to stabilize in the second season after planting, the roles of brush and Douglas-fir competition need to be better defined. Measuring the effects of Douglas-fir and understory competition separately would allow the manager to decide whether a given stand would need more thinning or brush control to achieve adequate survival of the nitrogen fixers, and whether it would be economically feasible to do so.

Because the underplanted alder and broom were not adapted to the site, they may be susceptable to freezing and cold injury. This could reduce their future survival and growth and should be monitored.

Nitrogen Fixation and Growth

Future nitrogen inputs can be surmised from a single year of data given the strong relationships between nitrogen fixation and plant size. To more accurately assess inputs, nitrogen contents, nodule masses and fixation rates should be periodically measured on the underplanted alder and broom. This would also allow clarification of the relationship between growth and nitrogen fixation and a better determination of the number of plants required to achieve a given level of nitrogen input.

Weed Potential

Seed production and germination of alder and broom should also be monitored. The conditions under which any germination and growth occurs should be noted. This will aid in the containment of these species.

Douglas-fir Response

Whether Douglas-fir will respond, and the timing and magnitude of the response to the underplanted nitrogen fixers is the most critical question. Also pertinent are related changes in soil characteristics such as pH, organic matter, bulk density, lowered C:N ratios and higher turnover rates for nitrogen in the stand (Tarrant and Miller, 1963). These variables should be monitored over time as with survival, nitrogen fixation and weed potential.

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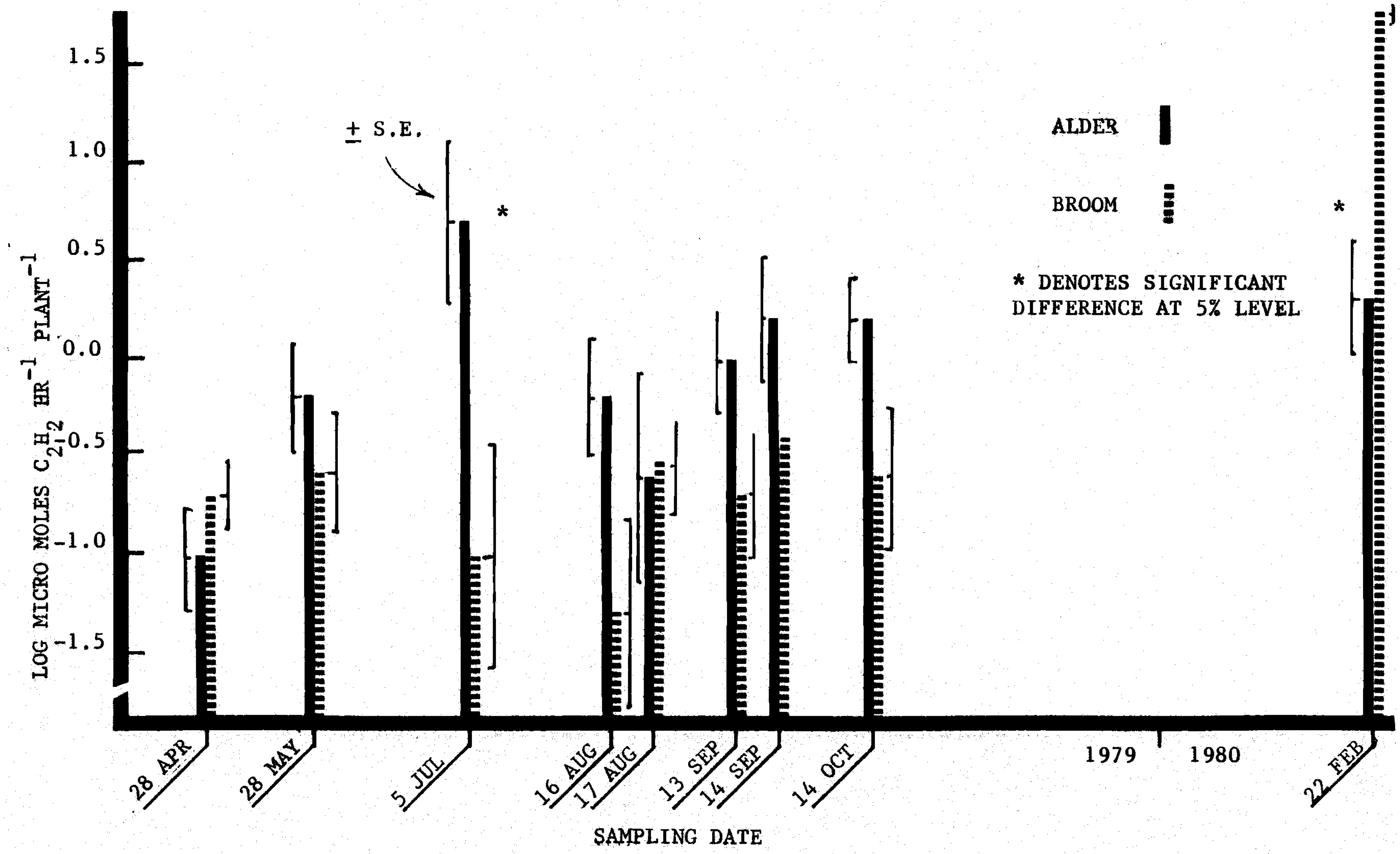
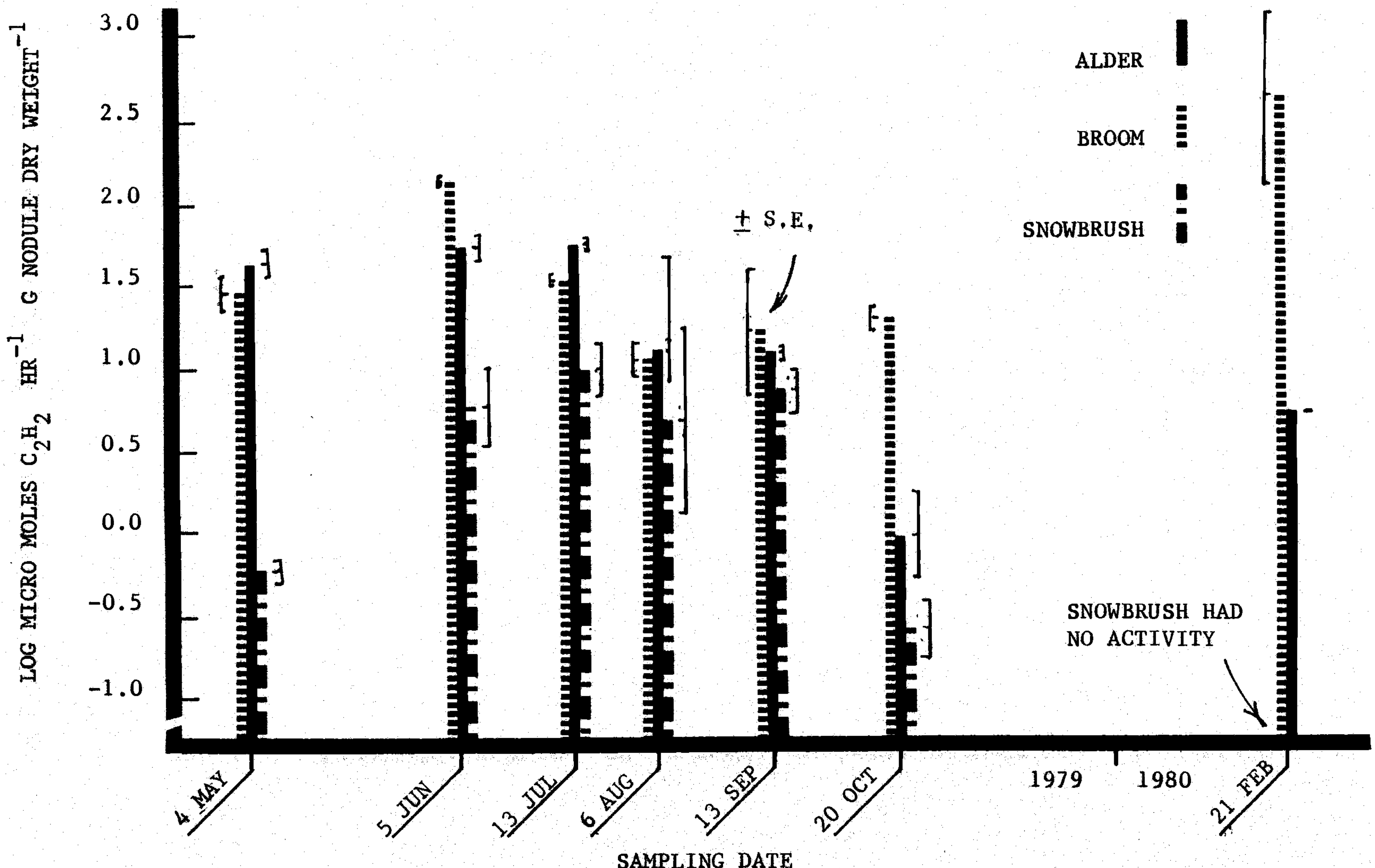
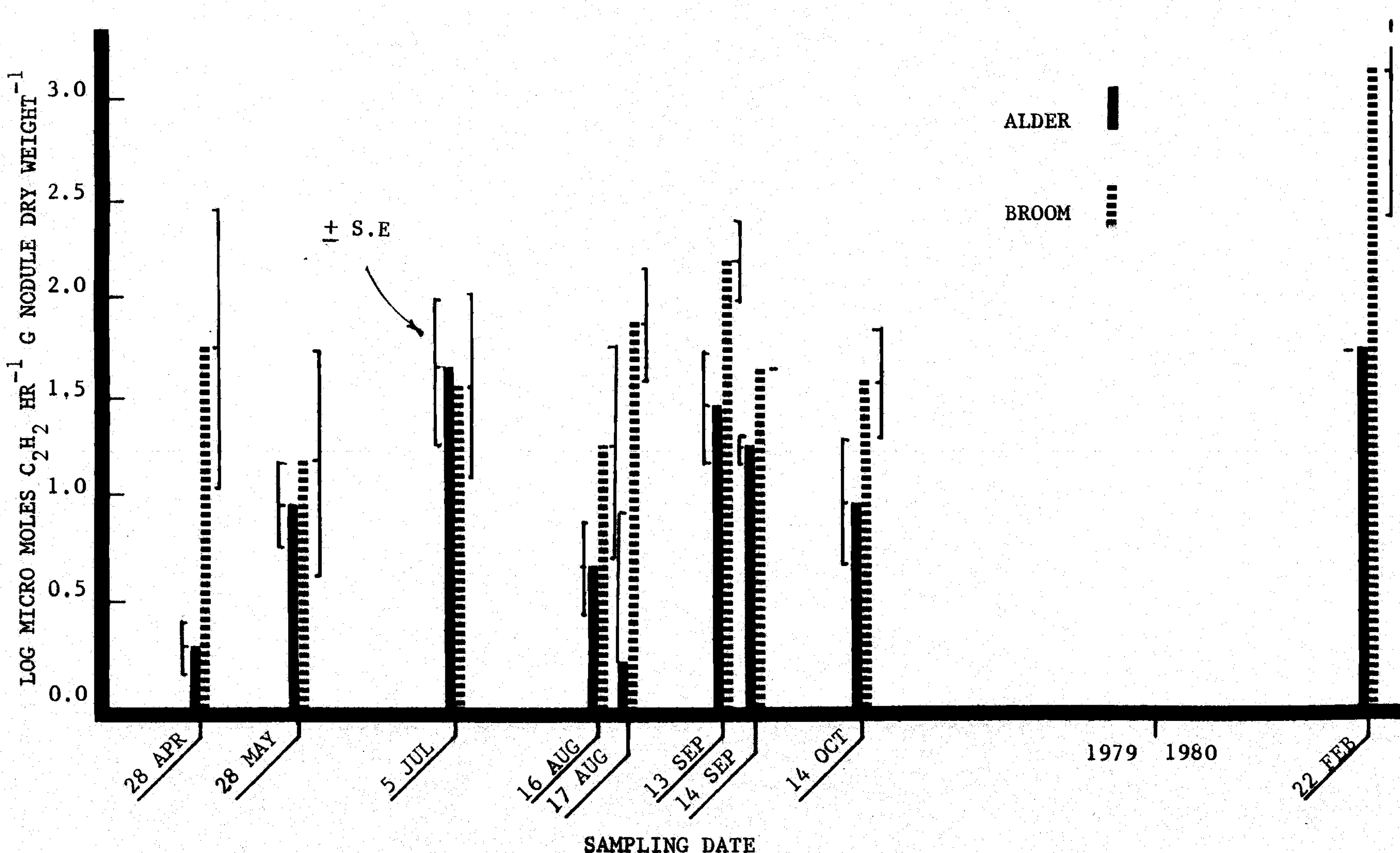
APPENDIX



