Case Studies of Red Alder and Sitka Alder in Douglas-fir Plantations: Nitrogen Fixation and Ecosystem Production

by

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Seven case studies of 11 ecosystems were used to examine the effects of nitrogen-fixing alders in Douglas-fir plantations. The first case study quantified nitrogen (N) fixation and aboveground net primary production in a young Sitka alder [*Alnus sinuata* (Regel) Rydb.] ecosystem. At 5 yr of age, the N fixation (C_2H_2 reduction) rate of 35 kg ha^{-1} yr^{-1} was near the middle of the reported range for this shrubby species. The second case study compared N fixation rates of Sitka alder and red alder (*Alnus rubra* Bong.) on the same sites. These species exhibited similar nodule activities and had similar nodule:leaf biomass ratios of 7-8%. A mixture of Sitka alder and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] was estimated to have a current N fixation rate of 20 kg ha^{-1} yr^{-1} based on acetylene reduction; N accretion measurements indicated an average N fixation rate of 30 kg ha^{-1} yr^{-1} for 23 yr. A mixture of red alder and Douglas-fir on the same site had a current N fixation rate of 130 kg ha^{-1} yr^{-1} based on acetylene reduction, with an N accretion rate of 65 kg ha^{-1} yr^{-1} for 23 yr.

The third case study evaluated the effects of Sitka alder on Douglas-fir growth and nutrition, and on ecosystem production and litterfall. Current Douglas-fir stem growth was 40% greater with Sitka

alder, and aboveground ecosystem net primary production was increased 70% with the alder. Litterfall nutrient content was 3 to 7 times greater under the mixed canopy.

The fourth and fifth case studies looked at 23 yr-old mixtures of red alder and Douglas-fir in comparison with pure Douglas-fir, on an infertile site and on a fertile site. Red alder had little effect on Douglas-fir size or growth rate on the infertile site, but ecosystem net primary production was tripled. Conversely, net primary production was not increased by red alder on the fertile site, and Douglas-fir size and growth were reduced.

The final two case studies evaluated: (1) the conclusions reached in the previous case studies for applicability to red alder/Douglas-fir mixtures in general, and (2) trends in production with stand development up to age 50. These case studies were consistent with the general conclusions of site fertility interactions with red alder/Douglas-fir mixtures. With further stand development, red alder continued to enhance ecosystem production and Douglas-fir growth on infertile sites, with opposite effects on fertile sites.

Sitka alder demonstrated a high potential usefulness for interplanting with Douglas-fir, and red alder greatly boosted ecosystem production on infertile sites. Both species merit further development as tools for forest management on N deficient sites.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PREFACE

Content

"The nitrogen in our DNA, the calcium in our teeth, the iron in our blood, the carbon in our apple pies were made in the interiors of collapsing stars. We are made of starstuff."

--Carl Sagan--

Context

"...everything interesting is a matter of organization, not of primal substance."

--Bertrand Russell--

Synthesis

"It is important to see the particular action as _part_ of the ecological subsystem called context and not as the product or effect of what remains of the context after the piece which we want to explain has been cut out from it."

--Gregory Bateson--

Corollary

"The division of the perceived universe into parts and wholes is convenient and may be necessary, but no necessity determines how it shall be done."

--Gregory Bateson--

CASE STUDIES OF RED ALDER AND SITKA ALDER IN DOUGLAS-FIR PLANTATIONS: NITROGEN FIXATION AND ECOSYSTEM PRODUCTION

SECTION I. INTRODUCTORY SUMMARY AND SYNTHESIS

SUMMARY

Low levels of nitrogen availability limits biomass production in many forests in the Pacific Northwest, and considerable interest has been shown in the potential of biological N fixation in forest management (c.f., Gordon et al. 1979). Much of the work in the region has focused on red alder (Alnus rubra Bong.), a rapidly growing tree with high rates of N fixation commonly ranging from 50 to 150 kg ha^{-1} yr^{-1} (for a summary see Section III). A study of interplanted Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] and red alder at Wind River, Washington demonstrated alder's ability to double wood production per hectare and increase the size of conifers on infertile sites (Miller and Murray 1978). The nitrogen benefits of interplanted alder are probably more than proportional to the increase in site N capital; red alder and mixed red alder/Douglas-fir ecosystems have been reported to increase site N capital by 30 to 60%, and to cycle 3 to 10 times the quantity of nutrients in aboveground litterfall measured in adjacent, pure-conifer stands (Tarrant et al. 1969, Cole et al. 1978, Binkley et al. 1982a). However, red alder's rapid juvenile growth can impede the successful establishment and early growth of conifers (Newton et al. 1968), and in some cases fails to increase wood production per hectare (Berntsen 1961).

Another common, though little-studied, alder species in the Pacific Northwest is Sitka alder [Alnus sinuata (Regel) Rydb.]. This high-elevation species with a shrubby growth form, has been reported to fix 20 to 65 kg of N ha^{-1} yr^{-1} (see Section III), grows well at low elevations and should offer less competition with interplanted conifers than red alder (Harrington and Deal 1982).

This thesis presents several case studies on the effects of these two alder species in Douglas-fir plantations. The overall thrust of my work was to evaluate the alder-induced changes in ecosystem functions (such as net primary production and nutrient availability) as a step toward gaining a predictive understanding of the potential of these species as tools for forest management. Three basic questions were addressed:

1. How much nitrogen is fixed by Sitka alder, and how does the rate compare to red alder on the same site?
2. What are the effects of two decades of Sitka alder in a poor-site-quality Douglas-fir plantation?
3. How do the effects of red alder on ecosystem production in Douglas-fir plantations vary with site fertility and stand age?

A summary and synthesis of the projects are presented in this section, and manuscripts describing five investigations comprise the remaining sections of the thesis.

Section II reports on a basic study of nitrogen fixation and net primary production in a 5-yr-old pure Sitka alder ecosystem. The estimated nitrogen fixation (C_2H_2 reduction) rate of 35 kg ha^{-1} yr^{-1} is near the middle of reported ranges for Sitka alder, and the aboveground net primary production of 6,000 kg ha^{-1} yr^{-1} was impressive given the stand age and the severity of the site.

Section III presents a comparison of N fixation (C_2H_2 reduction) rates of Sitka alder and red alder growing on the same sites at two ages. Vigorous 4- to 8-yr-old plants of both species exhibited average seasonal nodule activities of 10-12 µmole C_2H_2 reduced g^{-1} hr^{-1} dry nodule weight. A comparison of 21-yr-old plants revealed a higher nodule activity rate for red alder than Sitka alder; the difference was attributed to the declining vigor of the Sitka alder beneath an expanding Douglas-fir canopy. The annual N fixation rate estimate for the 21-yr-old red alder was 130 kg ha^{-1} yr^{-1}, compared with 20 kg ha^{-1} yr^{-1} for Sitka alder.

Section IV reports a case study of naturally established Sitka alder in a poor-site-quality Douglas-fir plantation. Current crop tree stocking was not affected by Sitka alder, but current crop tree biomass and stem growth were increased by 30 and 40%. Aboveground ecosystem net primary production was increased from 8,500 kg ha^{-1} yr^{-1} without alder to 14,400 kg ha^{-1} yr^{-1} in the mixed Douglas-fir/Sitka alder portion of the plantation. The nutrient content of aboveground litterfall was very low without alder, but with Sitka alder approached the highest levels reported for temperate forests. Despite the relatively moderate rate of N accretion (30 kg ha^{-1} yr^{-1}), Sitka alder's beneficial effects rivaled those reported for red alder, without severe competition with crop trees.

Section V presents case studies of two pairs of Douglas-fir and Douglas-fir/red alder ecosystems. Both pairs were 23 yr old; one was a fertile Site Class I and the other an infertile Site Class IV. Red alder did not change Douglas-fir biomass on the infertile site, but tripled net primary production. Conversely, red alder did not change total aboveground net primary production in the fertile site, but reduced Douglas-fir biomass by 35%.

Historic records from 2 U.S. Forest Service Experimental Forests allowed me in Section VI to: (1) evaluate the conclusions from Section V for broader applicability to red alder/Douglas-fir mixtures in general, and (2) assess the trends in ecosystem production through 50 yr of stand development. At age 27, the stands at Wind River Experimental Forest in Washington were remarkably similar to the infertile-site stands on Mt. Benson on Vancouver Island described in Section V; and at age 23 the stands at Cascade Head Experimental Forest in Oregon were slightly less productive than the fertile-site stands at Skykomish, Washington described in Section V. Further stand development on the infertile Wind River red alder site led to a marked increase in both Douglas-fir and total aboveground ecosystem net primary production through time. At Cascade Head, stand development with red alder through age 50 led to decreased Douglas-fir growth and total aboveground ecosystem biomass relative to the pure-conifer site.

SYNTHESIS

Nitrogen Fixation

For vigorous plants, nitrogen fixation rates per gram of nodule were similar for Sitka alder and red alder, and nodule biomass averaged 7-8% of leaf biomass for both species. Several studies report similar relationships between leaf biomass and N fixation. In general, alder appears to fix a quantity of nitrogen equaling 2 to 4% of its leaf biomass per year (Turner et al. 1976, Cole et al. 1978, Luken 1979, Tripp et al. 1979, and Bormann 1981). This relationship between leaf biomass and N fixation rate can be used to provide a first approximation of the number and size of alder required for a desired quantity of N fixation. My studies indicate 500 to 1,000 kg ha^{-1} of fixed N might be required to alleviate N limitations on infertile sites; 800 to 1,600 kg ha^{-1} of alder leaf biomass for 20 yr would probably supply this quantity of N. The size and number of alder required to provide this leaf biomass can be calculated from regression-equation derived tables (Table 1 and 2). These estimates should be viewed only as first approximations; actual rates may vary by ± 50% from the estimates. As the allometry between stem diameter and leaf biomass changes with plant and stand age, the values in Tables 1 and 2 should underestimate the N fixation rates of younger plants. Similar tables for young plants could be derived from regression equations developed for young plants.

Nitrogen Fixation and Nitrogen Availability

Nitrogen fixation under red alder on Mt. Benson doubled soil N concentrations in the upper profile, but the N availability index was tripled (Table 21). Similarly, the N concentration in the upper profile at Wind River was doubled by red alder and the N-availability index quadrupled (Binkley, unpublished data). It appears that alder-fixed N on infertile sites is either more active than "native" soil N, or that it increases the activity of the native N by a priming effect. Future research should consider the dynamics of alder-fixed N within

TABLE 1. FIRST APPROXIMATION OF NUMBER OF SITKA ALDER STEMS PER HECTARE REQUIRED FOR DESIRED RATES OF N FIXATION BASED ON BREAST HEIGHT DIAMETER.[a]

	N fixation rate kg ha^{-1} yr^{-1}			
Diameter (cm)	20	40	60	80
2	20,000	40,000	60,000	80,000
4	4,000	8,000	12,000	16,000
6	1,520	3,030	4,550	6,060
8	765	1,530	2,300	3,065

[a] Approximations based on 3% of leaf biomass, calculated from regression equations presented in Section IV for 22 yr old Sitka alder. The ratio of leaf:stem biomass is greater for younger plants, therefore approximate N fixation rates based on diameter would be higher for younger plants.

TABLE 2. FIRST APPROXIMATION OF NUMBER OF RED ALDER PER HECTARE REQUIRED FOR DESIRED RATES OF N FIXATION BASED ON BREAST HEIGHT DIAMETER.[a]

	N fixation rate kg ha^{-1} yr^{-1}				
Diameter (cm)	20	40	60	80	100
5	1,300	2,600	3,900	5,200	6,500
10	360	720	1,070	1,430	1,790
15	160	325	490	650	815
20	95	190	285	380	475
25	60	120	180	240	300

[a] Approximations based on 3% of leaf biomass, calculated from regression equations presented in Section V for 22 yr old red alder. The ratio of leaf:stem biomass is greater for younger plants, therefore approximate N fixation rates based on diameter would be higher for younger plants.

ecosystems, with a view toward a predictive understanding of the functional role of recently-fixed N.

Site Fertility Interactions

The ability of alder to increase ecosystem production appears limited by the fertility of a site. Only N-deficient sites appear to increase in net primary production with the inclusion of alder; fertile sites exhibit little change in ecosystem production. Conifer plantations may benefit from interplanted alder on N-deficient sites (if species dominance is controlled), but on fertile sites pure conifer plantations would probably be more valuable.

Nutrients other than N also may be limiting on infertile sites, and production may be further increased through fertilization with phosphorus and sulfur.

Canopy Interactions and Biomass Allocation

Canopy competition between interplanted conifers and alders regulates species dominance and canopy leaf biomass and distribution. Although dominance of Douglas-fir may be assured in a mixture with Sitka alder, the understory alder canopy will restrict the live crown of the Douglas-fir. At 23 yr of age on Mt. Benson, Douglas-fir with Sitka alder were producing 40% more stem growth than without alder, but the current Douglas-fir biomasses were similar between both portions of the plantation. Apparently, beneficial effects of Sitka alder early in the plantation's development were offset by the reduction in Douglas-fir live crowns. Similarly, increased Douglas-fir growth with red alder at Wind River required not only the achievement of a dominant crown position (at age 25 to 30), but also the development of a substantial canopy above the alder (at about age 45 to 50).

Data on Douglas-fir canopies in association with red alder are rare, but my results from Mt. Benson suggest that co-dominant Douglas-fir with red alder may carry only one-third the leaf biomass of similar-size, open-grown Douglas-fir. Despite this reduction in canopy, Douglas-fir stem growth was similar with and without red alder. Increased rates of net photosynthesis may have accounted for part of the increased stem growth per unit leaf biomass, but a shift in biomass allocation (away from roots and into stems) also probably occurred. The reduction in Douglas-fir canopies in association with red alder may be offset by an increased allocation of growth to stems. Improved soil fertility should maintain this favorable allocation to stem growth following the removal of alder; in combination with expanding canopies, sustained stem growth efficiency may greatly increase Douglas-fir biomass by the end of a rotation. This emergent pattern from the Mt. Benson and Wind River sites indicates a substantial potential for interplanted red alder to accelerate conifer stemwood production on poor sites. Therefore, the proposed mechanism of biomass allocation away from roots in favor of stems with improving soil fertility merits direct measurement and evaluation.

Selection of Alder Species

Red alder and Sitka alder appear to fix similar quantities of N per unit leaf biomass; high densities of red alder will carry larger canopies than Sitka alder, yielding higher maximum N fixation rates for red alder. The highest rates of N fixation by red alder would probably be associated with severe competition with associated conifers. If a market exists for red alder biomass, mixtures of red alder and Douglas-fir may yield the greatest economic returns. Maintenance of the desired species mix and dominance would probably require intensive stand treatments (Miller and Murray 1978). Where no market for red alder biomass exists, or where stand treatments will not be made, Sitka alder offers a low-risk, low-competition alternative for biological N fixation. The wide range of forestry objectives and practices in the Pacific Northwest suggests both species have potential uses in forest management strategies.

SECTION II. NITROGEN FIXATION AND NET PRIMARY PRODUCTION IN A YOUNG SITKA ALDER ECOSYSTEM[1]

INTRODUCTION

Sitka alder [Alnus sinuata (Regel) Rydb. = Alnus crispa (Ait.) Pursh ssp. sinuata (Regel) Hultén] is a promising candidate for biological nitrogen fixation in conifer plantations in the Pacific Northwest. The shrubby growth form of this species provides less competition for regenerating conifers than rapidly growing red alder (Alnus rubra Bong.) (Harrington and Deal 1982). Moreover, the range of rates of nitrogen fixation, reported to be 20 to 65 kg ha^{-1} yr^{-1} (Section III, Crocker and Major 1955, Crocker and Dickson 1957, Ugolini 1968), may be sufficient to alleviate nitrogen limitations on conifer growth (Miller and Murray 1979). Most studies have dealt with Sitka alder stands older than 20 years; information on both nitrogen fixation and biomass production for younger stands is needed to evaluate the potential of this species in forest management programs. Objectives of this project were to estimate the nitrogen fixation rate, total biomass, and biomass production in a young Sitka alder stand.

