

AN ABSTRACT OF THE THESIS OF

PAULA W. REID for the degree of Master of Science in
Forest Science presented on July 6, 1983

Title: ASSESSING THE INFLUENCE OF SILVICULTURAL PRACTICES ON
DOUGLAS-FIR NUTRITION, AND STEMWOOD PRODUCTION

Abstract approved: Signature redacted for privacy.
Professor Robert Tarrant

Nitrogen, phosphorus and sulfur concentrations were measured in the soil, foliage and litter of Douglas-fir growing in pure Douglas-fir and mixed conifer stands. On four sites of contrasting fertility and climatic conditions, plots had been modified by the introduction of alder, thinning, or by a single application of nitrogen fertilizer and thinning.

Samples were taken to look for differences between plots in soil, foliage and litter nutrient concentrations and ratios. Changes in canopy leaf area and wood production efficiency were calculated from estimates of stemwood diameter and sapwood area. Wood production efficiency, an index of stemwood production per unit of leaf area, remained steady or increased under all treatments, despite shading from higher canopy leaf areas. On the less fertile Washington and Vancouver Island sites, the alder/conifer plots, with higher

concentration up to a certain 'threshold level', above which higher nitrogen concentrations did not increase wood production as significantly. Stemwood production also tended to increase with higher N:P ratios and then leveled off above a ratio of twelve.

A nitrogen use efficiency was calculated as the amount of stemwood produced per unit of N in the foliage. Although higher foliar nitrogen values correlated with higher wood production/m² on the poorer quality sites, the nutrient use efficiency tended to be lower when the nitrogen concentration per m² was more than about three grams per m².

Stemwood production per m² of foliage tended to increase with higher foliar N:P ratios, but the correlation coefficient was low. Soil N (mineralizable and total) plotted against against foliar N/m² produced a coefficient of .7. Oregon coast site data alone showed a significant correlation between foliar N and percent N retranslocation ($r = .94$) and between foliar P and percent P retranslocation ($r = .91$).

Assessing the Influence of Silvicultural Practices
on Douglas-fir Nutrition and Stemwood Production

by
Paula W. Reid

A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed July 6, 1983

Commencement June 1984

ACKNOWLEDGEMENTS

I would like to acknowledge the people who helped me through this thesis project. Dr. Richard Waring provided me with the opportunity to do the research, as well as ideas and encouragement, for which I am extremely grateful. Dr. Kermit Cromack took on the role of major advisor in Dr Waring's absence and did everything possible to assist in all phases of the project. Dr. Phillip Sollins gave valuable criticism on the form and content of the first draft. I would also like to thank Prof. Robert Tarrant, Dr. Larry Boersma, Dr. John Gordon and John Marshall for reviewing the thesis.

I am most grateful to Dr. Dan Binkley for his field sampling assistance, thoughtful advice and constant encouragement throughout the completion of this project. Field and laboratory assistance was also provided by Cynthia McCain, Richard Boone, Marlene McDermott and Roger Martin. Carol Glassman made her laboratory facilities readily available and offered technical advice on chemical analyses.

This research project was funded by the following National Science Foundation grants; The Long Term Ecological Reserve Grant, and Stress-induced Wave Mortality in Subalpine Forest Ecosystems.

TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION	1
II. SITE DESCRIPTIONS	6
III. FIELD SAMPLING	9
IV. ANALYSES	11
Laboratory Analysis	11
Growth Efficiency Determination	16
Statistical Analysis	16
V. RESULTS	18
VI. DISCUSSION	26
Nutrient Analysis	26
nitrogen	27
phosphorus	29
balanced nutrition	31
litter measurements and the process of retranslocation before leaf abscision	32
sampling	37
summary table	41
Growth Efficiency	42
stemwood production efficiency	43
nutrient use efficiency	48
VII. SUMMARY AND CONCLUSION	54
BIBLIOGRAPHY	56