Mean log plant AR rate versus sampling date for underplanted broom and alder.



Mean log nodule AR rate versus sampling date for naturally occurring alder, broom and snowbrush.



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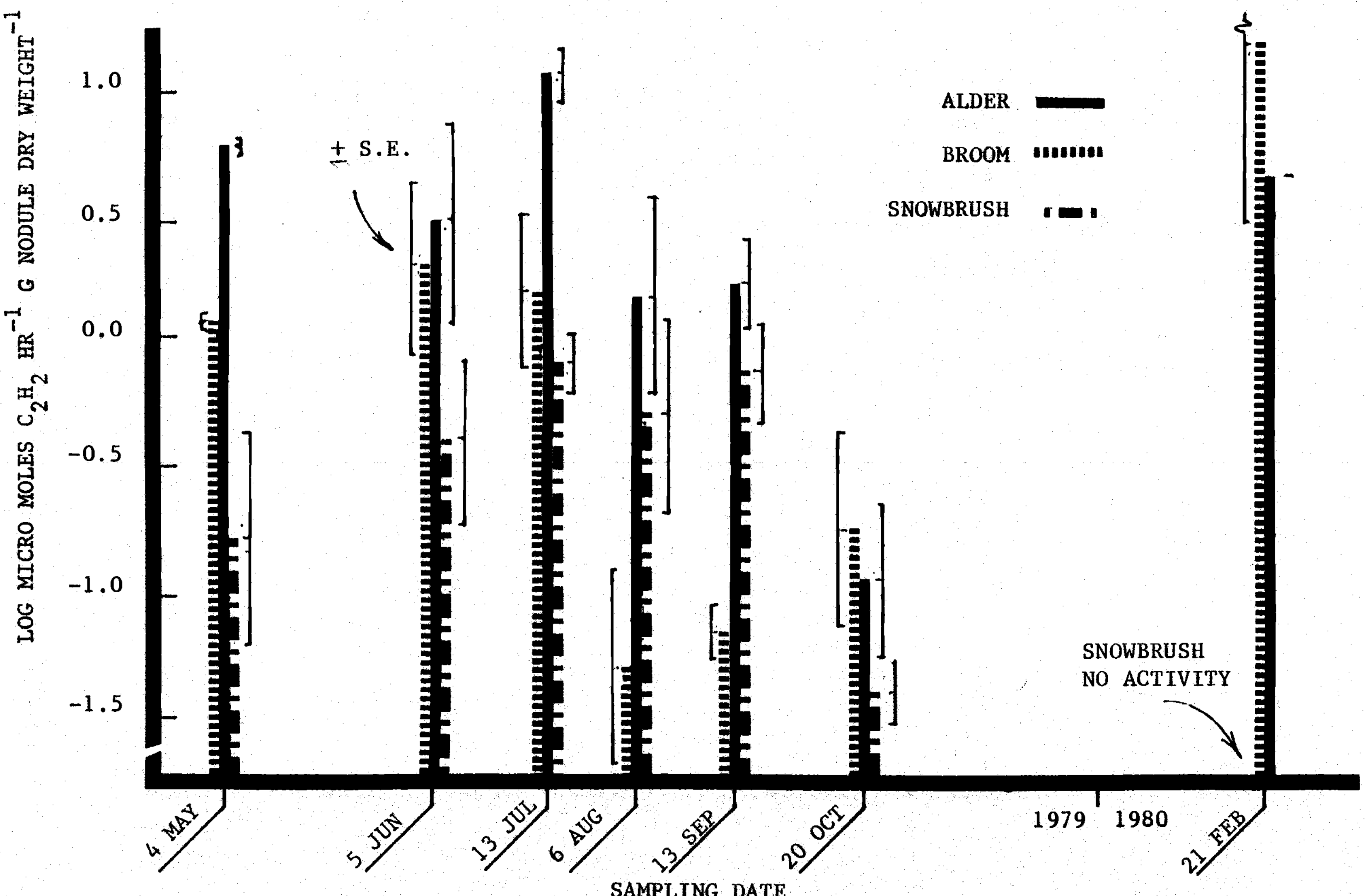