SITE DESCRIPTION AND METHODS

The study site was located at 820-m elevation on Butler Peak near Green Mountain in MacMillan Bloedel Limited Tree Farm 19 near Nanaimo,

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[1] Modified from Binkley, Dan. 1982. Nitrogen fixation and net primary production in a young Sitka alder stand. Can. J. Bot. in press. Used by permission.

British Columbia. The Sitka alder established naturally 5 years before the initiation of the study on an abandoned landing site in a clearcut. Soil of the landing was a shallow Orthic Regosol (Canada Soil Survey Committee 1978) (= Udorthent (U.S. Department of Agriculture 1975)) ranging in depth from 20 to 40 cm. Parent material was unconsolidated till overlying compacted basal till. The coarse (> 2 mm) fragment content exceeded 75% by volume. The site falls within the _Abies_ _amabilis_/_Vaccinium_ _alaskaense_/ _Vaccinium_ _parvifolium_ habitat type of the _Abies_ _amabilis_-_Tsuga_ _heterophylla_ Vegetation Zone (Beese 1981). Sitka alder comprised almost all of the biomass.

Three parallel, 30-m transects were established at 10-m intervals in the study site. Forest floor samples (25 x 25 cm) were taken every 3 m and mineral soil samples (0-15 and 15-30 cm) every 6 m along each transect. Four 25 m^2 circular plots (2.8 m radius) were located systematically along each transect. The number of shrubs and the diameter and length of each stem were measured in each plot.

Soil samples were analyzed for indices of nitrogen availability as ammonium-nitrogen after a 7-day anaerobic incubation at 40°C (Keeney and Bremner 1966), and for total nitrogen by colorimetry on semi-micro Kjeldahl digests (Allen _et_ _al_. 1974). Total calcium, magnesium and potassium in the forest floor samples were determinined by atomic absorption on a hydrochloric acid solution after dry ashing (Allen _et_ _al_. 1974). Extractable cations in the forest floor and mineral soil samples were also determined by atomic absorption on 1 _N_ NaCl extracts (Lavkulich 1977).

Twenty-five stems were selected from the study site in mid-July for calculation of biomass regression equations. The stems were chosen subjectively to span the range of diameters on the site (1.5 to 4.2 cm basal diameter). All leaves were stripped from the stems and air dried in the laboratory; stem fresh weights were recorded in the field. The root systems and nodules of eight shrubs were excavated; roots were field weighed and nodules were oven-dried and weighed in the laboratory.

Subsamples of leaves, stems, and roots were oven-dried for moisture content determinations and analyzed as mentioned for total nutrient content. Aboveground biomass regression equations were calculated using the model:

$$\log_e Y = A + B \log_e X$$

where Y = ovendry weight, A and B are coefficients, and X is the stem diameter at 10 cm from the root collar (Chapman 1976). Stem length did not increase the precision of the equations. Root and nodule biomass regressions were calculated as linear functions of total aboveground plant weight.

Biomass of each of the 12 plots was calculated by applying the regression equations to stem measurements. Stem production was derived by applying the stem biomass regression equation to the diameter of the previous year. Leaf production was assumed to equal the current biomass of leaves. Production of reproductive tissues appeared substantial but was not measured.

Acetylene reduction assays of nitrogen fixation rates were performed five times during summer 1980, following the procedure of McNabb and Geist (1979). The nodules were cut from 1-2 plants each time, leaving 2 cm of root attached, then incubated in an atmosphere of 10% acetylene for 30 min. Gas subsamples were stored in blood collection tubes for as long as 4 months before gas chromatographic analyses for acetylene and ethylene were performed. Changes in ethylene content should be less than 5% with storage less than 8 months (McNabb and Geist 1979).

RESULTS AND DISCUSSION

Table 3 gives the chemical properties of the soil. The low nutrient values combine with the high coarse-fragment content to indicate an infertile soil on the landing. At the current stage of stand development, the forest floor consisted of a discontinuous litter layer but contained substantial quantities of nutrients (Table 3).

Nitrogen fixation began in May concurrently with leaf emergence and peaked in July (Table 4). No assays were made after August, but nitrogen fixation probably ceased with leaf fall in late September (Wheeler and McLaughlin 1979). A series of calculations led to an approximation of the quantity of nitrogen fixed. Using 10 μmol C_2H_2 g^{-1} h^{-1} as a seasonal average for 24 h day^{-1} for 4 months gave 30 mmol C_2H_2 reduced per gram of nodule for the season. Assumption of a molar conversion ratio of three moles of C_2H_2 reduced per mole of N_2 fixed (Hardy _et al._ 1973) and multiplication by the molecular weight of nitrogen yielded a total seasonal estimate of 0.27 g of nitrogen fixed per gram of nodule. From the total nodule biomass of 130 kg ha^{-1} (Table 6), nitrogen fixation was estimated as 35 kg N ha^{-1} yr^{-1}. This value is based on several simplifying but untested assumptions: that the molar conversion ratio is 3.0, that measured rates equaled daily averages, and that within-plant variation in rates

TABLE 3. FOREST FLOOR AND MINERAL SOIL CHEMICAL PROPERTIES[a].

Component	Total N	Total P	Available N index[b]	Extractable cations,[c] meq 100 g^{-1}		
	%	%	µg g^{-1}	Ca	Mg	K
Forest floor (2,480 kg ha^{-1})	1.9 (0.2)	0.24 (0.01)	--	30.8 (2.2)	2.8 (0.3)	1.9 (0.0)
Mineral soil						
0-15 cm	0.15 (0.01)	0.14 (0.01)	25.2 (4.7)	3.3 (0.4)	0.2 (0.0)	0.2 (0.0)
15-30 cm	0.16 (0.02)	0.13 (0.01)	18.1 (3.4)	2.0 (0.3)	0.2 (0.0)	0.2 (0.0)

[a] Mean (standard error).

[b] Ammonium nitrogen contained in a 1 N KCl extract of sample incubated anaerobically at 40°C for 7 days.

[c] Cations extracted with 1 N NaCl.

TABLE 4. SITKA ALDER ACETYLENE REDUCTION ASSAYS, SUMMER 1980.

Date	C_2H_2 reduction rate $\mu mol\ g^{-1}\ hr^{-1}$ Mean	Standard error	No. of assays
May 29	3.1	0.4	21
June 19	6.0	0.8	22
July 6	22.0	1.6	4
July 16	10.5	1.3	26
August 20	7.9	1.3	10

approximates between-plant variation. Despite these potential sources of bias, the annual nitrogen fixation rate appears reasonable in comparison with estimates in the literature (Section III) and with the magnitudes of the nitrogen pools within the ecosystem (Table 6).

Biomass regression equations (Table 5) combined with the plot data provided the biomass and production estimates in Table 6. This young Sitka alder stand appeared to be accelerating in aboveground production; the stem biomass production in the current year almost equaled the previous 4 years of growth. Characteristic of young, rapidly growing stands, the aboveground biomass accumulation ratio (biomass divided by production) was 1.8.

If nitrogen fixation follows the trend of net primary production, the rates may increase in this ecosystem in the future. Typical nitrogen fixation rates for red alder exceed those of Sitka alder, but the difference may be partly attributable to the more favorable environments where red alder commonly grows. In comparisons of the two species on the same sites (Section III), similar rates of acetylene reduction activity in young stands were found, though red alder performed better at 20 years of age.

Nodule biomass of Sitka alder was 7.4% of leaf biomass; in a variety of field-grown alder species, the proportion ranged from 5.6% to 9.8% (Akkermans and van Dijk 1976, Akkermans and Houwers 1979, Tripp et al. 1979, Bormann 1981). This range of percentages is no greater than the errors commonly associated with estimates of nodule biomass. Accurate estimates of leaf biomass (from regression

TABLE 5. SITKA ALDER BIOMASS REGRESSION EQUATIONS, BIOMASS IN G AND DIAMETER AT BASE IN CM (N = 25, DIAMETER RANGE 1.5 to 4.2 CM FOR ABOVEGROUND PORTIONS; N = 8 FOR BELOWGROUND PORTIONS).

Component	Equation	r^2	s.e.[a]
Leaves	Log_e Biomass = 2.12 + 2.29 (Log_e Diameter)	0.87	0.25
Stems	Log_e Biomass = 3.09 + 2.93 (Log_e Diameter)	0.92	0.25
Roots	Biomass = 0.275 (Aboveground Biomass)	0.81	131
Nodules	Biomass = 0.0118 (Aboveground Biomass)	0.81	8.0

[a] Standard error of the estimate.

TABLE 6. SITKA ALDER BIOMASS, NET PRIMARY PRODUCTION, AND NUTRIENT CONTENT.

Component	Biomass kg ha^{-1}	Net primary production kg ha^{-1} yr^{-1}	Nutrient content of biomass kg ha^{-1}				
			N	P	K	Ca	Mg
Leaves	1,750 (460)[a]	1,750	44.0	6.9	15.0	19.7	3.3
Stems	8,910 (105)	4,250	57.3	13.6	21.0	20.3	3.6
Roots	2,930 (405)	--	18.8	4.5	6.9	6.7	1.2
Nodules	130 (48)	--	--	--	--	--	--
Forest floor	2,450 (500)	--	47.0	5.9	1.9	24.5	9.5

[a] Mean (standard error).

equations or litterfall collections) are obtained more easily than estimates of nodule biomass. If the proportion of nodule biomass to leaf biomass remains constant through the development of the stand, changes in leaf biomass could provide a useful surrogate measure for nodule biomass.

No literature on biomass production of Sitka alder is available for comparison with the results presented here. However, the biomass values are similar to those reported by Van Cleve et al. (1971) for 5-year-old thinleaf alder [Alnus incana (L.) Moench ssp. tenuifolia (Nutt.) Breitung] on a floodplain in Alaska and by Tripp et al. (1979) for 3-year-old red alder on coal-mine spoils in Washington.

The foliage assimilation efficiency (aboveground net primary production divided by leaf biomass) is an informative index for comparing ecosystems. In this study, the ratio was 3.4, slightly less than the average 3.7 for temperate forests of North America and Europe (Bray and Gorham 1964). Ratios for red alder range from 2.3 to 4.9 (Zavitkovski and Stevens 1972, Smith 1977, Tripp et al. 1979). Considering the harsh environment of the Sitka alder study site near Green Mountain, the foliage assimilation efficiency of 3.4 is remarkable.

Several criteria were listed by Miller and Murray (1979) for selecting nitrogen-fixing species for silvicultural purposes, including a nitrogen fixation rate of 20 to 50 kg N ha^{-1} yr^{-1} and minimal competition with crop trees for light. The 5-year-old Sitka alder on Green Mountain fit these criteria. The study provides a picture of the biomass, production, and nitrogen fixation rate of one stand at one point of development. Additional studies of this sort on other sites and at successive stages of development will allow an increasingly comprehensive understanding of the biomass and nutrient dynamics of Sitka alder ecosystems.

SECTION III. NITROGEN FIXATION BY SITKA ALDER AND RED ALDER ON THE SAME SITES[2]

INTRODUCTION

Red alder has received considerable attention in recent years both as a potential commercial species and as a source of biologically fixed nitrogen for other species (Trappe et al. 1968, Briggs et al. 1978, DeBell and Radwan 1979, Gordon et al. 1979). Strategies for incorporating red alder into forest management in the Pacific Northwest include short and long rotations of pure red alder as well as red alder interplanted with other commercial species (DeBell et al. 1978). The economic feasibility of these options is open to debate (Atkinson and Hamilton 1978, Atkinson et al. 1979), but energy costs and wood values could make symbiotic nitrogen fixation an attractive alternative to commercial forest fertilization. However, because land managers recognize red alder's ability to dominate disturbed sites and inhibit conifer regeneration, they are cautious about intentionally incorporating such a potential problem into their programs. Furthermore, current economic and social aspects of brush control can make red alder very difficult to manipulate in conifer plantations.

If alder is desired solely as a nitrogen fixer, conifers could be interplanted with a slow-growing alder that fixes substantial nitrogen. Recent discussion addressed the potential genetic development of a variety of alder with low growth rates and high nitrogen fixation

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[2] Modified from Binkley, Dan. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B.C. Can. J. For. Res. 11:281-286. Used by permission

ability (Newton and Howard 1979, Perry et al. 1979). However, with over 20 species in the genus Alnus (Hall and Maynard 1979), considerable genotypic diversity already exists. Existing species may exhibit these desirable characteristics.

Sitka alder has a desirable shrubby growth form and occurs on diverse sites from Alaska to California and eastward to Montana (Hitchcock and Cronquist 1973). On Vancouver Island, British Columbia, Sitka alder is common at elevations from 100 m to 1,500 m. Furthermore, conifers grow vigorously in association with Sitka alder. Therefore, a project was undertaken to compare the potentials of red alder and Sitka alder as sources of biologically fixed nitrogen in forest management programs by:

1. Using the acetylene reduction technique to measure the rates of nitrogen fixation by Sitka alder at several locations;
2. Comparing acetylene reduction rates for red alder and Sitka alder growing on the same sites;
3. Estimating the nodule biomass (kg ha^{-1}) for both species on the same site; and
4. Estimating annual nitrogen fixation rates for both species.

METHODS

The acetylene reduction procedure (McNabb and Geist 1979) involves incubating nodules in the field for 1 hr in an atmosphere of 10% acetylene. Then gas subsamples are removed and stored in vacutainer tubes and later analyzed by gas chromatography for acetylene (C_2H_2) and ethylene ($C_2H_{4\mu}$.

Between July 3 and July 9, 1979, acetylene reduction by Sitka alder nodules was assayed at four sites ranging in elevation from 510 to 820 m. At these sites, the trees ranged from 4 to 20 years of age and yielded nodules up to 3 cm in diameter. Two of these sites, Lizard Lake and Mt. Benson, were more intensively studied throughout the summer.

The Lizard Lake site, in Tree Farm License 20 near Port Alberni, was at a 660 m elevation on a parent material of glacial till. The soil was a sandy loam Humo-Ferric Podzol (Canada Soil Survey Committee 1978), which corresponds to the Typic Haplorthod subgroup (U.S. Department of Agriculture 1975). A recently clearcut area had 4- to 8-yr-old Sitka alder and red alder intermixed with coniferous species. Acetylene reduction by both species was assayed on the same day at three times during the summer. The quantities of nodules per plant were not estimated.

The second intensive study site, near Nanaimo, was located on Mt. Benson at 510 m elevation in Tree Farm License 19. The soil again was a Humo-Ferric Podzol derived from glacial till parent material with a layer of compacted basal till at a depth of 50 cm. The 15- to 20-yr-old (age at breast height) plantation was a mosaic of Douglas-fir either alone or mixed with Sitka alder or red alder that were naturally established. Two study plots were established, one in each type of alder vegetation.

A 1.0 ha plot contained Sitka alder ranging from 10 to 20 years of age as well as Douglas-fir. The Sitka alder formed a very dense canopy 5 to 7 meters above the ground; the Douglas-fir averaged about

11 m in height. Basal area was 10.6 and 8.2 m^2 ha^{-1} for the Sitka alder and the Douglas-fir.

An adjacent 1.0 ha plot of red alder and Douglas-fir had no discernably different site factors. The red alder were 12 to 20 years old and averaged 8 to 12 m in height. Some Douglas-fir had similar heights but many were suppressed beneath the alder canopy. The basal areas for the red alder and Douglas-fir were 13.9 and 6.4 m^2 ha^{-1}.

At Mt. Benson, soil pits (50 x 50 cm) were subjectively located and excavated to the depth of the basal till. Twenty-four pits were dug in the Sitka alder/Douglas-fir plot while 22 pits were dug in the red alder/Douglas-fir plot. The soil was sifted by hand to collect nodules which were assayed for acetylene reduction activity. Nodules were oven dried at 80°C for 24 hr to determine biomass.