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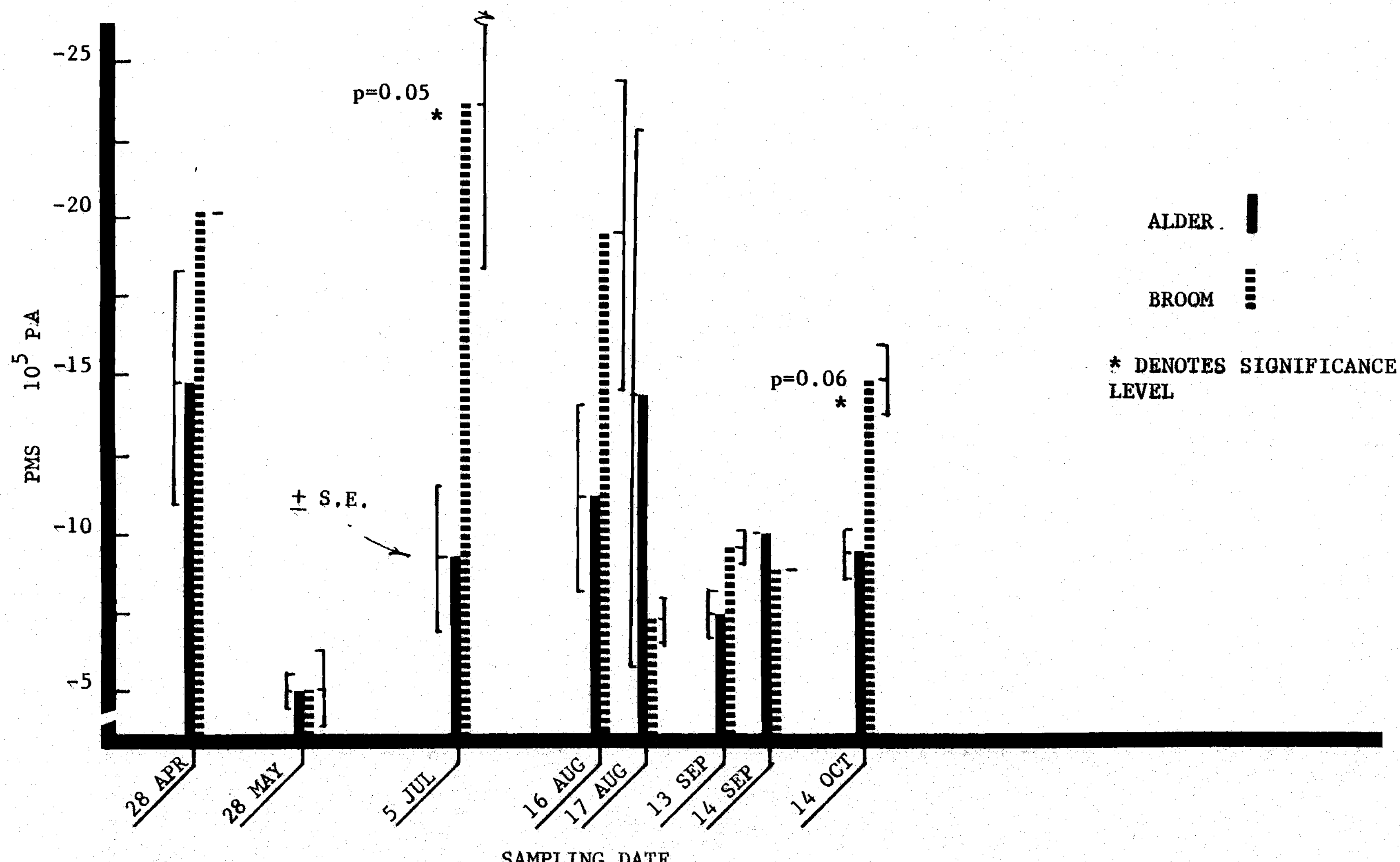
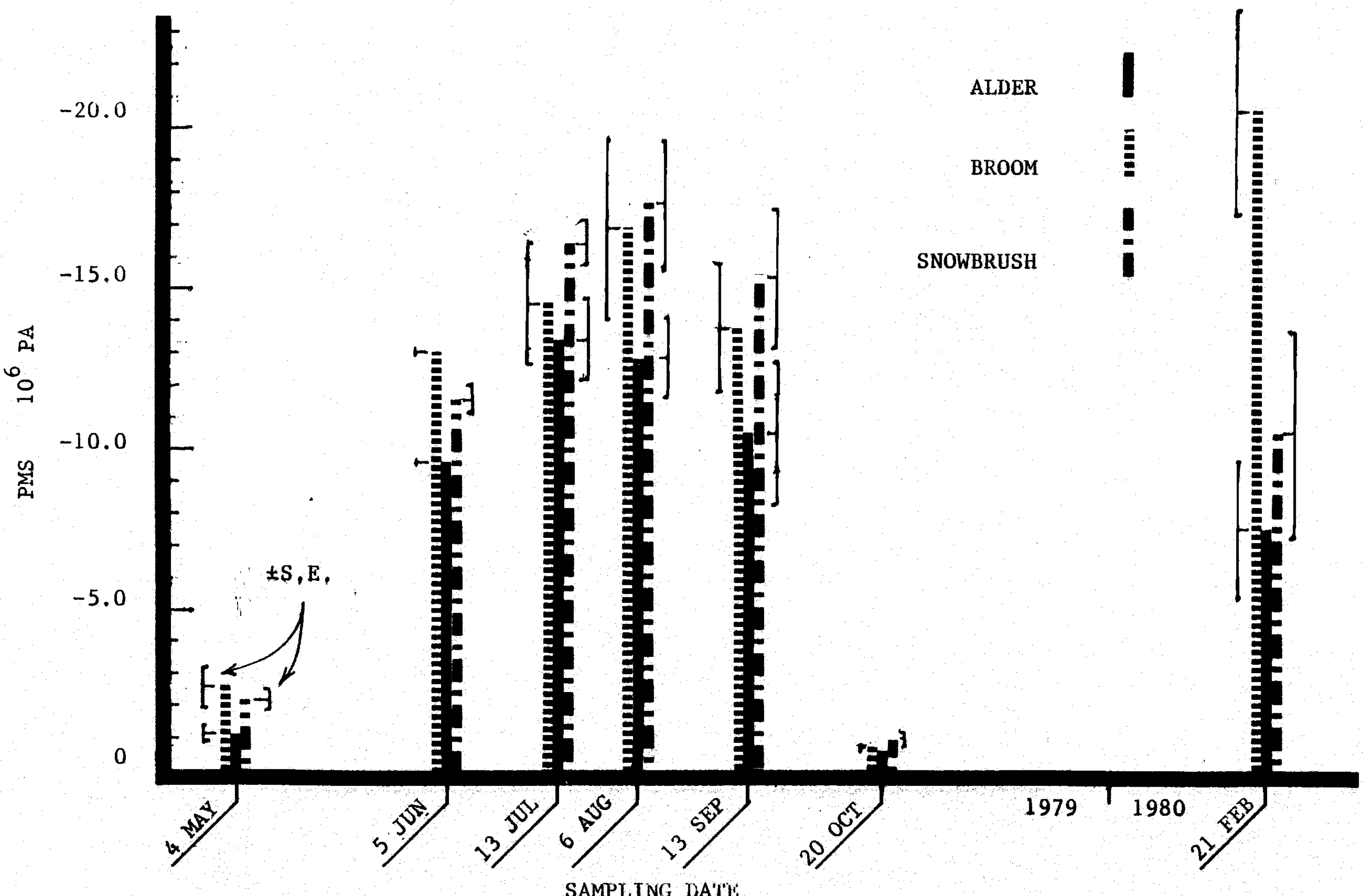
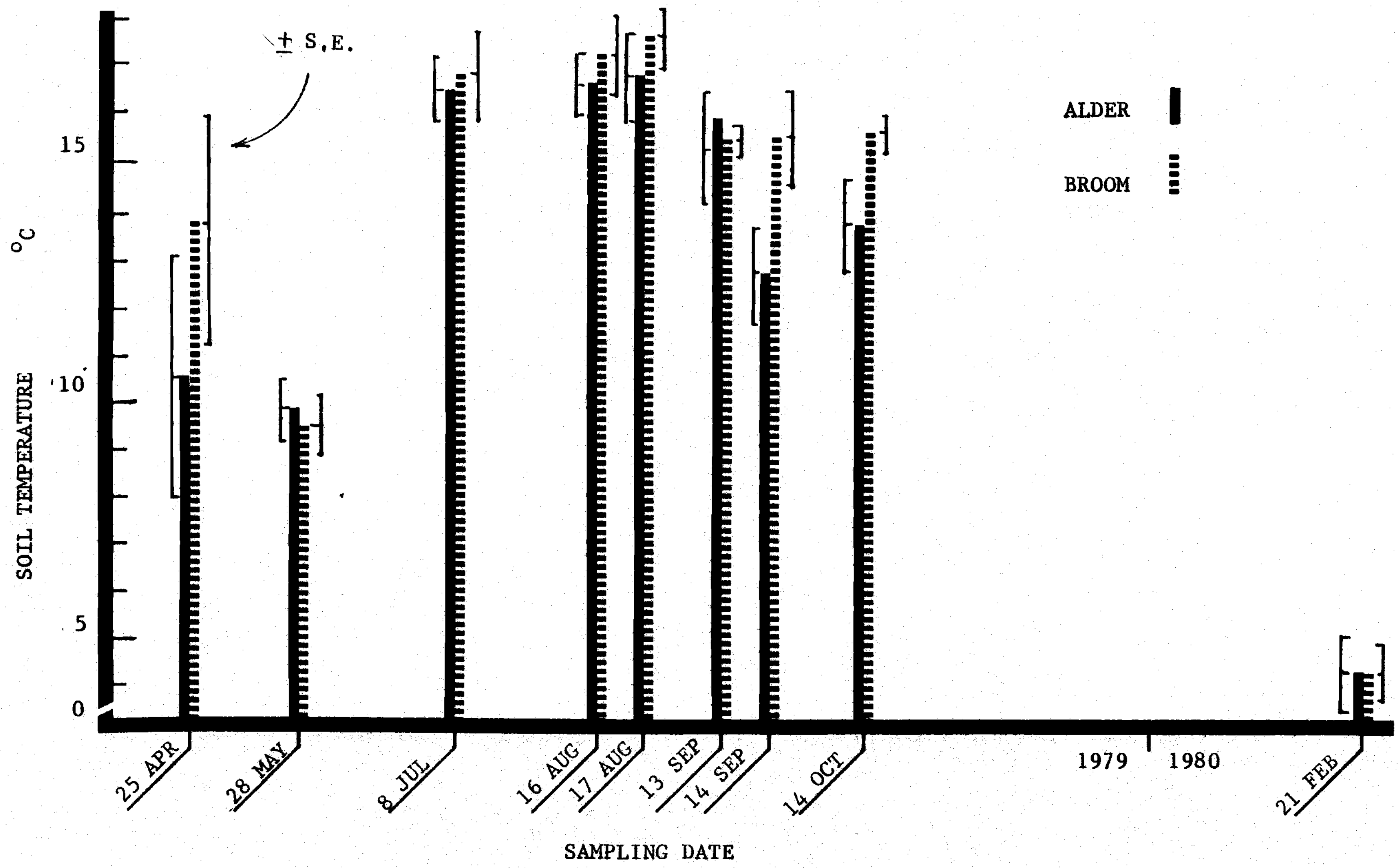