RESULTS AND DISCUSSION

The acetylene reduction assays for Sitka alder in early July showed higher rates for the smaller nodules and higher elevations (Table 7), but the differences in the four sites complicate interpretation. Sitka alder at Green Mountain and Pearl Lake tended to have smaller nodules well distributed throughout the rooting zone. At Mt. Benson, Sitka alder had larger nodules which were unevenly distributed along the roots. At Lizard Lake, Sitka alder had both types of nodules. Size differences may reflect nodule development over time or other physiological factors.

During the summer at Lizard Lake, acetylene reduction rates did not significantly differ between the two alder species (Table 8). Conversely, on Mt. Benson red alder acetylene reduction rates averaged

TABLE 7. ACETYLENE REDUCTION RATES OF SITKA ALDER NODULES ON VANCOUVER ISLAND, JULY 3-9, 1979.

Location	Elevation (m)	Age (yr)	No. of Assays	Nodule Mean Size (cm)	C_2H_2 Reduction Rate Mean	S.E.[a]
					--(μmol g^{-1}	hr^{-1})--
Green Mountain	820	4	4	< 1	22.0	1.6
Pearl Lake	700	5-10	3	< 1	19.4	4.1
Lizard lake	660	4-8	6	< 1-3	15.2	2.9
Mt. Benson	510	10-20	3	1-3	8.8	4.4

[a] Standard error.

TABLE 8. ACETYLENE REDUCTION RATES OF 4 TO 8 YEAR-OLD SITKA AND RED ALDER NODULES AT LIZARD LAKE.

Assay Date	Alder Species	C_2H_2 Reduction Rate Mean	 S.E.[a]	No. of Assays
		--(μmol g^{-1}	hr^{-1})--	
July 9, 1979	Sitka	15.2	2.9	6
	Red	21.8	7.4	4
July 18, 1979	Sitka	36.1	8.3	4
	Red	51.0	24.2	3
August 28, 1979	Sitka	20.5	4.5	10
	Red	18.8	7.6	6

[a] Standard error.

twice those of Sitka alder (Table 9). In these 15- to 20-yr-old stands, the red alder appeared vigorous while the Sitka alder was overtopped by the developing Douglas-fir canopy. Dead nodules were common in the Sitka alder site, yet none were found in the red alder site. Acetylene reduction rates for both species may have been similar on Mt. Benson in the past when the Sitka alder was more vigorous.

Assuming that the acetylene reduction values I measured approach the average 24-h rates, and assuming that activity occurs from leaf emergence to leaf fall (May through September), an estimate of C_2H_2 reduction for the intensively studied Mt. Benson site would average 5 and 10 $\mu mol \cdot g^{-1} \cdot hr^{-1}$ for Sitka and red alder for 24 hr per day over 5 months, or 18 and 36 $mol \cdot kg^{-1} \cdot yr^{-1}$.

Few studies have compared nitrogen fixation rates for different species on similar sites. Carpenter et al. (1979) assayed ten 3 to 4 year old Sitka alder and red alder; acetylene reduction rates averaged 12.1 and 26.2 $\mu mol\ C_2H_2\ g^{-1}\ hr^{-1}$ for Sitka and red alder. Based on the nodule weight per tree, rates averaged 430 and 490 μmol $C_2H_2\ tree^{-1}\ hr^{-1}$ for Sitka and red alder. These acetylene reduction values are well within the range I measured, although I found no significant rate difference between the species for young, vigorous plants.

The average values I report are below all of those listed by Tripp et al. (1979), who compared acetylene reduction rates for five published studies on four alder species. The high elevation of my sites (510 to 820 m) may be less favorable for nitrogen fixation.

In addition to greater acetylene reduction rates, red alder on Mt. Benson also had a greater nodule biomass than Sitka alder.

TABLE 9. ACETYLENE REDUCTION RATES OF 15- TO 20-YR-OLD SITKA AND RED ALDER ON MT. BENSON.

Assay date	Alder species	No. of assays	C_2H_2 reduction rate, µmol•g^{-1}•hr^{-1} Mean	s.e.[a]
May 22, 1980	Sitka	10	1.7	0.2
	Red	10	3.4	1.0
June 13, 1980	Sitka	10	3.4	0.8
	Red	10	10.5	1.9
June 22, 1980	Sitka	6	8.7	2.3
	Red	4	20.0	7.3
July 10, 1980	Sitka	13	12.4	2.1
	Red	10	20.1	4.1
July 28, 1980	Sitka	10	3.2	1.5
	Red	10	13.9	4.3
August 20, 1980	Sitka	10	2.7	0.2
	Red	8	4.4	1.1

[a] Standard error.

Nodule biomass (dry weight) averaged (± 1 standard error) 390 ± 150 kg•ha^{-1} on the red alder site and 110 ± 40 kg•ha^{-1} for the Sitka alder site. I have also found a proportionate difference in leaf biomass of the two species (Sections IV and V).

Few estimates have been published for alder nodule biomass under field conditions. Zavitkovski and Newton (1968) estimated nodule biomasses of 120 and 250 kg ha^{-1} in a 7-yr-old and a 30-yr-old pure red alder stand. Tripp et al. (1979) found average nodule biomasses of 30 to 55 kg ha^{-1} for 2- to 4-yr-old red alder growing on mine spoils, while Bormann and Gordon (1980) reported 50 to 175 kg ha^{-1} for 5-yr-old alder. Akkermans and van Dijk (1976) reported 450 kg ha^{-1} of nodules in a 1- to 20-yr-old stand of _A. glutinosa_. Both plots on Mt. Benson fall within this range.

To approximate the quantities of nitrogen fixed, the annual acetylene reduction for Sitka and red alder of 18 and 36 mol C_2H_2•kg^{-1}•yr^{-1} can be converted to moles of N_2 by using an assumed conversion ratio of 3 moles C_2H_2 per mole N_2 (Hardy et al. 1973). Then multiplying by the molecular weight of N_2 yields an annual nitrogen fixation rate of 170 and 340 g•kg^{-1} of nodules. Multiplying these quantities by the nodule biomass for each species yields nitrogen fixation estimates of 20 kg•ha^{-1}•yr^{-1} for Sitka alder and 130 kg•ha^{-1}•yr^{-1} for red alder.

My estimates of annual nitrogen fixation rates for Sitka and red alder are similar to others listed in Table 10 which groups taxonomically similar species. The group of _Alnus rugosa_ (Du Roi) Spreng., _A. tenuifolia_ Nutt. and _A. incana_ (L.) Moench has a growth form similar to Sitka alder, and these species have been found to fix more nitrogen

TABLE 10. AVERAGE ANNUAL ACCRETION OF NITROGEN IN ALDER ECOSYSTEMS.

Species and N Accretion kg ha^{-1} yr^{-1}	Component	Stand Age	Reference
Alnus rubra, pure stands			
320	Ecosystem[a]	2-15	Newton et al. 1968
140	Soil to 90 cm[a]	0-40	Franklin et al. 1968
100	Ecosystem[b]	0-1	Zavitkovski and Newton 1968
140	Ecosystem[b]	7	Zavitkovski and Newton 1968
209	Ecosystem[b]	30	Zavitkovski and Newton 1968
80	Soil to 15 cm[a]	0-4	DeBell and Radwan 1979
85	Ecosystem[a]	38	Cole et al. 1978
50	Forest floor + soil to 20 cm[a]	0-40	Bormann and DeBell, in prep.[d]
100+	Ecosystem[a]	0-40	Bormann and DeBell, in prep.[d]
50-106	Ecosystem[c]	5	Bormann and Gordon 1980
Mixed stands, with Douglas-fir			
130	Ecosystem[c]	22	This study
60	Ecosystem[a]	0-23	This study, Section V
40	Soil to 90 cm[a]	26	Tarrant and Miller 1963
13	Soil to 15 cm[a]	0-17	Berg and Doerksen 1975
51	Soil to 15 cm[a]	0-17	Berg and Doerksen 1975
26	Soil to 90 cm[a]	0-40	Franklin et al. 1968
Mixed stand, with *Populus trichocarpa* (T. & G.)			
32	Soil to 15 cm[a]	0-4	DeBell and Radwan 1979
Alnus sinuata, *A. Crispa*, pure to mixed stands			
20	Ecosystem[c]	22	This study

TABLE 10 (continued)

Species and N Accretion kg ha^{-1} yr^{-1}	Component	Stand Age	Reference
31	Ecosystem[a]	0-23	This study, Section IV
62	Soil to 60 cm[a]	0-50	Crocker and Major 1955
40	Soil to 60 cm[a]	0-50	Crocker and Dickson 1957
24	Forest floor and A horizon	0-55	Ugolini 1968
Alnus rugosa, *A. tenuifolia*, *A. incana*, pure stands			
360	Ecosystem[a]	0-5	Van Cleve et al. 1971
156	Ecosystem[a]	0-20	Van Cleve et al. 1971
85	Ecosystem[a]	0-16	Voight and Steucek 1969
170	Ecosystem[a]	0-18	Daly 1966
43	Soil to 70 cm[a]	0-21	Ovington 1956
56	Soil to 20 cm[a]	0-30	von Oberforter et al. 1925 (cited in Tarrant and Trappe 1971)
43	Ecosystem[c]	30	Johnsrud 1978
Alnus glutinosa			
58	Ecosystem[c]	5-20	Akkermans and van Dijk 1976
30	Greenhouse study[a]	7	Virtanen 1957 (cited in Tarrant and Trappe 1971)
12	Soil to 5 cm[a]	11	Holmsgaard 1960 (cited in Tarrant and Trappe 1971)

[a] Based on accretion studies.

[b] Based on greenhouse accretion per gram of nodule times nodule biomass in field.

[c] Based on acetylene reduction assays.

[d] Bormann, B. T. and D. S. DeBell. Relation of stand age to nitrogen content and other properties of soil beneath red alder. Manuscript in preparation.

than Sitka alder. Because study conditions varied, the different rates of fixation cannot be attributed solely to species or location. However, these other alder species with shrubby growth forms should also be considered for biological nitrogen fixation in forest plantations.

CONCLUSIONS

Although the acetylene reduction rates appeared similar for Sitka and red alder nodules from young plants at Lizard Lake, red alder was more active on Mt. Benson. However, the estimated 20 $kg \cdot ha^{-1} \cdot yr^{-1}$ nitrogen input to the Mt. Benson Sitka alder-Douglas-fir plot is still substantial, and may have been greater in the past. Miller and Murray (1979) estimated that a nitrogen fixation rate of 20-50 $kg \cdot ha^{-1} \cdot yr^{-1}$ might be sufficient to alleviate nitrogen as a growth limiting factor for Douglas-fir plantations. Therefore, Sitka alder with its shrubby growth form appears to be a feasible alternate source of biologically fixed nitrogen where commercial or competition concerns do not favor red alder.

Further research is needed to examine the mechanisms controlling nodulation and nitrogen fixation rates in the two alder species, i.e., the photosynthate supply of the host, the strain of nitrogen-fixing endophyte (Perry et al. 1979), the interactions of the host-endophyte-mycorrhizal fungi symbioses (Trappe 1979), nutrient demands, and environmental conditions. Until the mechanisms which regulate the nitrogen fixing symbioses are understood, the applicability of information obtained on one site for other sites will remain uncertain.

SECTION IV. A CASE STUDY OF SITKA ALDER IN A DOUGLAS-FIR PLANTATION

INTRODUCTION

The potential of symbiotic nitrogen fixation for increasing production in forest ecosystems has been the topic of much recent work (c.f., Haines 1978, Gordon et al. 1979). Research in the Pacific Northwest has focused on red alder; however, maintaining full stocking of conifers mixed with rapidly growing red alder may require intensive stand treatments (Miller and Murray 1978). Another common alder species in the region is Sitka alder. This high elevation species with a shrubby growth form has been reported to fix 20 to 65 kg of nitrogen ha^{-1} yr^{-1} (Section III), grows well at low elevations and should offer less competition with interplanted conifers than red alder (Harrington and Deal 1982). The objective of the present study was to take advantage of the natural occurrence of Sitka alder in a portion of a 23-year-old Douglas-fir plantation and evaluate impacts on Douglas-fir growth and nutrition, on ecosystem biomass, production and litterfall and on soils.

SITE DESCRIPTION

The study area is on Mt. Benson near Nanaimo, British Columbia (50° 8' N Latitude, 124° 2' W Longitude) in MacMillan Bloedel Tree Farm 19. The area is classified as a _Tsuga heterophylla_/_Gaultheria shallon_-_Berberis nervosa_ habitat type of _Tsuga heterophylla_ Vegetation Zone (Franklin and Dyrness 1973), or the East Vancouver Island Montane Wetter Maritime Coastal Western Hemlock biogeoclimatic variant of

Klinka et al. (1979). The climate is mild, with average temperatures in January and July of 1° and 17°C. The frost-free period is about 200 days, with 1,500 accumulated degree days over 6°C (Klinka et al. 1979). Precipitation averages 200 cm yr^{-1} only 40 cm of which falls from April through September. The soil is a gravelly clay loam Typic Haplorthod (= Humo Ferric Podzol, Canada Committee on Soil Classification 1978) developed on a 50 cm blanket of unconsolidated till overlying compacted basal till. The establishment pattern of the naturally-seeded Sitka alder did not appear to follow any soil patterns (Table 11); aerial photographs from 1958 show the probable seed source for the alder was restricted to one corner of the plantation. The plantation is in a midslope position and has a westerly aspect with slope varying from 5° to 15°. The site was logged and burned between 1952 and 1956 and planted with Douglas-fir seedlings in 1958. Current (1981) height of co-dominant and dominant Douglas-fir was 11 m, and Sitka alder averaged 6 m. The expanding canopy of the Douglas-fir will probably shade-out most of the alder within 5 yr. I have assumed that the adjacent sites used in this study were relatively similar prior to the establishment of Sitka alder in the late 1950's but lack of pre-establishment soils data and independent treatment replications preclude testing this assumption. However, the similarity in soil physical properties between the sites (Table 11) supports my assumption.

TABLE 11. SOIL PHYSICAL PROPERTIES, AVERAGES OF 10 SAMPLES.

		Site type	
Property	Depth, cm	No alder	Sitka alder
Depth to compacted till, cm	--	56	50 n.s.[d]
Rock volume[a], % > 5 cm	0-50	10	8 n.s.
Coarse-fragment-free bulk density[b], kg of < 2-mm-fraction l^{-1}	0-15	0.49	0.49 n.s.
Sand[c], %	0-15	39	38 n.s.
Silt, %	0-15	32	32 n.s.
Clay, %	0-15	29	30 n.s.

[a] Visually estimated from soil pits.

[b] Sample volume measured by sand displacement.

[c] Particle size analysis by hydrometer method (Lavkulich 1977).

[d] Site means do not differ significantly ($p < 0.10$) based on two-tailed T-tests.

METHODS

Vegetation

Eight plots each measuring 15 x 40 m (with 10 m buffers between plots) were established in the adjacent no alder and Sitka alder sites in the summer of 1981. Within each plot, all Douglas-fir crop trees (defined as those exceeding 7 cm breast-height diameter) were tagged and measured for diameter and 5 yr radial increment. Within the Sitka alder plots, all alder stems were tallied by 1 cm diameter classes. Regression equations applied to these measurements provided estimates of aboveground plant biomass and woody biomass increment. The equations for Sitka alder were developed as a part of this study and followed the model (Chapman 1976):

$$\text{Log}_e \text{ Biomass} = \text{Intercept} + \text{Coefficient } (\text{Log}_e \text{ Diameter}).$$

Fourteen stems were analyzed. All leaves were stripped from the branches, oven-dried for 24 hr at 80°C and weighed. Diameter measurements were taken every 2 m along the stems, and volume calculations were converted to biomass based on ash-free oven-dry weights of stem samples. These equations are listed in Table 12.

A regression equation for Douglas-fir stems (wood+bark) was obtained from Gholz et. al. (1979). Five trees ($\pm$ 1 cm diameter from site average) per site were randomly sampled for foliage biomass: each tree was divided into 2 m sections, and the number of branches per section tallied. One average branch per section was subjectively chosen and all leaves were stripped, oven-dried, and weighed. The ratio of leaf weight to basal area per tree did not differ between

TABLE 12. SITKA ALDER BIOMASS REGRESSION EQUATIONS, BIOMASS IN G AND DIAMETER AT BREAST HEIGHT IN CM (N = 14, DIAMETER RANGE 2 TO 7 CM).

Component	Equation	r^2	s.e.[a]
Leaves	$\log_e$ Biomass = 1.82 + 2.38 ($\log_e$ Diameter)	0.88	0.127
Stems	$\log_e$ Biomass = 4.50 + 2.30 ($\log_e$ Diameter)	0.97	0.276

[a] Standard error of the estimate.

sites ($p < 0.10$). The combined estimate of 910 kg m^{-2} (standard error of the mean = 80 kg m^{-2}) was multiplied by the average plot basal area to estimate foliage biomass per hectare (Ovington et al. 1967). Use of the foliage biomass regression equation from Gholz et al. (1979) (not shown) underestimated the reported values by 60 to 70%. Branch biomass was calculated as 140% of leaf biomass, based on leaf-to-branch allometry from Gholz et al. (1979).

The annual aboveground net primary production of Sitka alder was calculated as leaf biomass plus the annual average of the previous 5 years' stem increment. Douglas-fir production was estimated by summing one-fifth of the leaf biomass (Cole et al. 1967) with the average annual increment of stems and branches. Because plant mortality was not included, the reported net primary production estimates are minimum values.

Douglas-fir foliage was collected in early August 1979 for nutrient analysis. Ten samples per site were composited from 5 trees each. The samples included all ages of needles from the central rachis of a fifth-whorl branch from the top. All sample branches were in a fully illuminated position. Ten Sitka alder foliage samples were obtained in August 1981 by bending down randomly selected stems and picking upper-crown leaves. Three composited tissue samples were analyzed for nutrient concentrations from these categories: Douglas-fir stem+bark (obtained from increment cores), Douglas-fir branches (obtained from the foliage sampling operation), and Sitka alder stem+bark (obtained from the regression equation sampling).

Total nitrogen was determined on sulfuric acid, micro-Kjeldahl digests using Autoanalyzer techniques (Allen et al. 1974). Total phosphorus and metals were determined in nitric-perchloric acid digests (Allen et al. 1974). Foliar sulfate-sulfur was determined following boiling in 0.01 N HCl by the hydroiodic acid, bismuth reducible method (Kowalenko and Lowe 1972), and total sulfur by Autoanalyzer methods as sulfate following ashing-fusing with $NaHCO_3$ + Ag_2O (Lea and Wells 1980).

The biomass and nutrient content of understory conifers [western hemlock (*Tsuga heterophylla* [Raf.] Sargeant), western red cedar (*Thuja plicata* Donn ex D. Don) and Douglas-fir, generally less than 4 m tall] were calculated by applying equations developed for eastern hemlock [*Tsuga canadensis* (L.) Carr] by Young and Carpenter (1967) to stem tallies from 10 to 100 m^2 random plots in each site. Production arbitrarily was assumed to equal 10% of understory conifer biomass.

Shrub and herb biomasses were clipped and weighed from 10-1 m^2 plots per site. Ninety percent of the biomass was comprised of *Gaultheria shallon* (Pursh) and *Berberis nervosa* (Pursh). Minor species included *Pteridium aquilinum* (L.) Kuhn, *Vaccinium parvifolium* Smith and *Achlys triphyllum* (Smith) DC. Production of the understory was calculated at 26% of biomass (Turner and Long 1976), and nutrient content estimated from concentrations given by Turner et al. (1978).

Forest Floor and Soils

Forest floor biomass samples (25 x 25 cm) were collected at 30 random locations per site, air-dried and sorted into 3 categories: woody fraction, > 2 mm fraction and < 2 mm fraction. Three composite samples of each category were analyzed for nutrient concentrations as described for plant tissues. Forest floor biomass is reported on an ash-free (loss on ignition at 475°C for 4 hr) basis.

Ten soil pits were dug in each site, and the pit faces sampled at depths of 0-10 cm, 10-20 cm, 20-35 cm and 35-50 cm. Soil samples were air-dried and sieved. The < 2 mm fraction measured for: pH in a water paste, total nitrogen as mentioned, total carbon using the Walkley-Black wet oxidation method (Allen et al. 1974), Bray-extractable phosphorus and 1 N NaCl extractable potassium, calcium and magnesium (Lavkulich 1977). The anaerobic incubation method (ammonium-N after 7 days at 40°C) of Keeney and Bremner (1966) was used for an index of nitrogen availability.

Litterfall

Leaf and other non-woody litterfall was collected in plastic 80 liter buckets (45 cm diameter openings) lined with 1 mm nylon mesh bags. Twenty traps were located in each site from July 1, 1980 through June 15, 1981. Litter collections occurred just after autumn leaf fall on October 30, and on June 15. Woody litterfall was collected from 10-1 m^2 quadrats on June 15 from which the forest floor had been removed the previous July. Nutrient contents were based on nutrient concentrations from 3 composite samples each of non-woody and woody litterfall.

Statistical Analysis

The significance of differences between the means of the two sites was evaluated with 2-tailed t-tests, on the basis of the variance of the 8 estimated plot values per site. Sources of variation inherent in estimating individual plot values were unavoidably included in the comparison of the sites; therefore, my tests of significance should be conservative.

RESULTS

Soil Chemistry

The major effect of Sitka alder on the mineral soil was restricted to the top 10 cm (Table 13); significant increases at this depth were found for total and available N, total carbon, and extractable P, Ca and Mg. Only the available nitrogen index levels were greater at all sampling depths in the Sitka alder site.

Douglas-fir Crop Trees

The presence of Sitka alder did not appear to result in a significant change in Douglas-fir stocking or stand basal area, but average diameter was increased significantly by 13% and average basal area increment by 33% (Table 14). Greater current growth rates of Douglas-fir with Sitka alder, but similar current basal area,indicated the effect of Sitka alder was currently greater than at earlier stages of the plantation's development.

The Douglas-fir foliage from the Sitka alder site contained significantly higher concentrations of N, but lower concentrations of P, S, SO_4-S, Ca, Mn, Zn, and Fe (Table 15). The 0.93% N of the no alder site Douglas-fir was very low (van den Driessche 1979) and the P and S concentrations in the Sitka alder site Douglas-fir were low to very low (van den Driessche 1979).

TABLE 13. SOIL CHEMICAL PROPERTIES, AVERAGES OF 10 SAMPLES OF < 2 MM FRACTION.

Property	Depth (cm)	Site type	
		No alder	Sitka alder
Acidity, pH[a]	0-10	4.5	4.8 n.s.[e]
	10-20	4.8	4.6 n.s.
	20-35	4.9	4.9 n.s.
	35-50	4.9	4.0 n.s.
Nitrogen, %	0-10	0.09	0.16****
	10-20	0.07	0.08 n.s.
	20-35	0.06	0.07 n.s.
	35-50	0.05	0.06 n.s.
Available nitrogen index[b], μg g^{-1}	0-10	25	86****
	10-20	15	44****
	20-35	39	52**
	35-50	36	52**
Carbon, %	0-10	2.05	3.34****
	10-20	1.61	1.62 n.s.
	20-35	1.15	1.21 n.s.
	35-50	1.09	1.13 n.s.
Available phosphorus index[c], μg g^{-1}	0-10	8.23	21.29****
	10-20	13.65	11.31 n.s.
	20-35	8.88	12.14 n.s.
	35-50	9.94	11.55 n.s.
Extractable[d] calcium meq kg^{-1}	0-10	19.9	44.2**
	10-20	7.2	11.4 n.s.
	20-35	7.2	8.3 n.s.
	35-50	6.6	12.9 n.s.
Extractable magnesium, meq kg^{-1}	0-10	4.4	9.1**
	10-20	1.8	2.8 n.s.
	20-35	1.5	2.1 n.s.
	35-50	1.6	4.4*
Extractable potassium, meq kg^{-1}	0-10	2.4	2.6 n.s.
	10-20	2.2	1.3 n.s.
	20-35	0.9	1.9 n.s.
	35-50	1.0	1.6 n.s.

[a] In a water paste.

[b] As ammonium-N in 1 N KCl extract after 7 days anaerobic incubation at 40°C.

[c] Bray method (0.03 N NH_4F and 0.025 N HCl).

[d] Extracted with 1 N NaCl.

[e] Significance of site differences based on 2-tailed t-tests: n.s. = not significant ($p > 0.10$), * = $p < 0.10$, ** = $p < 0.05$, *** = $p < 0.01$, **** = $p < 0.001$.

TABLE 14. DOUGLAS-FIR CROP TREE AVERAGES OF 8 600 M^2 PLOTS PER SITE.

Property	Site type No alder	 Sitka alder
Stocking, trees ha^{-1}	650	570 n.s.[c]
Average breast height diameter[a], cm	13.8	15.6**
Basal area, m^2 ha^{-1}	10.5	10.9 n.s.
Basal area increment[b], m^2 ha^{-1} yr^{-1}	0.9	1.2****

[a] Based on average basal area of trees.

[b] Average of 1977 to 1981 growth.

[c] Significance levels as in Table 13.

TABLE 15. FOLIAR NUTRIENT CONCENTRATIONS, AVERAGES OF 10 SAMPLES.

Nutrient	No alder site	Sitka slder site	
	Douglas-fir[a]	Douglas-fir[a]	Sitka alder[b]
%			
N	0.93	1.10***[c]	3.10
P	0.22	0.12****	0.30
K	0.59	0.55 n.s.	0.90
Ca	0.49	0.42**	0.56
Mg	0.09	0.07 n.s.	0.27
S	0.37	0.21****	0.29
SO_4-S	0.13	0.05****	--
$\mu g\ g^{-1}$			
Na	53	51 n.s.	--
Mn	730	430***	--
Zn	20	11***	--
Fe	140	90***	--
Cu	1.9	2.9**	--

[a] Collected early August, 1979; each sample was a composite of all ages of needles from the central rachis of a fifth-whorl branch from the top from 5 trees. Projected leaf area was 56 $cm^2\ g^{-1}$ (oven dry basis) for Douglas-fir in both sites.

[b] Collected early August, 1981. Projected leaf area was 205 $cm^2\ g^{-1}$ (oven dry basis) for Sitka alder.

[d] Significance levels as in Table 13.

Aboveground Biomass, Production and Nutrient Content

The estimate of total Douglas-fir biomass on the Sitka alder site was 20% greater than on the no alder site (Table 16), but the difference was not significant with a 2-tailed t-test ($p = 0.80$). Stem biomass was significantly increased by 30% with Sitka alder, and the annual stem increment was increased by 40%. Inclusion of alder biomass and understory and forest floor components resulted in an estimated 56% increase in aboveground ecosystem biomass, and a 70% increase in aboveground net primary production.

The nutrient content of aboveground biomass pools was greater in the Sitka alder site (Table 17 and 18); most of the differences were due to the alder and forest floor pools. The total nitrogen content of the plant plus forest floor pools in the Sitka alder site exceeded the estimate for the no alder site by 350 kg ha^{-1}.

Litterfall Biomass and Nutrient Content

The two sites differed more in litterfall biomass and nutrient content than in any other parameter (Table 19). Total litterfall in the Sitka alder site exceeded the no alder site by 3.6 fold, with nutrient content increases ranging from 3 to 7 fold.

DISCUSSION

Nitrogen Fixation

The total soil nitrogen content of the no alder site was 1,560 kg ha^{-1} (calculated from Table 11 and 17). This is less than almost all values reported for Pacific Northwest forest soils (c.f., Turner et al.

TABLE 16. ABOVEGROUND BIOMASS AND NET PRIMARY PRODUCTION[a] ESTIMATES, AVERAGES OF 8 600 M^2 PLOTS PER SITE.

	Biomass (kg ha^{-1})		Production (kg ha^{-1} yr^{-1})[b]	
	Site type		Site type	
Component	No alder	Sitka alder	No alder	Sitka alder
Douglas-fir				
Foliage	9,600	9,900 n.s.[c]	1,900[d]	2,000 n.s.
Branches	13,300	13,900 n.s.	900	1,200 n.s.
Stems	35,000	45,900*	4,100	5,800**
Subtotal	57,900	69,700*	6,900	9,000***
Sitka alder				
Foliage		1,800		1,800
Stems+branches		23,800		3,100
Subtotal		25,600		4,900
Understory				
Conifers	9,500[e]	1,700**	1,000[e]	200**
Shrubs+herbs	2,500	1,100 n.s.	600[f]	300 n.s.
Subtotal	12,000	2,800**	1,600	500**
Plant total	69,900	98,100***	8,500	14,400***
Forest floor	7,000	22,100****		
Grand total	76,900	120,200****		

[a] Mortality not included.

[b] Douglas-fir and Sitka alder stem and branch production estimates are based on regression-calculated biomasses using breast height diameter from 5 yr previously.

[c] Significance levels as in Table 13.

[d] Current year foliage is assumed to be 20% of total foliage for Douglas-fir (Cole et al. 1967).

[e] Understory conifer biomass estimated using equations for eastern hemlock from Young and Carpenter 1967.

[f] Understory conifer production was assumed to equal 10% of biomass; shrub+herb production was assumed to be 26% (Turner and Long 1975).

TABLE 17. BIOMASS NITROGEN AND PHOSPHORUS CONTENTS[a] (KG HA $^{-1}$).

	Site type and nutrient			
	Nitrogen		Phosphorus	
Component	No alder	Sitka alder	No alder	Sitka alder
Douglas-fir				
Foliage	89	110	20	11
Branches	13	17	2	3
Stems	27	28	3	5
Subtotal	129	155	25	19
Sitka alder				
Foliage		56		5
Stems+ branches		50		3
Subtotal		106		8
Understory				
Conifers[b]	16	3	3	1
Shrubs+herbs	27	12	3	2
Subtotal	43	15	6	3
Plant total	172	276	31	30
Forest floor	36	282	14	42
Grand total	208	558	45	72

[a] Based on average nutrient concentration times biomass listed in Table 16. Nutrient concentrations were based on 10 samples of foliage, and on 3 composited samples for other tissue types.

[b] Estimated from Young and Carpenter (1967) for eastern hemlock.

TABLE 18. BIOMASS POTASSIUM, CALCIUM AND MAGNESIUM CONTENTS[a] (KG HA^{-1}).

	Site type and nutrient					
	Potassium		Calcium		Magnesium	
Component	No alder	Sitka alder	No alder	Sitka alder	No alder	Sitka alder
Douglas-fir						
Foliage	57	54	47	42	9	7
Branches	7	11	6	6	< 1	< 1
Stems	12	31	14	18	2	2
Subtotal	76	96	67	66	11	9
Sitka alder						
Foliage		16		10		5
Stems+ branches		13		12		4
Subtotal		29		22		9
Understory						
Conifers[b]	7	1	11	2	2	1
Shrubs+herbs	23	10	18	8	5	2
Subtotal	30	11	29	10	7	3
Plant total	106	136	96	98	18	21
Forest floor	6	16	31	160	17	51
Grand total	112	152	127	258	35	72

[a] Based on average nutrient concentration times biomass listed in Table 16. Nutrient concentrations were based on 10 samples of foliage, and on 3 composited samples for other tissue types.

[b] Estimated from Young and Carpenter (1967) for eastern hemlock.

TABLE 19. ABOVEGROUND LITTERFALL BIOMASS AND NUTRIENT CONTENT ($KG\ HA^{-1}$).