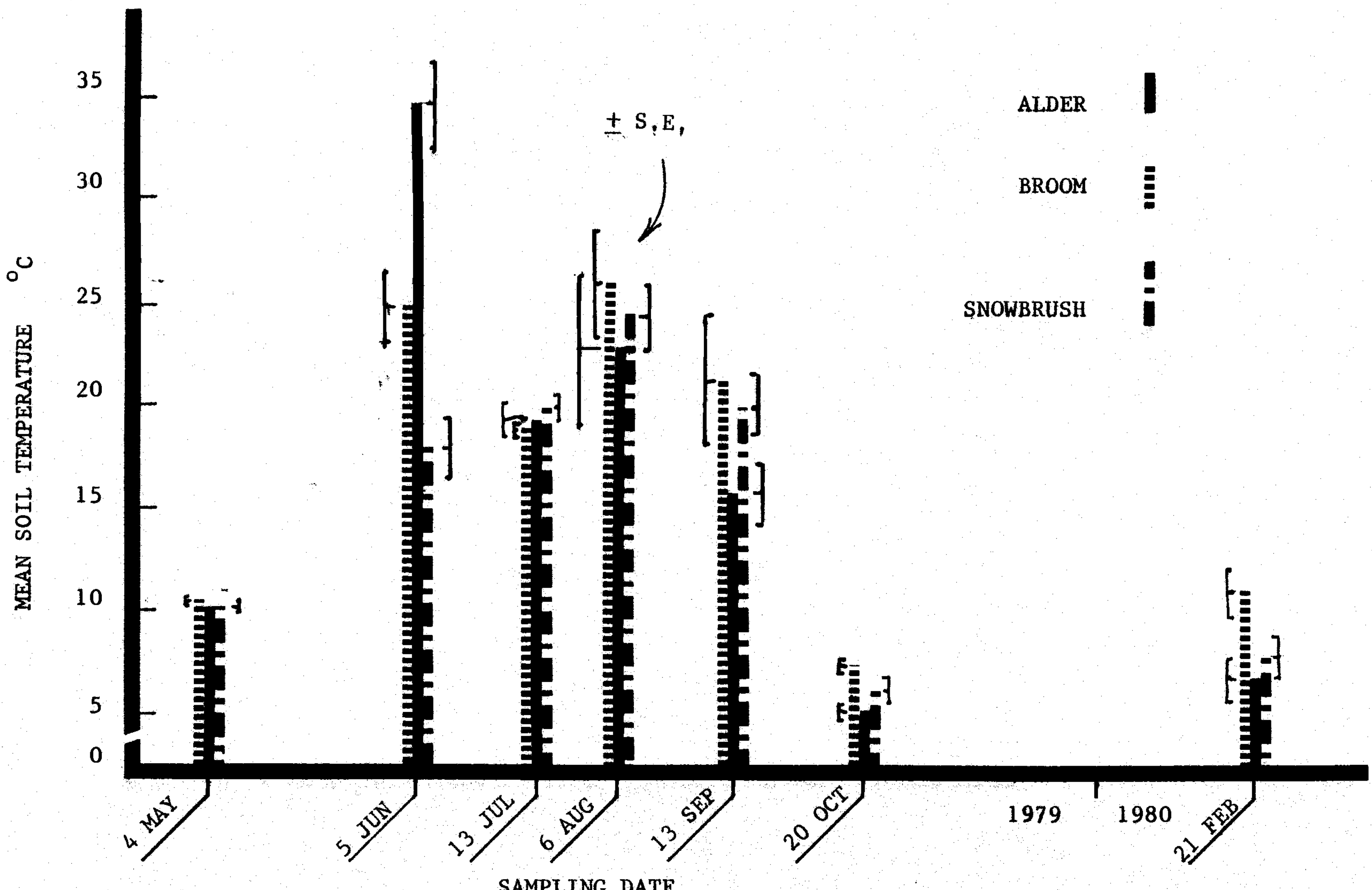
Mean PMS versus sampling date for underplanted broom and alder.