Component	Site type[a] No alder	 Sitka alder
Biomass		
Fine litterfall	1,350	3,840
Woody litterfall	80	1,370
Total litterfall	1,430	5,210
Nutrients		
Nitrogen	16	112
Phosphorus	2	7
Potassium	2	15
Calcium	14	44
Magnesium	2	13

[a] All site means differ at $p < 0.001$.

1979, Cole and Rapp 1981). In combination with the low foliar-N concentrations of the Douglas-fir and low available-N indexes, the low soil nitrogen content indicates a severe nitrogen limitation in the no alder site. The increase in mineral soil N (0-10 cm) in the Sitka alder site of 336 kg ha^{-1} can be added to the increase in plant and forest floor biomass N content for a total ecosystem accretion estimate of 686 kg ha^{-1}. Dividing by stand age yields an annual fixation estimate of 30 kg ha^{-1} yr^{-1}. The current rate of fixation in 1980 by the acetylene reduction technique was 20 kg ha^{-1} yr^{-1} (Section III). The declining vigor of the alder probably resulted in the current rate being lower than the long-term average.

Douglas-fir Nutrition

The presence of Sitka alder significantly increased the N concentrations in Douglas-fir foliage, but even the 1.1% N level is low (van den Driessche 1977). A growth response to additional N might occur (Turner et al. 1979). The Douglas-fir with Sitka alder may be experiencing phosphorus or sulfur limitations on growth, but a Douglas-fir seedling bioassay of soils from this site showed no response to added N, P or S (Binkley et al. 1982b). A fertilizer field trial is under way.

Ecosystem Effects

Grier (1979) reported an average aboveground net primary production of 13,400 kg ha^{-1} yr^{-1} for the Douglas-fir region. Our no alder site was 36 percent below this average, and our Sitka alder site was marginally above average. The increase in N content of litterfall was even larger; Vitousek (1982) compiled an extensive list for temperate forests, and only those containing N fixers had greater than 80 kg ha^{-1} yr^{-1} in litterfall. Despite the relatively low rate of N fixation, the N content of litterfall on the Sitka alder site ranked as high as any temperate ecosystem listed by Vitousek. My results demonstrated a high potential for increasing forest nutrient cycling rates and production by incorporating N-fixing Sitka alder into management strategies.

Contrasts with Red Alder

Nitrogen fixation estimates for red alder typically range from 50 to 150 kg ha^{-1} yr^{-1} (Section III) which substantially exceeds rates for Sitka alder in the present study and in the literature. However, the impact of Sitka alder on ecosystem functions is remarkably similar to red alder. For example, a 30 year-old stand of red alder had 46% greater net aboveground primary production than an adjacent 42 year-old Douglas-fir stand, and cycled 4.6 times more N in litterfall (Cole et al. 1978, Cole and Rapp 1981). In a red alder/Douglas-fir stand (Section V) adjacent to the sites discussed here, neither aboveground net primary production nor litterfall N content significantly exceeded the estimates for the Sitka alder/Douglas-fir stand. It appears that the benefits of mixtures of N-fixing species with conifers on Mt. Benson were not simply proportional to the quantity of N fixed. The relatively moderate quantity of 686 kg ha^{-1} in the Sitka alder site rivaled the effect of the greater fixation (1,490 kg ha^{-1}) of red alder.

My study demonstrated a high potential for incorporating Sitka alder into conifer plantations, but designed experiments are needed to develop the usefulness of this management tool. Some of the major areas to be addressed are the site-to-site differences in Douglas-fir response to Sitka alder, the response of other conifer species, and the whole-rotation interactions of the species. Finally, on sites where nutrients in addition to N may be limiting, the nutritional interactions of the species must be elucidated.

SECTION V. INTERACTION OF SITE FERTILITY AND RED ALDER ON ECOSYSTEM PRODUCTION IN DOUGLAS-FIR PLANTATIONS

INTRODUCTION

Nitrogen-fixing red alder is a promising species for mixture with commercially valuable conifers on N-deficient sites (c.f., Tarrant and Trappe 1971, Atkinson et al. 1979). For example, inclusion of red alder in a Douglas-fir plantation at Wind River, Washington doubled total wood volume production and increased bole volume of average-size Douglas-fir by 60% (Miller and Murray 1978). The contribution of red alder to conifer ecosystem production involves both the biomass production of the alder itself and any stimulatory effect of increased N availability on conifer growth. Therefore, the greatest benefits from alder may be exhibited on the most N-deficient sites. In the present study, I hypothesized that red alder would greatly increase ecosystem production and biomass accumulation in a 23-year-old Douglas-fir plantation of poor site quality, but would have little effect in a stand of the same age on a fertile site. Nitrogen accretion and availability were assessed to help explain observed patterns of response to alder.

SITE DESCRIPTION

The fertile site is near the Skykomish River in northwestern Washington (47° 50' N Latitude, 121° 50' W Longitude) on private land. Stand composition was reported by Miller and Murray (1978). At an elevation of 35 m, the climate at the Skykomish site is mild. Average January and July temperatures are 3° and 18°C. Precipitation averages

120 cm yr^{-1}, with 35 cm falling between April and September. The soil is a Kitsap series silty clay loam (Dystric Xerochrept, U.S. Department of Agriculture 1975) derived from deep, fine-textured sediments of former glacial lakes. The site is classified as a _Tsuga heterophylla/Polystichum munitum_ habitat type of the _Tsuga heterophylla_ Vegetation Zone (Franklin and Dyrness 1973). Two-year-old Douglas-fir seedlings were machine planted in a pasture in 1958. Naturally established red alder seedlings were hand-cleared from half the plantation between 1962 and 1964 (R. Miller, personal communication 1981). The Douglas-fir seedlings presumably had a 2 yr advantage in age-from-seed over the red alder. Site index (expected height at 50 yr) is 45 m for Douglas-fir. At age 23, the average height of co-dominant Douglas-fir and red alder was 21 to 22 m.

The infertile site study area is at 510 m elevation on Mt. Benson near Nanaimo, British Columbia (50° 8' N Latitude, 124° 2' W Longitude) in MacMillan Bloedel Limited Tree Farm 19. Nitrogen fixation rates for the red alder are reported in Section III, and the effects of Sitka alder in this plantation are reported in Section IV. The climate on Mt. Benson is slightly cooler than Skykomish; average temperatures for January and July are 1° and 17°C. Precipitation averages about 200 cm yr^{-1} with 40 cm falling from April through September. The soil is unclassified as to series, and is a gravelly clay loam Typic Haplorthod developed on a 50 cm blanket of uncompacted till overlying compacted basal till. Soil physical properties are uniform between the red alder and no alder units of the plantation. The site is in a mid-slope position with a westerly aspect and a slope of 5° to 15°. The site falls into the _Tsuga heterophylla/Gaultheria_ *shallon*-*Berberis nervosa* habitat type (Franklin and Dyrness 1973). Logging and slash-burning occurred between 1952 and 1956; Douglas-fir seedlings were planted in 1958. Red alder seedlings were naturally established in one portion of the plantation. Aerial photographs from 1958 show a probable seed source which may account for the limited distribution of the alder in the plantation. Breast-height ages of Douglas-fir and alder were similar, but exact ages-from-seed are unknown. Site index on Mt. Benson is 24 m at 50 yr for Douglas-fir, and the site is near the upper-elevation limit of the range of red alder (Lloyd 1965). At age 23, the average height of the co-dominant and dominant Douglas-fir was 11 m, and co-dominant red alder was 9 to 11 m. Without alder, the Douglas-fir was approaching closed-canopy conditions, with live crowns extending to the ground. In the red alder unit, Douglas-fir canopies were restricted to the upper 8 m of the stems.

METHODS

Skykomish

The Skykomish plantation was small; each of the no alder and red alder units occupied about 1,000 m^2. Within each of the two units, 5 random machine-planted rows (each row occupied about 40 m^2) were measured for Douglas-fir diameters and 5 yr increments. Seven rectangular 40 m^2 plots were established randomly for measuring alder diameters and increments. Calculations of biomass were made by applying regression equations to plot measurements. Stem production was based on regression-estimated biomass calculated on stem diameter

5 yr previously. Douglas-fir foliage production was assumed to equal 20% of the total foliage biomass (Cole et al. 1967). Alder production was calculated as for Douglas-fir, but with all leaf biomass counted as annual production. Regression equations for Douglas-fir were obtained from Gholz et al. (1979). Red alder biomass calculations used the equations developed on Mt. Benson.

Five soil pits were dug randomly in each unit and sampled at depths of 0-10, 10-20, 20-35 and 35-50 cm. Five additional samples of 0-10 cm depth also were taken. Coarse-fragment-free bulk density (kg of the < 2 mm fraction per l of soil volume) was measured for 10 soil cores (5 cm diameter x 15 cm depth) per unit. Forest floor biomass was sampled with a 25 x 25 cm frame at 10 points in each unit. Soils were air-dried and analyzed by standard methods for total nitrogen by Autoanalyzer techniques (Allen et al. 1974), available N index (ammonium-N following 7 day anaerobic incubation at 40°C, after Waring and Bremner 1964), total organic carbon by the Walkley-Black method (Allen et al. 1974), pH in a water paste, and extractable cations by atomic absorption on 1 N NaCl extracts (Lavkulich 1977). Three composite samples of forest floor per unit were analyzed for total N and P (Allen et al. 1974).

Ten foliage samples of Douglas-fir and 10 of alder were obtained from mid-crown positions with a shotgun in late September 1981. Samples of all-ages of needles were analyzed (as above) for total N and P. Values for N concentrations of stems and branches were taken from the Mt. Benson analyses.

Mt. Benson

Measurement plot dimensions on Mt. Benson were 15 x 40 m with a 10 m buffer between plots. A total of 12 plots were established in two units as part of a long-term study. The red alder/Douglas-fir unit accommodated 4 plots, and the no alder/Douglas-fir unit was large enough for 8 plots. Tree measurements were the same as at Skykomish. Douglas-fir stem biomass was calculated using an equation from Gholz et al. (1979). Because of the difference in canopy morphology between units, foliage biomass calculations were based on sampling from 5 random, average-size ($\pm$ 1 cm diameter from mean) trees in each unit (Ovington et al. 1967). This foliage sampling involved tallying the number of branches in 2 m stem sections, and harvesting one representative branch per section for laboratory determination of foliage weight. The ratio of foliage biomass to basal area [50 g cm^{-2} (standard error = 5) for the red alder unit, and 96 g cm^{-2} (s.e. = 7) for the no alder unit] was then multiplied by the plot basal areas. Use of the standard Douglas-fir foliage biomass equation from Gholz et al. (1979) (not shown) would have yielded values close to those reported here for the red alder unit, but would have underestimated the open-grown Douglas-fir canopies in the no alder unit by 60 to 70%. Branch biomass was calculated as 140% of leaf biomass, based on branch to leaf allometry from Gholz et al. (1979).

The red alder biomass equations followed the model (Chapman 1976):

$$\text{Log}_e \text{ Biomass} = \text{Intercept} + \text{Coefficient } (\text{Log}_e \text{ Diameter}).$$

Twelve trees were sampled; stem diameters were measured every 2 m, the number of branches per section tallied and one branch per section sampled for branch and leaf weights. Stem volume calculations were converted to biomass based on density of oven-dried subsamples. These equations are listed in Table 20.

Soil samples were collected from 10 pits per unit, as described for Skykomish. Ten coarse fragment-free bulk density samples were taken using a sand displacement method. Forest floor samples were collected from 30 locations in each unit. Chemical analyses were the same as described above.

Douglas-fir foliage was collected in early August 1979 from the central rachis of a fifth-whorl branch from 50 trees per unit. Five samples went into each of 10 composites for nutrient analysis. All foliage came from fully illuminated branches. Red alder leaves were sampled from upper-crown positions of 10 trees. Three composite samples of stem and branch tissues were analyzed as mentioned for N concentrations.

RESULTS

Soil Properties

Red alder appeared to have had no effect on the top 10 cm of soil at the fertile Skykomish site (Table 21), but at deeper levels significant accretions of nitrogen and carbon occurred. Alder did not greatly affect the anaerobic available N index. In general, the Skykomish no alder unit soils had less extractable calcium and magnesium.

TABLE 20. RED ALDER BIOMASS REGRESSION EQUATIONS, N = 12, BIOMASS OVEN-DRY IN G, BREAST HEIGHT DIAMETER IN CM, RANGE 6 TO 20 CM.

Component	Equation	r^2	s.e.[a]
Leaves	$\log_e$ Biomass = 3.20 + 1.89 ($\log_e$ Diameter)	0.85	0.331
Branches	$\log_e$ Biomass = 2.20 + 2.70 ($\log_e$ Diameter)	0.91	0.344
Stems	$\log_e$ Biomass = 3.97 + 2.56 ($\log_e$ Diameter)	0.98	0.113

[a] Standard error of the estimate.

TABLE 21. SOIL PROPERTIES.

		Sites			
		Infetile Mt. Benson		Fertile Skykomish	
Property	Depth (cm)	No alder	Red alder	No alder	Red alder
Coarse fragment-free bulk density (kg l^{-1})	0-15	0.48	0.49 n.s.[e]	0.57	0.55 n.s.
Acidity, pH[a]	0-10	4.5	4.4 n.s.	4.2	4.1 n.s.
	10-20	4.8	4.9 n.s.	4.7	4.6 n.s.
	20-35	4.9	5.0 n.s.	4.9	4.5*
	35-50	4.9	5.1 n.s.	4.6	4.6 n.s.
Nitrogen %	0-10	0.09	0.19****	0.31	0.29 n.s.
	10-20	0.07	0.11****	0.21	0.25***
	20-35	0.06	0.08*	0.13	0.16*
	35-50	0.05	0.08**	0.09	0.14*
Available[b] nitrogen index, μg g^{-1}	0-10	23	77****	82	61*
	10-20	15	52****	29	29 n.s.
	20-35	39	48*	9	8 n.s.
	35-50	35	56***	4	5 n.s.
Carbon %	0-10	2.05	3.92****	4.98	4.72 n.s.
	10-20	1.61	2.13*	3.74	5.03****
	20-35	1.15	1.52*	2.11	2.85 n.s.
	35-50	1.09	1.44 n.s.	1.26	2.33**
Extractable[d] calcium, meq kg^{-1}	0-10	19.9	38.9**	12.50	5.25***
	10-20	7.2	21.0*	3.41	6.35**
	20-35	7.2	16.5**	1.74	1.44 n.s.
	35-50	6.6	16.8**	2.00	1.29**
Extractable[d] magnesium, meq kg^{-1}	0-10	4.4	6.8 n.s.	2.10	1.03**
	10-20	1.8	3.9**	0.98	0.99 n.s.
	20-35	1.5	3.0*	0.78	0.20***
	35-50	1.6	3.9**	1.10	0.43****
Extractable[d] potassium, meq kg^{-1}	0-10	2.4	3.7 n.s.	1.32	1.21 n.s.
	10-20	2.2	2.5 n.s.	0.86	1.46*
	20-35	0.9	1.4 n.s.	0.85	0.92 n.s.
	35-50	1.0	0.9 n.s.	0.83	0.77 n.s.

[a] In a water paste.

[b] As ammonium-N following 7 day anaerobic incubation at 40°C.

[c] As net production of mineral-N following 30 day aerobic incubation at 20°C at field capacity.

[d] 1 N NaCl extractable; multiplication by 2.08 yields meq kg^{-1} units for Mt. Benson, and multiplication by 1.79 yields meq kg^{-1} for Skykomish.

[e] n.s. = not significant at $p < 0.10$, * = significant at $p < 0.10$, ** at $p < 0.05$, *** at $p < 0.01$, **** at $p < 0.001$ based on 2-tailed T-tests.

The infertile Mt. Benson site showed large increases in total and available-N index, total C, and extractable Ca and Mg.