Mean PMS for naturally occurring alder, broom and snowbrush.



Mean soil temperature <u>versus</u> sampling date for underplanted alder and broom.



Mean soil temperature *versus* sampling date for naturally occurring alder, broom and snowbrush.

II. EXPECTED NITROGEN INPUTS FROM RED ALDER PLANTED UNDER PRECOMMERCIALLY THINNED DOUGLAS-FIR

NITROGEN AND DOUGLAS-FIR YIELD

Nitrogen fertilization is now an accepted and widely successful technique for increasing the yield of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) in the Pacific Northwest. By 1978, 1.2 million acres in this region - primarily of Douglas-fir had received 168 to 224 kg/h (150 to 200 lb/ac) of elemental nitrogen as urea prill or the larger forest grade granules (Bengtson, 1979), with stands on lower site classes (III and IV) yielding greater responses than higher sites (I and II). At four years after application, Miller and Fight (1979) report average annual gains for Douglas-fir ranging from 27 cu ft on site I land to 91 cu ft on site IV, with an estimated duration of fertilizer response of about 10 years.

Future Costs and Uncertainties

Although the price of urea has increased greatly in recent years, the value of Douglas-fir has increased even more, thus maintaining urea application as a profitable practice (Miller and Fight, 1979). Moreover, the energy requirements for reducing nitrogen have decreased more than ten times from 1930 to 1970 and the present world production of industrially-fixed nitrogen exceeds demand and is expected to do so for the short term (Evans, 1980). Despite these positive trends, the cost of nitrogen fertilization and uncertainty of its supply can, for forestry, be expected ultimately to increase.

Urea is derived from ammonia reduced from atmospheric dinitrogen by the Haber-Bosch process which requires high temperatures and pressures and a source of hydrogen. Natural gas very conveniently satisfies all of these requirements. Unfortunately it is becoming increasingly expensive and scarce in the U.S., forcing an increased reliance on imported gas. A freezing of fertilizer prices in 1971 discouraged domestic ammonia plant production forcing an increasing reliance on overseas ammonia production in countries with good supplies of natural gas but often, however, centrally planned economies (Bengston, 1979). The political goals of some of these countries are often not congruent with those of the U.S.

Barring the discovery of a cheap pollution-free source of hydrogen, or a more efficient catalyst for industrial nitrogen reduction, the probabilities of increased prices and lowered availabilities for nitrogen fertilizer will certainly increase. If world or national shortages of ammonia do occur, the allocation of nitrogen fertilizers to food production will most likely occur at the expense of forest nitrogen fertilization (Gordon _et al_., 1979).

Symbiotic Nitrogen Fixation

Nitrogen-fixing legumes and actinorhizal (plants with _Alnus_ type nodules) species, which reduce atmospheric nitrogen to ammonia in root nodules, can increase the yield of associated non-nitrogen fixing crop trees. The use of nitrogen fixed by green plants is attractive because the reduction of atmospheric nitrogen is powered by photosynthesis, which in turn is powered by solar energy, which by our standards is inexhaustable. Using nitrogen fixing plants could thus potentially reduce the use of better concentrated but exhaustable sources of energy such as petroleum or coal. Some amount of petroleum will, however, still be required to grow, transport and plant an effective number of nitrogen fixing plants within the target stand.

In the Pacific Northwest, red alder planted shortly after stand establishment markedly increased the yield of Douglas-fir on a low quality site after 50 years. The rapid juvenile growth of alder was, however, checked by frost damage for its initial two years. This most likely prevented the Douglas-fir from being suppressed by the alder (Miller and Fight, 1979). Normally Douglas-fir requires a six to eight year head start to escape suppression from alder (Newton et al., 1968).

Red alder thus has the proven capability to increase the yield of Douglas-fir. The gains in growth resulting from increased nitrogen must, however, be balanced against possible growth losses caused by competition from the nitrogen fixer. Suppression of Douglas-fir by red alder can range from several years loss of growth to loss of the stand.

Red alder can also fix nitrogen when planted under precommercially thinned Douglas-fir (Helgerson, 1981) and when naturally seeded under commercially thinned Douglas-fir (Berg and Doerksen, 1975). Alder thus has the potential to increase the yield of Douglas-fir with a minimal probability of causing growth loss from competition. The problem remains, however, of predicting the amount of nitrogen that will be added to the stand over time.

AMOUNTS AND COSTS OF NITROGEN FROM ALDER

The amount of nitrogen added to an underplanted Douglas-fir stand can be found by first determining the average amount of nitrogen underplanted alder might fix over time beneath the Douglas-fir canopy. The reliability of this estimate can be tested by multiplying the single tree estimate by an appropriate stocking level for comparison with studies of nitrogen fixation in pure alder stands. The average estimate also allows determination of the number of underplanted alder required to equal the nitrogen input from conventional urea fertilization.

Estimating Future Nitrogen Fixation

An estimate of future nitrogen fixation for an individual alder can be based on its expected duration of fixation, its active nodule mass, and the fixation rate of its nodules. These variables are dependent on the amount of Douglas-fir and understory competition at the time of planting and the Douglas-fir growth rate.

The duration of the fixation period is controlled by the time after thinning until the Douglas-fir fully suppresses the alder. This probably coincides with the time until crown closure for the Douglas-fir. The active nodule mass (proportional to the size the alder attains), and the nitrogen fixation rate of the nodules are also sensitive to surrounding plant competition.

Uncertainty exists, however, in determining accurate values for each of these variables. If the duration of the nitrogen fixation period, the active nodule mass and fixation rates can be estimated then cost of nitrogen and Douglas-fir response can also be estimated.

Crown closure times, Douglas-fir densities and expected nitrogen fixation per alder are in Table I. The time for crown closure was estimated from the size of trees crowns at thinning and their lateral growth. A standard precommercial thinning regime is 630 leave trees per ha (255 per acre) for Site III Douglas-fir in the central Oregon Cascades. The crown radii of 30 trees from an 18 year old similarly thinned stand averaged 1.64 m at time of thinning and their radial growth increment averaged 0.11 m over the last four years. Extrapolating this growth rate produces crown closure in seven years.

A probability tree diagram can calculate the expected amount of nitrogen fixed by an individual alder over time and can organize and display the uncertainties associated with estimating nitrogen fixation (Figure 1). This diagram illustrates the expected average future amount of nitrogen fixed over 15 years by an individual alder planted under mid-site III Douglas-fir precommercially thinned at age 18 to about 321 trees per ha (130 per acre). The series of branches and probabilities denote three possible outcomes for the nodule mass the alder will produce and whether the nodule nitrogen fixation rate will stay constant or decline with age. Six (3 x 2) possible outcomes thus exist that individual trees may follow. Expected values for nitrogen fixation over the other time periods were similarly calculated.