Foliar Nutrient Concentrations

Red alder had little effect on Douglas-fir foliage concentrations of N and P at Skykomish (Table 22); N concentrations were adequate and P concentrations were low in both stands (van den Driessche 1979). On Mt. Benson, Douglas-fir foliage N concentrations were very low without alder, but approached adequate levels with alder (van den Driessche 1979). Conversely, P concentrations were adequate without alder, but extremely low with alder. Foliar N and P concentrations in red alder were higher on Mt. Benson than at Skykomish.

Biomass and Production

The dominant pattern of the effect of red alder on the infertile Mt. Benson site was one of marginal impact on Douglas-fir and large increases in total stand stocking, basal area and growth (Table 23). Similarly, the two- to three-fold increases in ecosystem biomass and net primary production in the red alder unit were due to the added complement of the alder itself, with little difference between units in the Douglas-fir components (Tables 24 and 25). An opposite pattern emerged from the fertile Skykomish sites where Douglas-fir stocking, size and growth were decreased by alder, but ecosystem totals were only marginally affected.

One of the largest effects of red alder on Douglas-fir on the infertile site was in the production of stemwood per unit leaf biomass. Douglas-fir from the red-alder unit produced 25% greater

TABLE 22. FOLIAR NUTRIENT CONCENTRATIONS, AVERAGES OF 10 SAMPLES.

		Site			
		Infertile Mt. Benson		Fertile Skykomish	
Nutrient	Species	No alder	Red alder	No alder	Red alder
Nitrogen, %	Douglas-fir	0.93	1.41****[a]	1.54	1.55 n.s.
	Red alder		3.05		2.35
Phosphorus, %	Douglas-fir	0.22	0.09****	0.14	0.16*
	Red alder		0.23		0.14

[a] Significance levels as in Table 21.

TABLE 23. STAND DESCRIPTIONS.

Component	Sites Infertile Mt. Benson No alder	 Red alder	 Fertile Skykomish No alder	 Red alder
Stocking, trees ha^{-1}				
Douglas-fir	650	540**[a]	1860	1600 n.s.
Red alder		2200		290
Diameter, cm breast height				
Douglas-fir	13.8	15.3*	19.3	16.7**
Red alder		9.8		21.1
Basal area, m^2 ha^{-1}				
Douglas-fir	10.5	10.0 n.s.	54.1	34.9****
Red alder		16.5		9.9
Basal increment, m^2 ha^{-1} yr^{-1}				
Douglas-fir	0.89	0.92 n.s.	3.73	2.59****
Red alder		1.52		1.07

[a] Significance levels as in Table 21.

TABLE 24. ABOVEGROUND ECOSYSTEM BIOMASS (KG HA^{-1}) [MEAN (STANDARD DEVIATION)].

	Site			
	Infertile Mt. Benson		Fertile Skykomish	
Component	No alder	Red alder	No alder	Red alder
Douglas-fir				
Foliage	9,600 (1,900)	3,390 (810)****[a]	15,480 (2,960)	11,000 (1,400)**
Branches	13,300 (6,100)	5,500 (3,180)***	24,600 (3,690)	16,540 (2,840)**
Stems	35,000 (12,800)	41,240 (11,840) n.s.	218,200 (26,300)	140,890 (30,870)***
Subtotal	57,900 (20,300)	50,130 (15,850) n.s.	258,280 (32,340)	168,430 (35,100)***
Alder				
Foliage		2,900 (1,850)		2,300 (2,180)
Branches		7,490 (3,130)		10,090 (9,290)
Stems		53,520 (15,220)		38,300 (35,190)
Subtotal		63,910 (17,430)		50,690 (46,620)
Plant subtotal	57,900 (16,800)	114,040 (23,560)****	258,280 (32,340)	219,120 (58,360) n.s.
Forest floor	6,970 (5,260)	33,600 (17,690)****	21,150 (14,460)	23,040 (26,100) n.s.
Grand total	64,870 (17,600)	147,640 (29,460)****	279,430 (35,430)	242,160 (63,930) n.s.

[a] Significance levels as in Table 21.

TABLE 25. ABOVEGROUND NET PRIMARY PRODUCTION[a] (KG HA^{-1} YR^{-1}).

	Site			
	Infertile Mt. Benson		Fertile Skykomish	
	No alder	Red alder	No alder	Red alder
Douglas-fir				
Foliage	1,920	790****[b]	3,100	2,200**
Branches	900	450****	1,840	1,240**
Stems	4,110	5,180*	18,320	12,130***
Subtotal	6,930	6,420 n.s.	23,260	15,570***
Red alder				
Foliage		2,900		2,300
Branches		1,250		1,050
Stems		5,140		3,620
Subtotal		9,290		6,970
Grand total	6,930	15,710****	23,260	22,540 n.s.

[a] Mortality not included.

[b] Significance levels as in Table 21.

stem growth with 65% less leaf biomass than on the no alder unit. Stem-growth-to-leaf-biomass ratios were 1.53 for Douglas-fir in the red alder unit, and 0.43 in the no alder unit. In contrast, this production efficiency ratio was little affected by alder at Skykomish, with a stem-production-to-leaf-biomass ratio of 1.18 without alder and 1.10 with red alder.

Ecosystem Nitrogen Content

Summing the nitrogen content of the major ecosystem pools (Table 26) revealed an accretion of 1,493 kg ha^{-1} for Mt. Benson and 972 kg ha^{-1} at Skykomish. The Skykomish value is a minimum estimate, as changes in soil N below 50 cm were not examined. Average nitrogen accretion rates for 23 yr were 65 kg ha^{-1} yr^{-1} at Mt. Benson and 42 kg ha^{-1} yr^{-1} at at Skykomish.

DISCUSSION

Soil Properties

Increased soil total nitrogen and decreased extractable Ca and Mg as a result of alder on the fertile Skykomish soil followed the pattern reported by Franklin et al. (1968) for a fertile red alder/Douglas-fir ecosystem in coastal Oregon. These authors also found a decrease in soil pH associated with the red alder, but the soils from both Skykomish units were marginally more acidic than the 4.6 to 5.0 pH of the Oregon sites. Franklin et al. (1968) suggested that leaching losses of cations from more acidic, nitrate-rich alder stands could be substantial. However, Cole et al. (1978) found only

TABLE 26. ECOSYSTEM NITROGEN CONTENT (KG HA^{-1}).

	Site			
	Infertile Mt. Benson		Fertile Skykomish	
	No alder	Red alder	No alder	Red alder
Douglas-fir				
Foliage	90	55	240	171
Branches	13	7	31	20
Stems	27	32	170	109
Subtotal	130	94	441	300
Red alder				
Foliage		89		54
Branches		48		65
Stems		110		79
Subtotal		247		198
Plant subtotal	130	341	441	498
Soil				
Forest floor	36	502	280	280
0-10 cm	432	912	1,680	1,680
10-20 cm	336	528	1,160	1,410
20-35 cm	432	504	1,100	1,335
35-50 cm	360	432	710	1,140
Subtotal	1,596	2,878	4,930	5,845
Grand total	1,726	3,219	5,371	6,343

slightly greater leaching losses of cations from a red alder stand in comparison with an adjacent Douglas-fir stand in Washington. For the Washington sites, the increased cation content of the vegetation exceeded the decrease in the soil, resulting in a net increase of Ca and K in the alder system. In contrast to Skykomish and the studies cited, red alder increased the level of soil extractable Ca and Mg at Mt. Benson. The effect of alder on soil cation levels is probably the result of interacting effects on cation accumulation in vegetation, changes in cation exchange capacity and soil pH, the production of hydrogen ions and nitrate (Johnson and Cole 1980) and any change in soil weathering rate (Binkley et al. 1982a). These factors vary with soil fertility and parent material, and generalization of the effects of alder on soil cations appears tenuous at present.

The increase in anaerobic available N index in the red alder unit at Mt. Benson was greater than the proportional increase in soil total N, indicating a greater availability of the recently-fixed N or an increase in the availability of "older" soil N. This apparent difference in availability of alder-fixed N may be a major component of long-term responses of Douglas-fir to N fixation early in a rotation, and merits further investigation.

Soil carbon was increased 50% under red alder on Mt. Benson, representing an increase of 16.8 tons ha^{-1}. Increases in soil organic matter should increase soil water holding capacity, cation exchange and nutrient retention capacities, and should improve soil structure (c.f., Black 1978, Russell 1973). These properties were not examined directly in the present study, but may constitute a significant portion of the enhancement of site fertility by red alder.

Growth Interactions of Douglas-fir and Red Alder

The dominant pattern emerging from the Mt. Benson data was one of red alder marginally affecting Douglas-fir growth, while tripling aboveground ecosystem production. As the red alder component of the ecosystem decreases in the future, the Douglas-fir biomass at harvest age will probably be greater (and distributed on larger stems) from the red alder unit than the no alder unit. An opposite pattern was apparent for the N-rich Skykomish site. The addition of the alder component to the fertile-site Douglas-fir plantation proportionately reduced the growth of Douglas-fir. Even with the removal of alder (either naturally or by stand treatment), it is doubtful that the Douglas-fir biomass of the red alder unit could catch-up with that of the no alder unit.

The greater stem-growth-to-leaf biomass of the Douglas-fir in the red-alder unit on Mt. Benson indicated a greater rate of net photosynthesis per unit leaf area or a change in biomass allocation within the trees. Fertilization studies with Douglas-fir have shown 10 to 30% increases in net photosynthetic rates with improved nutrition (Brix and Ebell 1969, Brix 1981), and ecosystem analysis studies have shown large decreases in belowground (particularly fine root) biomass allocation with improved soil conditions (e.g., Santantonio 1979, Keyes and Grier 1981). These processes probably accounted for the observed increase in Douglas-fir stem growth per unit leaf area and deserve direct assessment as an avenue of interaction between conifers and N-fixing alder.

Douglas-fir Nutrition

Red alder had little effect on Douglas-fir foliage N and P concentrations at Skykomish; on Mt. Benson, red alder appeared to enhance N nutrition of Douglas-fir but impair P nutrition. Bioassays with Douglas-fir and red alder seedlings verified P limitations in the red alder unit soils (Binkley et al. 1982b). Phosphorus fertilization on Mt. Benson might increase Douglas-fir growth, as well as growth and N fixation of red alder.

Nitrogen Fixation

Red alder fixed substantial quantities of N at both sites, despite large differences in soil total N contents and N availability index levels. The N accretion values are within reported ranges for mixed red alder/Douglas-fir ecosystems, but the accretion-based estimate of N fixation on Mt. Benson is half the estimate based on acetylene reduction assays in the same ecosystem (Section III). In addition to the variability inherent in both methods, potential explanations for the difference include: (1) the current N fixation rate (measured by acetylene reduction assays) may exceed the 23 yr average, (2) unexamined diurnal variation in acetylene reduction rates could have resulted in an over-estimate of daily averages, or (3) N losses from the system could have resulted in an N accretion rate substantially below the N fixation rate. The first explanation cannot be examined at present; no study has quantified rates of N fixation for varying ages of red alder in conifer plantations. Diurnal variations in nodule activity may have resulted in a 30 to 40% overestimate of N fixation (Johnsrud 1978, Tripp et al. 1979). Few estimates of N losses from alder ecosystems are available, but a range of 6 to more than 40 kg ha^{-1} yr^{-1} has been reported (Cole et al. 1978, Miller and Newton 1982). Precise estimates of N dynamics in alder ecosystems will require further investigation of these potential sources of difference between acetylene-reduction and N-accretion estimates of N fixation rates.

CONCLUSIONS

The inclusion of red alder in a poor-site quality Douglas-fir plantation greatly increased ecosystem production, as well as Douglas-fir stem growth per unit leaf biomass. On a fertile site, the red alder did not increase ecosystem production, and substantially decreased Douglas-fir growth. Mixtures of Douglas-fir and red alder may be an attractive forest management strategy on N deficient sites, but would be of limited value on highly fertile sites. As forest production on infertile sites may be constrained by other nutrients, consideration should be made of non-nitrogen nutrient interactions between the species.

SECTION VI. DEVELOPMENT OF DOUGLAS-FIR AND ALDER MIXTURES THROUGH TIME

INTRODUCTION

Mixtures of red alder and Douglas-fir were established in two U.S. Forest Service experimental forests in the 1920's. At Cascade Head, Oregon, naturally established alder/conifer stands were thinned from 1935-1937 (at age 8-10) to produce fifth-hectare stands of pure alder, mixed alder/conifer, and pure conifer. A 20-m wide red alder firebreak was interplanted in a Douglas-fir plantation at Wind River, Washington in 1928. Data collected from these stands by USFS personnel over the past 50 yr provided an opportunity to examine some of the conclusions reached from the Mt. Benson and Skykomish studies (Section V) for broader applicability to red alder/Douglas-fir mixtures in general. Specifically, I hypothesized that a mixture of red alder and Douglas-fir would greatly increase ecosystem production (in relation to a pure Douglas-fir stand) at infertile Wind River, but have little effect at the more fertile site at Cascade Head. Further, the increased production with red alder at Wind River should have persisted as the stands matured beyond the age of the younger Mt. Benson stands. These comparisons will be presented in more detail elsewhere.

SITE DESCRIPTION

The Cascade Head stands are described by Berntsen (1961), Franklin et al. (1968), Tarrant et al. (1969), and Miller and Murray (1978), and the Wind River sites are described by Tarrant (1961), Miller and Tarrant (1963) and Miller and Murray (1978). Table 27

TABLE 27. SITE AND STAND CHARACTERISTICS FOR CASCADE HEAD AND WIND RIVER, FROM SOURCES CITED IN TEXT.

Property	Cascade Head	Wind River
Elevation, m	200	600
Precipitation, cm yr^{-1}	250	230
Site index, m at 50 yr	40	25
Total soil N, kg ha^{-1} to 80 cm		
Without alder	13,000 (in 1966)	3,200 (in 1959)
With alder	14,200 (in 1966)	4,200 (in 1959)
Anaerobic available N index[a], μg g^{-1}		
Without alder	115 (in 1981)	25 (in 1981)
With alder	120 (in 1981)	100 (in 1981)

[a] Binkley, unpublished data.

summarizes some site characteristics; Wind River resembles the site at Mt. Benson, and Cascade Head is more similar to the Skykomish site.

METHODS

Stand measurements were taken at 7 times during the development of the Cascade Head stands (data made available by J. Franklin and S. Greene). For the Wind River sites, data published by Tarrant (1961) and Miller and Murray (1978) were used to represent stand development at 2 points in time. Regression equations from Gholz et al. (1979) were used to estimate biomasses of Douglas-fir and western hemlock. No equations were available for Sitka spruce, so the equation for Douglas-fir was used, with wood biomass reduced by 35% to account for the lower density of spruce. The red alder equations developed for Mt. Benson appeared to overestimate leaf biomass for larger trees; therefore, leaf estimates for trees greater than 25 cm diameter were reduced by 20%.

Stand averages for Cascade Head were calculated based on the number of stems in 2.5 cm diameter classes at the 7 ages, with production calculated as the average stem+branch increment plus 20% of Douglas-fir and spruce leaf biomass, 28% of hemlock leaf biomass, and 100% of alder leaf biomass. Similar calculations on dead trees yielded the mortality component of the net primary production estimate. The 1974 biomass estimate for Wind River was calculated as described for Cascade Head, except the trees were tallied by 7.5 cm diameter classes. Douglas-fir production for Wind River in 1974 was based on the average diameter increment of dominant Douglas-fir over the previous 5 yr and the number of stems ha^{-1} in 1974. Alder production was assumed to equal 10% of the stem+branch biomass (from the relationship at Mt. Benson and Skykomish) plus all leaf biomass. The 1958 Wind River estimates are based on the size and increment of the average-basal-area tree and the number of trees per hectare given by Tarrant (1961). No estimate of mortality was included in the Wind River calculations, and the understory contributions to aboveground biomass and production were not considered for either site.