The marginal probability of a given outcome is the product of probabilities leading to that outcome. For example, the marginal probability of the uppermost outcome ($p = 0.02$) is the product of

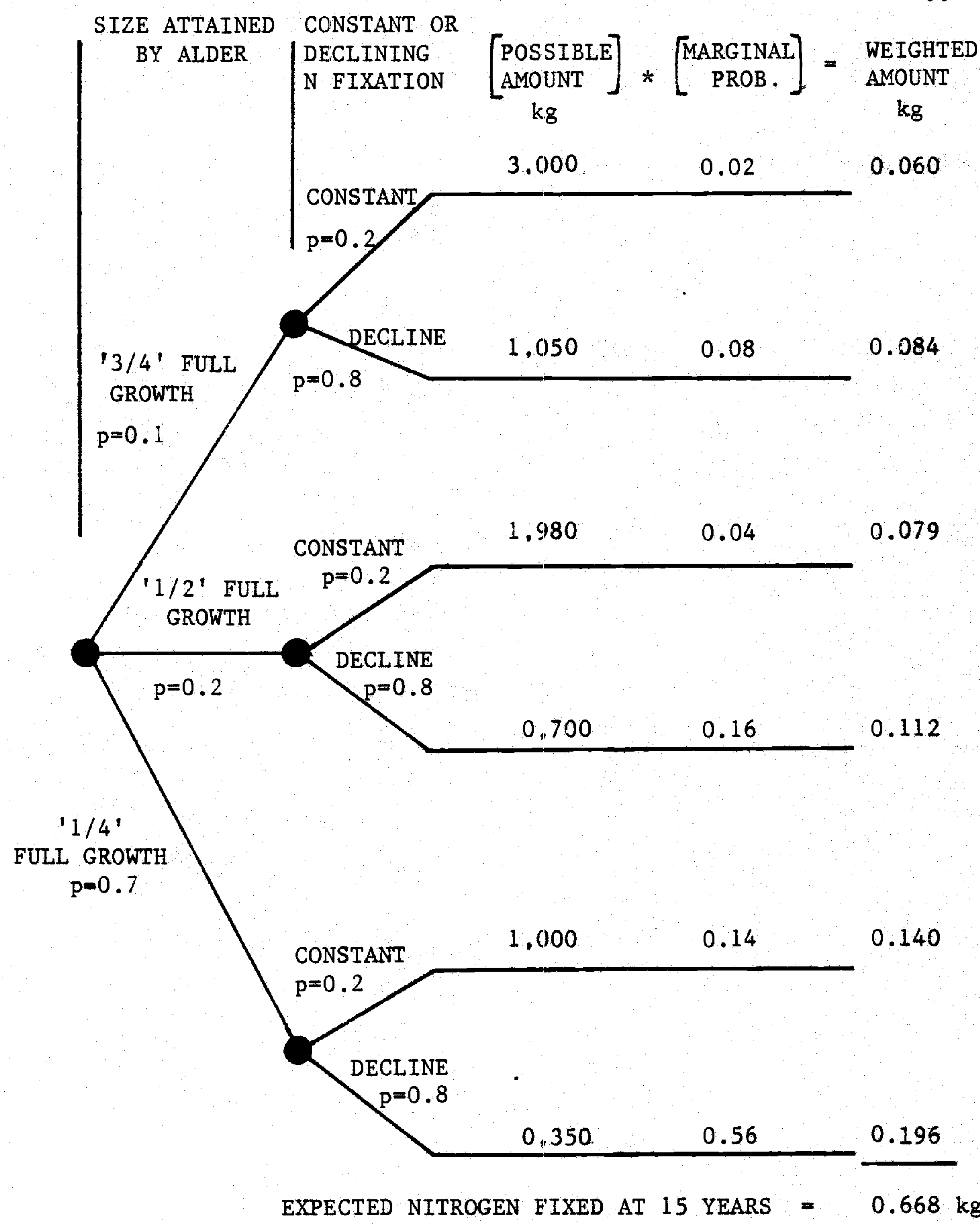


Figure 1. Probability tree diagram illustrating possible pathways and expected total nitrogen fixation after 15 years for individual underplanted red alder.

TABLE I. DOUGLAS-FIR DENSITIES, CROWN CLOSURE TIMES AND EXPECTED TOTAL NITROGEN FIXATION PER UNDERPLANTED ALDER.

Douglas-fir Density stems ha^{-1}	Time to Crown Closure Years	Expected Total Nitrogen Fixation Per Alder kg	Expected Annual Fixation Year Per Alder kg	Expected Nitrogen Annual Fixation by a Fully Stocked Alder Stand kg
630 (255 ac^{-1})	7	0.146	0.02	--
454 (184 ac^{-1})	10	0.240	0.024	130
321 (130 ac^{-1})	15	0.668	0.045	121
240 (97 ac^{-1})	20	1.616	0.081	139

Note: The expected values were based on probabilities of 0.1, 0.2 and 0.7, respectively, for three-quarters, one-half and one-quarter of "full" growth and probabilities of 0.2 and 0.8, respectively, for constant and declining rates of nitrogen fixation.

0.1 x 0.2; respectively, the probabilities of maximum nodule mass and a constant nitrogen fixation rate. The expected amount of nitrogen fixed is the sum of each of the 6 possible values from the probability tree multiplied by its individual marginal probability, e.g. (4.475)(0.02) + (1.571)(0.08) + ... (0.523)(0.56) = 1.003 kg. The expected values of nitrogen were likewise calculated for the other time periods.

This technique's advantages rest with its simplicity and flexibility. Because the number of variables that can be readily handled is small, the decision maker must concentrate on the pertinent ones. Because the model is small, it can be very easily changed as more accurate information becomes available.

Past studies estimate nodule mass as three to eight percent of the above ground biomass (Helgerson _et al_., in press; Dawson, 1978; Akkermans, 1971). Growth curves for red alder in British Columbia (Smith, 1968), height growth curves for red alder in the Cascades (Newton _et al_., 1968) and biomass equations (Gholz _et al_., 1978) were used to estimate the top weight of alder over time. The active nodule mass was presumed to stay at a constant three percent of the top dry weight of the alder over its fixation period. The alder may not, however, achieve its full rate of growth because of the harsher higher elevation site, and competition from the overstory Douglas-fir and understory brush. Total height at 15 years reported by Newton _et al_. (1968) was only about three fourths the height at 15 years for poor site alder in British Columbia (Smith, 1968). The reduction in growth is reflected by the 3/4, 1/2 and 1/4 growth possibilities in the probability tree. The nodule mass is presumed to also be proportionally reduced. Because fixation rates are dependent on the photosynthate supply (Gordon and Wheeler, 1978), they also should be directly affected by Douglas-fir and understory competition. This is reflected by the alternatives of a constant and declining fixation rate.

The average annual nitrogen fixation rate used was based on the seasonal average (51×10^{-6} moles C_2H_2 g nodule dry weight^{-1} hour^{-1}) observed by Helgerson (1981) using the theoretical 1:3 conversions ratio to convert acetylene reduction to nitrogen fixation. No appreciable nitrogen fixation was presumed to occur between leaf fall and bud burst - November to May. This reduced the average rate by half. A further reduction was made because of reduced fixation rates at night. The true 24 hour average was presumed to be two thirds of the daytime average (Tripp *et al*., 1979). The net annual result was a three fold reduction of the average seasonal nitrogen fixation rate observed by Helgerson (1981).

Another use of the probability tree approach is that the marginal probabilities can be rearranged as a plot of cumulative probability versus amount of nitrogen fixed (Figure 2). This allows the decision maker a view of the certainty of achieving a given nitrogen input.

COMPARISON WITH OTHER ESTIMATES

Given the initial assessments of what may happen, the expected nitrogen accretion from fixation for the 15 year period is 0.668 kg