RESULTS

Cascade Head

At age 23 in 1951, all three plots carried similar aboveground tree biomasses (Figure 1), but at age 52 (1980) the biomass of the pure conifer stand exceeded that of the mixed stand which in turn was greater than that of the pure alder stand. Net primary production (Figure 2) peaked in the pure alder stand in 1946 at age 15-20 yr, which coincided with the peak production age reported by Zavitkovski and Stevens (1972). The maximum production in the mixed stand occurred in 1951 (age about 25 yr), while the peak production for the pure conifer stand was attained in 1956 (age about 30 yr). The greater tree biomass in 1980 in the pure conifer plot was a result of both greater net primary production and lower mortality (data not shown).

Wind River

Douglas-fir production at Wind River was not altered by red alder in 1956 (age about 28), but the addition of the alder component increased ecosystem production by 2.5 fold (Table 28). Eighteen years

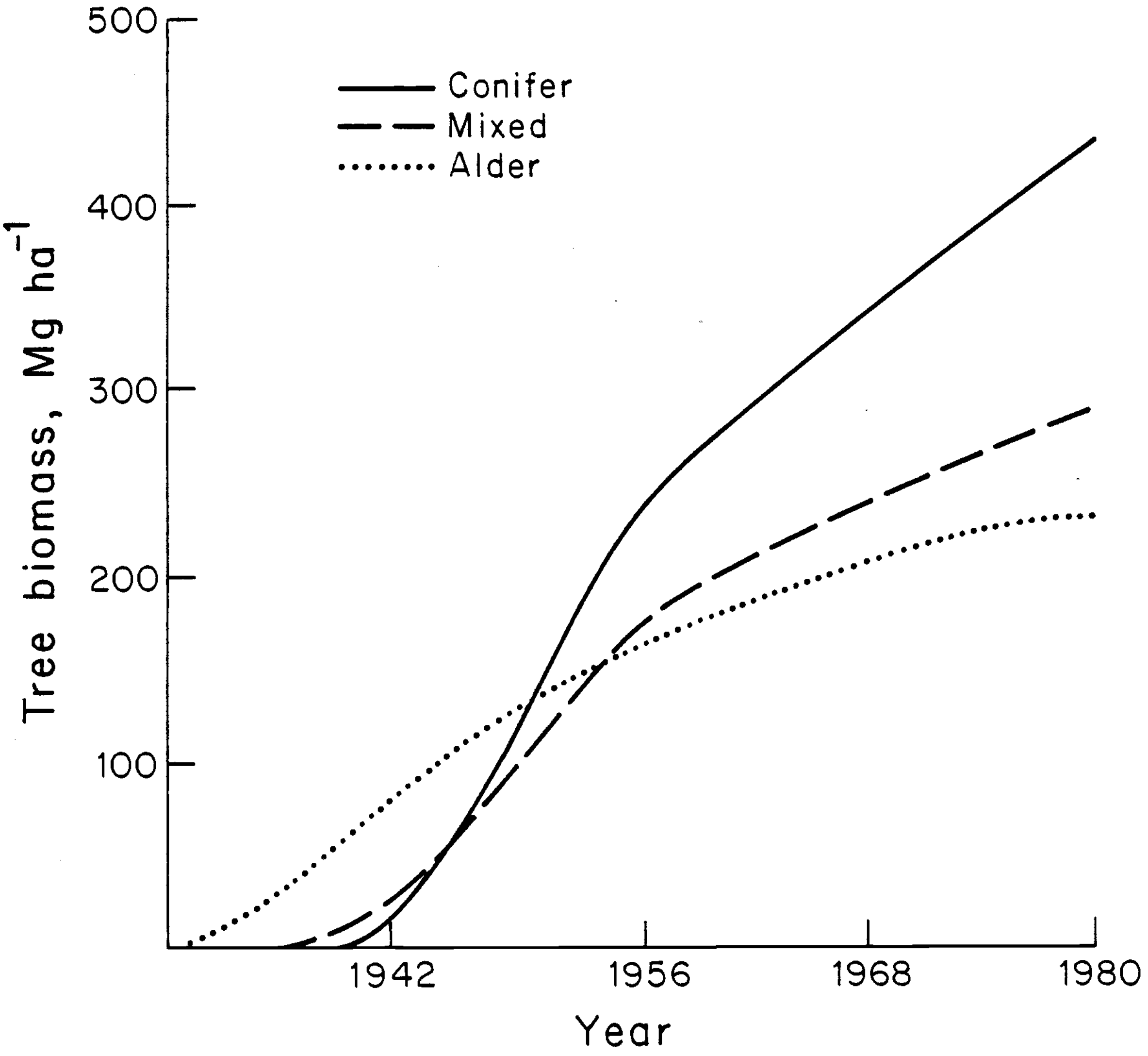

Figure 1. Aboveground ecosystem biomass at Cascade Head.

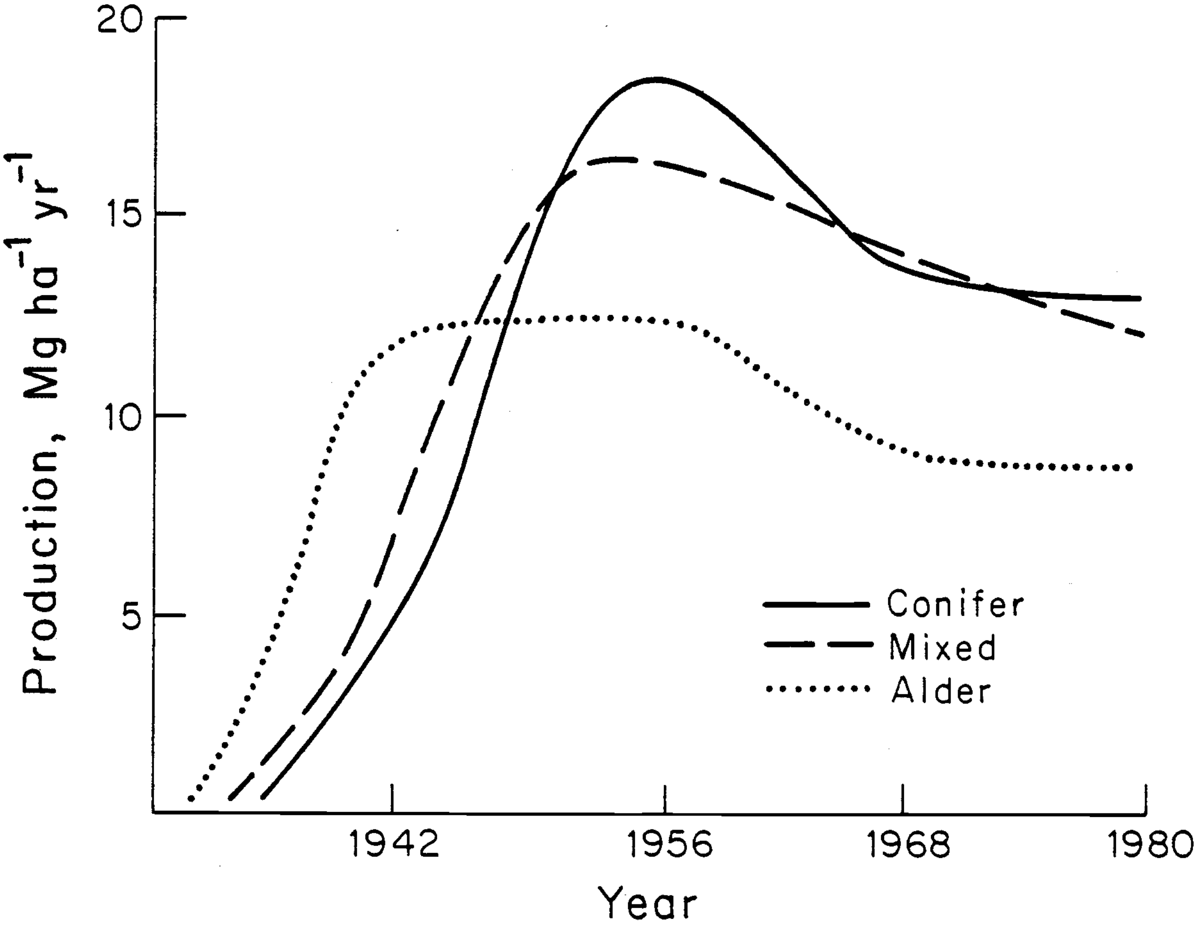

Figure 2. Aboveground net primary production at Cascade Head.

TABLE 28. WIND RIVER TREE BIOMASS AND PRODUCTION.

Component	Stand type and year			
	1956		1974	
	No alder	Red alder	No alder	Red alder
Production, kg ha^{-1} yr^{-1}				
Douglas-fir				
Foliage	1,020	860	1,640	1,440
Branches	590	480	540	765
Stems	4,790	4,010	5,790	9,870
Subtotal	6,400	5,350	7,970	12,075
Red alder				
Foliage		4,400		4,000
Branches		1,040		1,280
Stems		5,070		7,700
Subtotal		10,510		12,980
Grand total	6,400	15,860	7,970	25,055
Biomass, kg ha^{-1}				
Douglas-fir				
Foliage	5,100	4,280	8,175	7,180
Branches	6,370	5,440	13,220	12,820
Stem	44,370	38,610	120,810	130,670
Subtotal	55,840	48,330	142,210	150,670
Red alder				
Foliage		4,400		4,000
Branches		10,400		12,760
Stem		50,690		76,960
Subtotal		65,490		93,720
Grand total	55,840	113,820	142,210	244,390

later, Douglas-fir stem growth in the mixed stand was 70% greater than in the pure Douglas-fir stand. Net primary production in 1974 in the mixed stand was 3 times greater than in the pure Douglas-fir stand. Interestingly, at age 46 the mixed stand appeared to have achieved the productivity of the 23 yr old stands at the Site Class I Skykomish site (Section V).

DISCUSSION

Despite differences in sites, treatments and biases in estimation, the Cascade Head and Wind River comparisons were remarkably similar to Skykomish and Mt. Benson. Both of the fertile sites (Cascade Head and Skykomish) showed no difference in ecosystem biomass or production between alder/conifer and pure conifer stands at age 23. The infertile sites (Wind River and Mt. Benson) demonstrated little effect of the alder on conifer growth at age 27 and 23, but aboveground net primary production was increased from 2.5 to 3.0 fold by the alder.

It appears that red alder in general can substantially increase ecosystem production in Douglas-fir plantations on N-deficient sites. However, where red alder stocking is high, any increased conifer production will not be realized until the conifers achieve: (1) a dominant status, and (2) an expanded canopy above the alder. Lower stocking of alder may accelerate the time of Douglas-fir dominance, as might a delay in alder establishment. On fertile, N-rich sites, the competitive interactions of alder and conifers will probably negate any beneficial effects of N-fixation on conifer growth. However, the current fertility of high site soils may be the result of repeated successional cycles of red alder, and long-term maintenance of site fertility may require attention to the long-term implications of mixed alder/conifer plantations. Finally, designed experiments are needed to assess the interactions of alder and a variety of conifer species across a range of spacings and site fertility levels.

SECTION VII. CONCLUSIONS

1. Nitrogen fixation rates by Sitka alder ranged from 20-35 kg ha^{-1} yr^{-1} in the ecosystems studied. As a first approximation, rates should be expected to be proportional to Sitka alder leaf area.
2. Douglas-fir experiences less competition with interplanted Sitka alder than with red alder. At age 23 on Mt. Benson, Douglas-fir stem growth was 40% and 25% greater with Sitka alder and red alder than without alder. The benefits of each species must be considered over an entire rotation, which may alter the relative usefulness of the two species.
3. Consistent with previous studies, I found red alder N fixation rates of 40-65 kg ha^{-1} yr^{-1} in Douglas-fir plantations.
4. The benefits of alder-fixed N should be expected to decrease with increasing site fertility. I found aboveground net primary production of two Douglas-fir plantations was tripled by red alder on Site Class IV, but was unaffected on two Site Class I.
5. Alder species commonly increase ecosystem N capital by 30-80 percent, but the N content of litterfall is increased by 5-8 fold. The benefits of alder-fixed N seem to be more than proportional to the increase in site N capital, suggesting alder-fixed N may remain more active than "native" N.

6. Boosting ecosystem production through N fixation on N deficient sites may result in the ecosystem encountering a new production limit regulated by the availability of other nutrients. Phosphorus and sulfur appear to merit further attention.
7. Increased Douglas-fir stem growth in association with alder may be due in part to altered within-tree carbohydrate allocation patterns. Enriched soil conditions may reduce the requirement for fine root production, resulting in a greater allocation of carbohydrates to stemwood growth.
8. Major topics meriting research include:

   --Optimal stocking densities of N-fixers and crop trees;

   --Interactions of alder and conifer species other than Douglas-fir;

   --Whole rotation interactions of mixed plantations;

   --Non-nitrogen nutrient interactions of alders and conifers, including nutrient demands and competition;

   --Carbohydrate allocation patterns, especially the fine root production of conifers in association with alder; and

   --The activity of alder-fixed N within ecosystems.

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APPENDICES

APPENDIX 1. ASSESSING FOREST NUTRIENT AVAILABILITY BY AN ION EXCHANGE RESIN BAG TECHNIQUE

A variety of techniques has been used to estimate the availability of nitrogen in forest soils, but none is widely accepted (Keeney 1980). An ideal method would be capable of integrating temporal variability due to fluctuations in soil moisture, temperature and seasonal inputs of fresh detritus, and should also deal effectively with the high spatial variability common in forest soils. Finally, the method should be relatively simple and inexpensive. In this study, an *in situ* ion exchange resin bag method was evaluated under greenhouse and field conditions. I hypothesized the ion exchange resin (IER) method would correlate well with traditional laboratory techniques for sieved, well-mixed soils under controlled conditions, but that the IER method would provide more realistic evaluations of nitrogen availability under field conditions.

PROCEDURES

The study sites were those described in the thesis body on Mt. Benson, British Columbia. Soil samples for the greenhouse and laboratory work were collected at 9 random sites within each of the no alder, Sitka alder and red alder units. Forest floor material plus 0-5 cm depth mineral soil were passed through a 2 mm sieve in the field and the fine fraction was returned to the laboratory and air-dried. The soil was then mixed 1:1 by volume with perlite. Soil analysis methods included a variety of N availability indexes, and are described in Binkley et al. (1982b); soil sample chemical descriptions are listed in Table 29.

The ion exchange resin bags were prepared by placing approximately 17 g (oven-dry weight, or 35 g moist weight) of a mixed bed (cation + anion) resin (J. T. Baker #M-614) in knee-high nylon stockings. Anion exchange capacity was furnished by an amide group, and cation exchange by a sulfonic group. Approximately 5% of the cation exchange capacity was loaded with mercury (as mercuric chloride) to prevent microbial removal of nutrients. Following the *in situ* period described below, the resin was air-dried and transferred to 125 ml polyethylene bottles and extracted with 100 ml of 1 *N* KCl. Ammonium and nitrate were determined by standard Autoanalyzer techniques on 1:20 diluted samples. Ammonium determinations using a selective ion electrode were not possible due to the apparent interference of amides leached from the resin.

The greenhouse evaluation of the IER method involved placing IER bags in soil-filled cups during the period of the Douglas-fir seedling bioassay (described in Binkley et al. 1982b). The field evaluation used 30 IER bags buried at the forest floor/mineral soil interface in each of the three study units on Mt. Benson. The *in situ* period lasted from June 30, 1980 through May 31, 1981.

RESULTS

Correlation coefficients between the IER method and the traditional methods were very good (Table 30), and no method gave a significantly better correlation with seedling available N (Table 31).

TABLE 29. SOIL CHEMICAL PROPERTY AVERAGES (STANDARD DEVIATIONS) BY UNIT TYPE (N = 9 PER TYPE).

Unit	pH[a]	Organic matter (%)[b]	Nitrogen (%)	Extractable (meq 100 g^{-1})[c] Ca	Extractable (meq 100 g^{-1})[c] Mg	Extractable (meq 100 g^{-1})[c] K
No alder	5.5 (0.3)	8.4 (1.5)	0.09 (0.02)	1.47 (0.81)	0.23 (0.11)	0.23 (0.08)
Sitka alder	5.3 (0.3)	10.5 (1.6)	0.24 (0.07)	4.30 (0.96)	0.86 (0.15)	0.32 (0.09)
Red alder	5.5 (0.3)	12.8 (2.2)	0.30 (0.07)	4.97 (1.59)	0.75 (0.23)	0.18 (0.03)

[a] In water paste.

[b] As loss-on-ignition at 475°C for 4 hours.

[c] Extracted with 1 N NaCl, determined by atomic absorption spectrophotometry.

TABLE 30. CORRELATION COEFFICIENTS (R) BETWEEN THE NITROGEN AVAILABILITY INDEX METHODS.

Methods	1.	2.	3.	4.	5.	6.
1. Total N	--					
2. Initial NH_4-N + NO_3-N	0.73	--				
3. Anaerobic[a] NH_4-N	0.93	0.76	--			
4. Aerobic NH_4-N + NO_3-N	0.85	0.92	0.91	--		
5. Boiling water[b] total N	0.87	0.84	0.91	0.91	--	
6. Autoclave[b] total N	0.86	0.84	0.89	0.84	0.92	--
7. IER NH_4-N + NO_3-N	0.79	0.71	0.87	0.78	0.77	0.79

[a] Values based on net production of mineral N (post incubation concentrations minus initial). Gross and net mineralization values were highly correlated (r = 0.99 for anaerobic, r = 0.97 for aerobic).

[b] Total nitrogen produced by the chemical treatment methods was highly correlated with ammonium production (r = 0.94 for boiling water, r = 0.96 for autoclave).

TABLE 31. RANKED CORRELATION COEFFICIENTS (R) OF NITROGEN AVAILABILITY INDEXES WITH DOUGLAS-FIR SEEDLING N UPTAKE.[a]

Method	Initial NH_4-N+NO_3-N	Total N	Aerobic NH_4-N+NO_3-N	Autoclave total N	Boiling water total N	Resin NH_4-N+NO_3-N	Anaerobic NH_4-N
Seedling N uptake	0.67	0.79	0.81	0.82	0.86	0.87	0.91

[a] Lines join coefficients which do not differ significantly ($p < 0.10$), after Sokal and Rohlf (1981, p. 583).

Further, the coefficient of variation was lower for the IER method than any other index (Table 32).

The IER estimates of nitrogen availability differed greatly between the greenhouse and field studies. The greater values obtained in the field (Table 33) reflected in part the longer in situ period (11 months field vs. 5 months greenhouse). However, the relative magnitudes among the three study units also differed. In the greenhouse, no differences were evident between the two alder-site soils; in the field, the red alder unit IER bags collected four times the nitrate and two times the total amount of inorganic N collected in the Sitka alder unit. Variability was also greater in the field, but 30 samples per unit generally provided standard errors of the means of about 15% of the means.

DISCUSSION

As no method provides an unequivocal index of nitrogen availability, it is difficult to evaluate precisely the usefulness of the IER method. The method correlated well with more traditional indexes under controlled greenhouse conditions with sieved, well-mixed soils, indicating the IER index predicted N availability on par with other indexes under similar conditions. Therefore, the divergence of the field IER values from the greenhouse values demonstrated the sensitivity of IER bags to field factors not evaluated by the traditional indexes. The field values were consistent with the forest floor development of the three study units, and probably reflected the importance of forest floor morphology and the fluctuations of moisture and temperature (through an annual cycle) in regulating N availability.

TABLE 32. AVERAGES AND COEFFICIENTS OF VARIATION ($S/\bar{X}$) FOR THE GREENHOUSE ION EXCHANGE RESIN BAGS AND VARIOUS ESTIMATES OF SOIL NITROGEN AVAILABILITY.

Study unit soil:	No alder	Sitka alder	Red alder
Method:			
Total N (%)	0.08 (13%)	0.24 (8%)	0.29 (7%)
Seedling uptake (mg plant^{-1})	1.62 (19%)	9.60 (25%)	7.13 (28%)
Aerobic NH_4 (μg g^{-1})	6.9 (72%)	33.8 (33%)	34.8 (26%)
Aerobic NO_3 (μg g^{-1})	0.0 (0%)	39.9 (117%)	32.2 (96%)
Anaerobic NH_4 (μg g^{-1})	7.4 (97%)	83.0 (31%)	80.3 (28%)
Resin NH_4 (μg g^{-1} resin)	382.0 (5%)	627.0 (5%)	614.0 (5%)
Resin NO_3 (μg g^{-1} resin)	0.0 (0%)	91.0 (35%)	62.0 (18%)

TABLE 33. ION EXCHANGE RESIN AVERAGES (STANDARD ERRORS) FOR GREENHOUSE AND FIELD EXPERIMENTS ($\mu g\ g^{-1}$ DRY RESIN).

	Study units		
Experiment	No alder	Sitka alder	Red alder
Field			
NH_4-N	505 (60)	4,200 (600)	5,700 (1,100)
NO_3-N	40 (20)	1,100 (400)	4,700 (800)
Sum	545 (75)	5,300 (600)	10,400 (1,800)
Greenhouse			
NH_4-N	382 (20)	630 (30)	610 (30)
NO_3-N	0	90 (30)	60 (10)
Sum	382 (20)	720 (50)	670 (30)

The results of the IER method evaluation reported here are encouraging and the method deserves further testing. Several areas require attention. Sources of methodological bias need to be examined, such as varying the types of resin or method of confinement in the soil, and the effects of repeated wetting and drying cycles on the resin exchange characteristics. The method should also be evaluated against *in situ* versions of aerobic or anaerobic incubations (c.f., Eno 1960, Ellenberg 1977, Powers 1980). Further refinement of this technique may provide a simple and inexpensive technique for evaluating the effects of forest management practices which alter the processes regulating nutrient availability. The ion exchange resin bag method may come closer to meeting the requirements of an ideal method for assessing forest soil nutrient availability than methods currently in use.

APPENDIX 2. CELLULOSE DECOMPOSITION AS AN INDEX OF NITROGEN AVAILABILITY

Decomposition rates are generally considered to be regulated by resource quality, microenvironmental conditions, and the availability of exogenous nutrients. Therefore, the use of a standard resource, such as cellulose, can allow relative comparisons of the effects of microenvironment and nutrient availability (Chapman et al. 1976). Two investigations with cellulose decomposition were used to assess the interactions of environment and nutrient availability in the Mt. Benson sites.

METHODS

Standard litterbags (7.5 x 7.5 cm, of 1 mm mesh nylon) were filled with approximately 1.2 g of cellulose (Whatman #1 filter paper). To assess decomposition under the combined influence of environment and nutrient availability, thirty bags were placed randomly in each of the three site types: no alder, Sitka alder and red alder. Bag placement was at the forest floor/mineral soil interface, or at 2 cm below the mineral soil surface where the forest floor was absent in the no alder site. The treatment period lasted from June 1, 1981 to August 1, 1982. To remove environmental differences, a 3 month decomposition period under greenhouse conditions was examined (conditions described by Binkley et al. 1982b).

RESULTS

Cellulose decomposition under controlled environmental conditions revealed greatest nutrient availability in the Sitka alder soils, followed by the red alder soils, with the no alder soils showing markedly lower rates of decomposition (Table 34). In contrast, the three sites differed little in the field experiment. Apparently, the beneficial effects of greater nutrient availability in the alder soils demonstrated in the greenhouse experiment were counteracted in part by environmental conditions in the field study. The sparse forest floor and canopy in the no alder site probably resulted in greater litter bag temperatures relative to the alder sites. Similarly, the greater forest floor biomass in the red alder stand probably resulted in lower litterbag temperatures than in the Sitka alder site.

Under natural conditions, the forest floor resource quality differed greatly between the sites, and therefore the cellulose decomposition experiments cannot be used to estimate litter decomposition rates. The experiments did indicate a major interaction between enhanced forest floor nutrient availabilities in the alder stands and more favorable environmental conditions in the no-alder stand. These demonstrated interactions merit closer examination.

TABLE 34. CELLULOSE DECOMPOSITION, MEAN (%) AND STANDARD ERROR.

		Site type		
Experiment	n	No alder	Sitka alder	Red alder
Greenhouse	9	11 (2)	63 (5)	46 (4)
In field	30	44 (7)	52 (5)	40 (5)

APPENDIX 3. IMPROVEMENT OF DOUGLAS-FIR VIGOR INDEX BY SITKA ALDER AND RED ALDER

Recent work by Waring and coworkers (c.f. Waring 1980, Waring et al. 1980, Waring 1982) proposed a measure of tree vigor which relates stem growth to leaf area. By expressing stem growth as a function of leaf area, the index appears to be a sensitive indicator of overall tree vigor. The key to measuring this tree vigor index is a linear relationship between sapwood crossectional area and tree leaf area (Grier and Waring 1974, Snell and Brown 1978, Whitehead 1978, Long et al. 1981). In the present study, I assessed the effects of two nitrogen-fixing alder species on 3 methods of calculating Waring's tree vigor index for 21-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]. I hypothesized that slow-growing, shrubby Sitka alder [*Alnus sinuata* (Regel) Rydb.] would improve the Douglas-fir vigor index more than highly competitive, rapidly growing red alder (*Alnus rubra* Bong.).

SITE DESCRIPTION

Three study sites were the Mt. Benson sites described in Sections III, IV, and V. One site contained no alder, another portion contained naturally-seeded Sitka alder, and the third contained naturally-seeded red alder. The Douglas-fir canopy in the no alder site was open, with live crowns extending to the ground. In the Sitka alder site, the dense Sitka alder canopy at 5-6 m restricted the Doughelpfir live crowns to the upper 5 m of the stems. Douglas-fir crowns were mixed with the alder crowns for the entire tree height on the red alder site.

METHODS

Measurements

Douglas-fir crop trees in the plots described in Sections IV and V were measured for diameter, sapwood radius, height, and 5 year increments in diameter and height (1977-1981). Five average-diameter (mean ± 1 cm) Douglas-fir were randomly chosen in each site for leaf area determinations. Each tree was divided into 2 m stem sections, and the number of branches per section was recorded. One representative branch was chosen subjectively from each section and returned to the laboratory. All needles were stripped from each sample branch, oven dried and weighed. Projected leaf areas for subsamples of the leaves from each branch were measured using a Lycor leaf area meter.

Calculations

Three versions of the tree vigor index were calculated. Method 1 divided basal area growth over 5 years by stem crossectional sapwood area at breast height (Waring et al. 1980). This method assumed (1) that basal area growth is a suitable measure of stand growth, and (2) that sapwood area to leaf area ratios are the same for all stands. The second method utilizes biomass regression equations (from Kurucz 1969) and assumed conversion ratios of sapwood area to leaf area to calculate stem biomass increment per unit leaf area. Method 2 avoids the potential bias involved in using basal area as a surrogate measure of stem growth, but is subject to any bias and error involved in the application of the regression equations. The conversion factors for sapwood area to leaf area for Method 2 were assumed from values listed by Waring et al. (1980) for Douglas-fir. Method 3 uses the same stem growth estimates as Method 2, but sapwood area to leaf area conversions were based on the measured values for each of the three study sites.

Two-tailed T-tests were used to test for significant differences between means at $p < 0.05$.

RESULTS

The ratios of leaf area to leaf weight did not differ between the three sites (Table 36), and were very close to the value given by Waring et al. (1980). However, the conversion ratio of leaf biomass to sapwood area was reduced 65 to 80 percent in the red alder site relative to the Sitka alder and no alder sites. As a result, the leaf area to sapwood area ratio was much lower for the red alder site.

The apparent effects of the alders varied with the methodology used to calculate the vigor index. The estimates of Douglas-fir vigor calculated by the first two methods (Table 37) supported my hypothesis of greatest vigor in association with Sitka alder. Based on basal area growth (Method 1), Douglas-fir vigor with red alder was greater than without alder; based on stem growth (Method 2), the vigor was similar between the sites. This relative difference between the two methods is due to the marginally lower stocking and tree size in the red alder site yielding a smaller stem biomass estimate per unit basal area. The calculation of vigor index by the Method 3 exhibited a very

TABLE 35. DOUGLAS-FIR CROP TREE AVERAGE STOCKING, SIZE AND 5-YEAR GROWTH.

	Site type		
Property	No alder	Sitka alder	Red alder
Stocking,			
crop trees/ha	650b[1]	570ab	540a
Basal area,			
m^2/ha	10.5a	10.9a	10.0a
cm^2/tree	162a	191b	185b
Sapwood area,			
m^2/ha	6.7b	6.4b	5.4a
cm^2/tree	103a	112a	100a
Leaf area index[2],			
m^2/m^2	5.3b	5.4b	1.9a
Breast height diameter,			
cm	13.8a	15.6b	15.3b
Basal area growth,			
m^2/ha	4.5a	6.0b	4.6a
cm^2/tree	69a	105c	85b

[1] Means followed by the same letter do not differ significantly at $p < 0.05$.

[2] Projected basis, calculated from measured conversion ratios in Table 36. Sitka alder and red alder leaf area indexes were 2.2 and 3.5 (Binkley, unpublished data).

TABLE 36. DOUGLAS-FIR LEAF AREA RELATIONSHIPS FROM WARING ET AL. (1980) IN COMPARISON WITH THOSE MEASURED ON THE STUDY SITES.

Property	Site type		
	No alder	Sitka alder	Red alder
Leaf biomass/sapwood area, g/cm^2			
Assumed[1]	74	74	74
Measured	114b	102b	62a
Leaf area/leaf weight, cm^2/g			
Assumed	60	60	60
Measured[2]	55a	57a	53a
Leaf area/sapwood area, cm^2/cm^2			
Assumed	4440	4440	4440
Measured	6320b	5810b	3290a

[1] Assumed values from Waring et al. (1980).

[2] Weighted average of leaf area/leaf weight ratios for each 2 m canopy section (oven-dry basis).

TABLE 37. DOUGLAS-FIR VIGOR INDEXES.

Vigor Index Method	Site type No alder	 Sitka alder	 Red alder
1. 5 yr basal area growth/sapwood area, cm^2/cm^2	0.66a	0.71a	0.71a
2. 5 yr stem growth/leaf area; conversion ratios assumed[1], g/m^2	600a	830b	670a
3. 5 yr stem growth/leaf area; conversion ratios measured, g/m^2	390a	540b	1360c

[1] Conversions ratios are listed in Table 36.

different pattern; the vigor index ratings for the Sitka alder site and red alder site were 40 and 86 percent higher than the no alder site. The superior vigor index in the red alder site resulted from the lower leaf area to sapwood area ratio found for this site.

Method 3 was based on leaf area to sapwood area ratios directly measured for each study site, and therefore probably provides the most realistic estimate of stem growth per unit leaf area. The 40 to 86 percent increase in stem growth per unit leaf area in association with alder is substantially greater than can be explained by increased net photosynthetic rates. Brix (1981) found improving Douglas-fir nutrition through fertilization increased net photosynthesis rates by a maximum of 30%. An additional source of carbohydrates for stem growth per unit leaf area could be a reallocation within the trees. A number of recent studies have documented decreased below-ground carbohydrate allocation for fine root production with increasing soil fertility (c.f. Santantonio 1979, Keyes and Grier 1981, Waring 1982). Soil enrichment by the nitrogen-fixing alders may have resulted in decreased fine root production by the Douglas-fir, providing a greater proportion of the total carbohydrate budget to stem growth. This proposed carbohydrate allocation mechanism of interaction between nitrogen-fixing plants and associated trees merits direct evaluation.

The application of Waring's tree vigor index to my study sites was complicated by the anomalies in conversion ratios of leaf biomass to sapwood area. The expedient use of this simple index in the future will require a more thorough evaluation of the factors responsible for variations in this relationship.