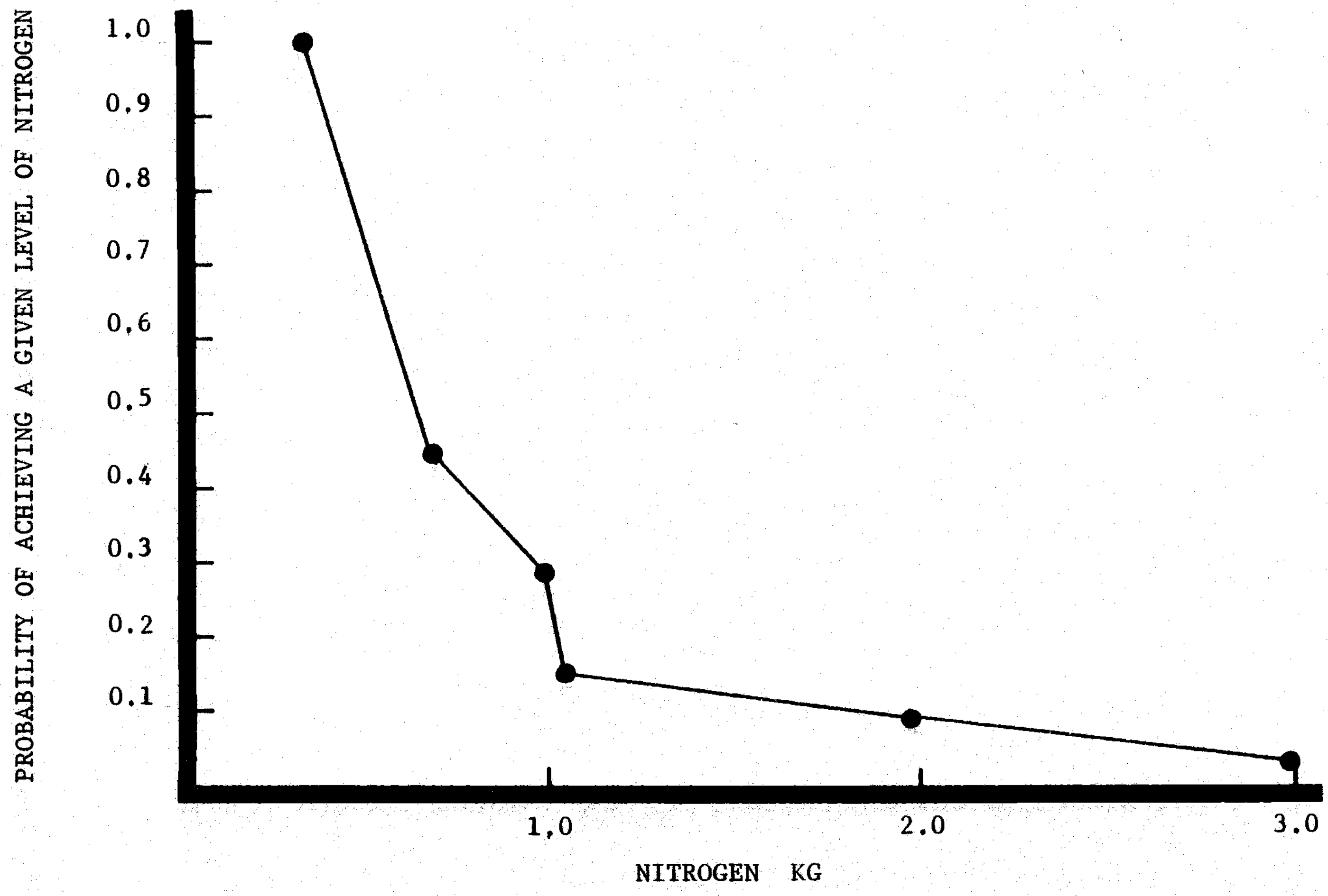


Figure 2. Probabilities of achieving a given level of nitrogen fixation after 15 years *versus* possible amounts of nitrogen fixation.

(Figure 1). But, is this value realistic? For comparison with other studies, the expected nitrogen accretion at 15 years was multiplied by the average stocking levels at that age for poor site alder (2,640 trees/ha) from yield tables of Smith (1968) and averaged over 15 years. The initial estimate for expected nitrogen addition from fixation from this hypothetical alder stand is thus 121 kg/ha/yr.

Other estimates of nitrogen accretion by alder have been made by comparing plant and soil nitrogen contents on red alder stands and adjacent non-alder communities. These estimates range from 40 to 320 kg/ha/yr (Table II).

The projected estimate here is greater than some others, although well below the 320 kg/ha/yr reported by Newton _et al_. (1968). The differences between the projected estimate and the others may be related to differences in methodology, the effects of competition on nitrogen fixation rates, or the assumptions used in the expected value model.

Possible Causes of Differences

The previously cited studies assessed nitrogen accretion by measuring nitrogen content of vegetation and soil in alder and adjoining non-alder stands. Nitrogen accretion in an alder stand is thus the difference between nitrogen fixation and other inputs and losses in the alder stand compared to the differences between inputs and losses in the adjoining non-alder stand. Nitrogen fixation by alder was not directly estimated.

For fully stocked alder stands, nitrogen losses appear to exceed those of adjacent Douglas-fir stands. This is suggested by the high

TABLE II. NITROGEN ACCRETION RATES FOR RED ALDER IN PURE STANDS AND WITH DOUGLAS-FIR. (ADAPTED FROM BORMANN, 1977).

Stand	Location	N Accretion Rate (kg N/ha/yr)	Stand Age(s)	Stand Component Measured	Methods Used & Comments	References
A. rubra	West Oregon	139	40	Mineral soil & forest	Paired plots: adjacent Douglas-fir used as time-zero estimate. Stands naturally established on forest clearing at the same time.	Tarrant *et al.*, 1969
A. rubra	Coast Range, Oregon	300 320	2-15 2-15	Mineral soil (0-60 cm) & forest floor ecosystem	16 stands (2-15 yrs) established on landings and other areas of subsoil were measured and the relationship between stand age and N content was developed.	Newton *et al.*, 1968
A. rubra	Cedar River	85	38	Ecosystem	Paired plots: adjacent Douglas-fir and red alder were measured for N content. Stands on low site alderwood soil.	Cole *et al.*, 1978
A. rubra	Capitol Forest	100 (0-10 yrs) 40 (10-40 yrs)	5-45	Mineral soil (0-20 cm; 20-60 cm) Forest floor Red alder understory & overstory Douglas-fir understory & overstory	Chronosequence and paired plots; 18 red alder stands (5-45 yrs) and 11 Douglas-fir stands (26-47 yrs) on high site Boistfort soil series.	Bormann, 1977
Mixed	Wind River Exp. Station, Cascade Mountains, Washington	40	30	Mineral soil & forest floor	A mixed plantation of red alder and Douglas-fir established on low-site land. N was compared to adjacent pure Doulgas-fir.	Tarrant & Miller, 1963
Mixed	West Oregon	45	17	Mineral soil only	Understory alder in heavily thinned Doulgas-fir stand. N content compared to adjacent Doulgas-fir stand without alder. Bulk density not taken into account. Because alder lowers bulk density, N values may be somewhat high.	Berg & Doerksen, 1975

levels of nitrate and the high nitrification capacity found in soil from red alder stands compared to Douglas-fir (Bollen and Lu, 1968). This may, however, be age-dependent. Cole et al. (1978) reported very similar nitrate/ammonia ratios for 10 year old red alder and Douglas-fir (0.01 and 0.02). A 38 year old alder stand had, however, a nitrate/ammonium ratio of 0.29 compared to a ratio of 0.02 for an adjacent stand of 48 year old Douglas-fir.

If nitrogen losses from the alder stand exceed inputs from other sources, nitrogen inputs from fixation by alder may be greater than those indicated by accretion values. Bormann (1977) cites unpublished data from Grier[1] that indicates that annual leaching losses of nitrate in pure alder stands may range from 30-60 kg N/ha/yr. Cole et al. (1978) report, however, a leaching loss of only 2.2 kg N/ha/yr for a 38 year old alder stand compared to 0.6 kg N/ha/yr for the adjoining 48 year old Douglas-fir. In addition, denitrification of nitrate nitrogen and ammonium nitrogen dependent on soil water availability (Bremner and Blackmer, 1979) will likely cause further nitrogen losses. A likelihood thus exists that annual nitrogen fixation exceeds the accretion rate. Our estimate should thus be adjusted downward to better reflect nitrogen losses from a pure alder stand.

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[1]Charles Grier, College of Forestry, University of Washington, Seattle, Washington.

RED ALDER VERSUS UREA

Current silvicultural practice in the Pacific Northwest is to apply 224 kg/ha (200 lbs/ac) nitrogen as urea most commonly at about 7 to 10 years before a commercial thinning or final harvest.

Based on our revised expected nitrogen fixation values, an accretion of 224 kg/ha of nitrogen (200 lb/ac) after 15 years by red alder fixation would require a minimum of 335 alders per ha (136 per acre). Allowing for 40% mortality (Helgerson, 1981) increases the planting density to 558/ha (339/ac).

Tree planters currently like to make $100/day with planting rates ranging from 500 to 1,200 seedlings/day and 0.40 to 0.80 ha (one to two acres) per day depending upon terrain. A planting rate of 0.50 ha per day seems a reasonable conservative estimate for planting 558 seedlings per ha under precommercially thinned Douglas-fir. Combined with a seedling cost of $120 per thousand this produces an initial cost for 224 kg/ha nitrogen at 15 years of about $267/ha ($108/ac). The range of current industrial costs of applying 224 kg/ha of nitrogen as urea run from $116 to $141 per ha ($47 to $57 per acre). Thus in terms of nitrogen inputs, the initial cost of underplanting red alder appears to be roughly twice that of a single application of urea.

Further cost differences arise because of the different periods of time each cost must be carried. The underplanted alder require 15 years to add 212 kg N/ha, and the Douglas-fir may require another 5 to 10 years to make full use of the added nitrogen. Thus the costs must be carried for a minimum of 20 years before they are recovered in a commercial thinning or final harvest.

The more rapid and certain response of Douglas-fir to urea greatly reduces the amount of time the cost of urea application must be carried. If urea is applied to large trees, the increased growth can be recovered in five to 10 years in a commercial thinning or in the final harvest. Because of the longer time involved, the discounted cost of nitrogen from alder is greater than urea. For example, with an interest rate of 7%, and carrying periods of 20 and 10 years, respectively, for underplanting alder and applying urea, the future compounded cost of underplanting alder is \$267/ha (F/P, 7%, 20; 3.8696) = \$1033 per ha compared to \$57/ha (F/P, 7%, 10; 1.9671) = \$112 per ha for urea. This indicates that for the two alternatives to be equivalent, the value increase of Douglas-fir harvested resulting from alder underplanting would have to be considerably greater than the increase in Douglas-fir value resulting from urea application. The amount of increase depends on the discount rate used and the exact time required before the cost is recovered as increased growth of Douglas-fir plus any salvage value from the alder.

Douglas-fir Response

The payoff to forest management rests ultimately with increased Douglas-fir yield resulting from the additional nitrogen input. A problem in estimating Douglas-fir response is determining the proportion of nitrogen fixed that is ultimately taken up by the Douglas-fir. Numerous fates await nitrogen fixed by red alder.

Some nitrogen may be leached directly from living alder and its litter. Some denitrification will undoubtedly also occur. Nitrification produces easily assimilated nitrate nitrogen, which unfortunately is also easily leached out of the system. Similar losses, however, also await nitrogen applied as urea. Hot dry weather can cause as much as 30% to be volatalized off as ammonia gas (Miller et al., 1976). Ammonium nitrogen from either source may be converted to N_2O and lost during nitrification as well as denitrification. Losses during nitrification are enhanced by soil water availablility (Bremner and Blackmer, 1979). The lowering of soil bulk density observed by Tarrant and Miller (1963) may offset this by providing better soil drainage.

Losses of nitrogen following urea application would seem to be more rapid and immediate, however, than losses of nitrogen from underplanted nitrogen fixers. Underplanted alder is analogous to a slow-release nitrogen fertilizer. Nitrogen availability thus should be much closer to the Douglas-fir rate of assimilation.

As mentioned previously, Douglas-fir stands have lower rates of nitrification and lower nitrate/ammonium ratios than red alder stands. Cole et al. (1978) also report a 6.5 year residency time for nitrogen in the foliage of their Douglas-fir stand compared to 1.1 years for the alder stand, and a 10.2 year residency time for nitrogen in the Douglas-fir forest floor compared to 7.5 years for the alder's. These facts and the increased carbon/nitrogen ratios caused by thinning suggest that more of the nitrogen fixed under the Douglas-fir stand by underplanted red alder will stay in the stand longer than would a single application of urea. As nitrogen fixed by the alder accumulates, however, its turnover rate and nitrification will likely become more rapid, increasing losses from the ecosystem.

A plot of cumulative nitrogen fixation over the 15 year span for an individual alder suggests that the greatest accretion comes in the last five years (Figure 3). Because nitrogen availability probably follows a similar trend, Douglas-fir response should also be greatest during or shortly after this time period. The slower rate of application of nitrogen supplied by red alder combined with its longer turnover time suggest that acceleration of the Douglas-fir growth rate will be slower but may last longer than it would be from an equal amount of nitrogen applied as urea.

FUTURE INFORMATION NEEDS

Although uncertainty exists regarding Douglas-fir's response to nitrogen applied as urea (Miller and Fight, 1979) greater uncertainty exists regarding Douglas-fir's response to an equivalent amount of nitrogen fixed by red alder underplanted after precommercial thinning.

The true value of underplanted alder could be better predicted if nitrogen inputs (alder survival, growth and nitrogen fixation), losses (leaching and denitrification) and Douglas-fir uptake rates, and growth response following precommercial thinning were better known. Of these, the most important seem to be the relationships between growth and nitrogen fixation for underplanted alder in competition with the surrounding underbrush and Douglas-fir and the fate of the additional nitrogen brought into the system.

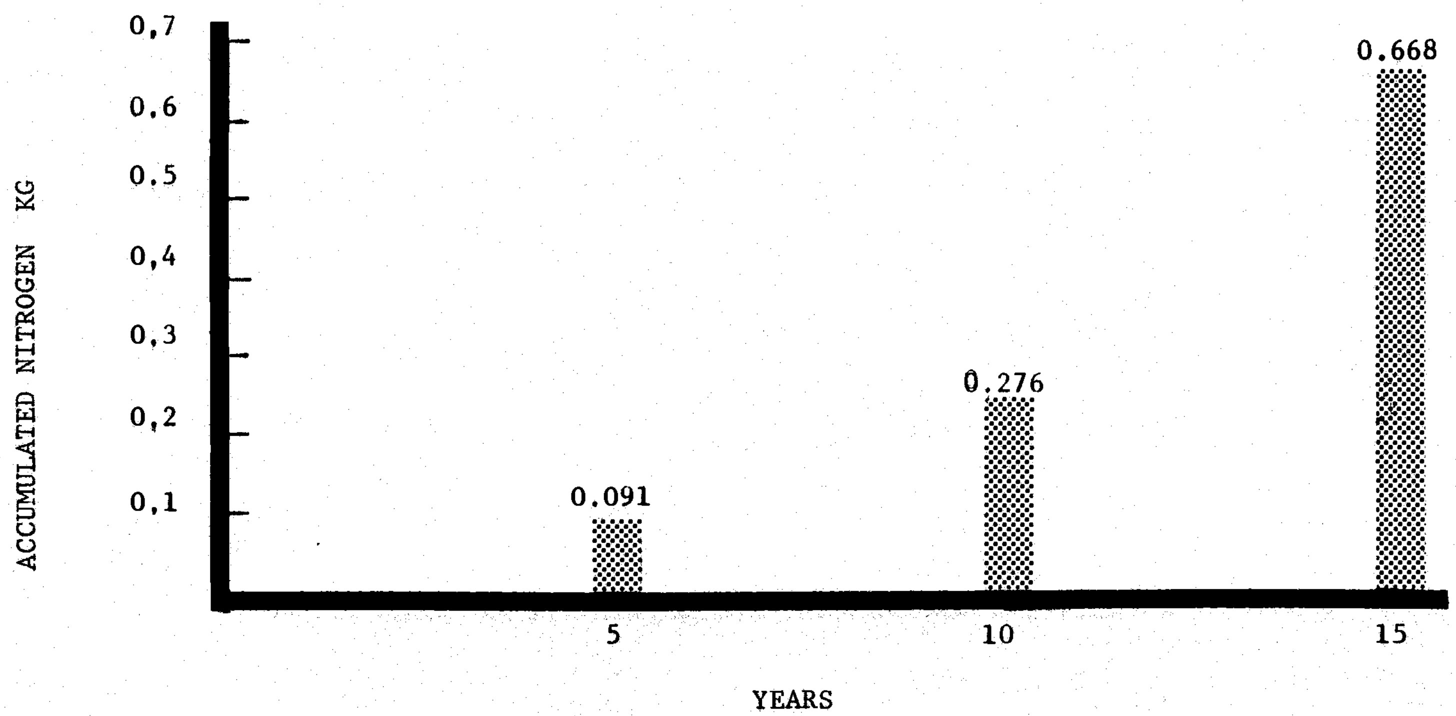

Figure 3. Accumulated nitrogen *versus* time for 15 year period.

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