LIST OF TABLES

<u>Table</u>	<u>Page</u>
I Site descriptions	7
II Douglas-fir foliage weight per unit leaf area g/m^2	12
III Growth Efficiency	12
IV Foliar and litter nutrient concentrations, and per cent retranslocation of nutrients on S. Washington, Oregon Coast and Vancouver Island sites	13
V Foliar and litter nutrient concentrations, and per cent retranslocation for the Oregon Cascades site	14
VI Soil N, P and S measurements for top 15 cm of mineral soil	15
VII Ratios of Douglas-fir foliar and litter nutrients	20
VIII Foliar and litter nutrient concentrations, percent values	21
IX Summary table, showing treated plot measurements whose values significantly ($p \leq .05$) differed from their controls, either higher (\uparrow) or lower (\downarrow)	39
X Current and 1-yr-old Douglas-fir foliar nutrient concentrations from Vancouver Island	40
XI Total stand and individual Douglas-fir leaf area	44

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Change in growth efficiency with leaf area	5
2	Change in growth efficiency with leaf area after fertilization	5
3	Efficiency of wood production vs. total stand leaf area	19
4	Wood production/ha/yr vs. Douglas-fir foliar N/ha (x) and wood production/ha/yr vs. Douglas-fir leaf area (·)	23
5	Foliar nitrogen, phosphorus and sulfur concentrations vs. stemwood production	24
6	Foliage and litter nitrogen concentrations vs. stemwood production/m ² foliage	33
7	N:P ratio in Douglas-fir foliage and litter vs. wood production	34
8	Nitrogen productivity vs. foliar biomass	49
9	Vitousek's data showing litterfall dry weight per year vs. nitrogen content of the litterfall	50
10	Vitousek's data showing the relationship between the amount of nitrogen in the litterfall and the dry mass-to-nitrogen ratio of that litterfall	51
11	Stemwood production per unit of nitrogen in the foliage vs. nitrogen in Douglas-fir foliage per m ²	52

ASSESSING THE INFLUENCE OF SILVICULTURAL PRACTICES ON DOUGLAS-FIR NUTRITION AND STEMWOOD PRODUCTION

CHAPTER I

INTRODUCTION

The efficiency with which trees produce wood is important because it reflects the ability of these trees to fully utilize site resources. The amount and availability of resources like nutrients, moisture and light are among the factors which determine the production of photosynthate, and its subsequent allocation towards wood production as height and diameter growth.

Forest management practices modify the ecosystem and thus affect the efficiency with which wood is produced. When resources are added to a forest system through fertilization, redistributed through thinning, or affected by changes in species composition, not only is the growth of the crop tree influenced, but the cycling of nutrients is altered as well. We need to know the effects of silvicultural practices on wood production, which occur through changes in mineral mobilization and uptake, internal redistribution within trees, and the eventual recycling of nutrients through litterfall, throughfall and root death.

Important elements like nitrogen are in part recycled through the ecosystem by plant uptake, utilization and release in litterfall back to the soil. A stimulus like soil nitrogen input may affect not only the available N in the soil but also uptake by vegetation, and

litter nutrient concentrations (Keeney 1980, Turner 1977). We might be able to recognize changes in the cycling of nutrients by making certain discriminate measurements at these key nutrient transfer points (soil, foliage, litter). Nitrogen in particular should be important to measure because it limits growth on forest sites. As an essential component of proteins, including the light-capturing pigments, it might be expected to mirror changes affecting photosynthesis and even wood production (Miller, Miller and Cooper 1981).

This paper reports a study in which Douglas-fir wood production was estimated, and a series of simultaneous measurements were made of several elements in the soil, foliage and litter. Four different sites were sampled; a fertile coastal Oregon site, two less fertile sites on Vancouver Island, B.C. and in southern Washington, and a site of intermediate fertility in the Oregon Cascades. Nutrient availability at each site had been modified by introduction of alder, thinning, or the application of fertilizer and thinning. The effects of these treatments on wood production per leaf area were compared, as were foliar, litter and soil N,P&S contents and ratios. These nutrient variables were tested for their correlation with changes in wood growth efficiency.

Previous research has offered some hypotheses on the effect of silvicultural practices on wood production and nutrient cycling. Wood production efficiency, the amount of stemwood produced per unit leaf area, has been shown to be negatively correlated with canopy leaf area, probably as a result of shading (Newman 1979, as cited in

Waring et al., 1980) (see Figure 1). Treatments like thinning, and fertilization combined with thinning have increased the amount of wood produced per unit leaf area at comparable canopy leaf areas (Waring et al., 1978) (Figure 2).

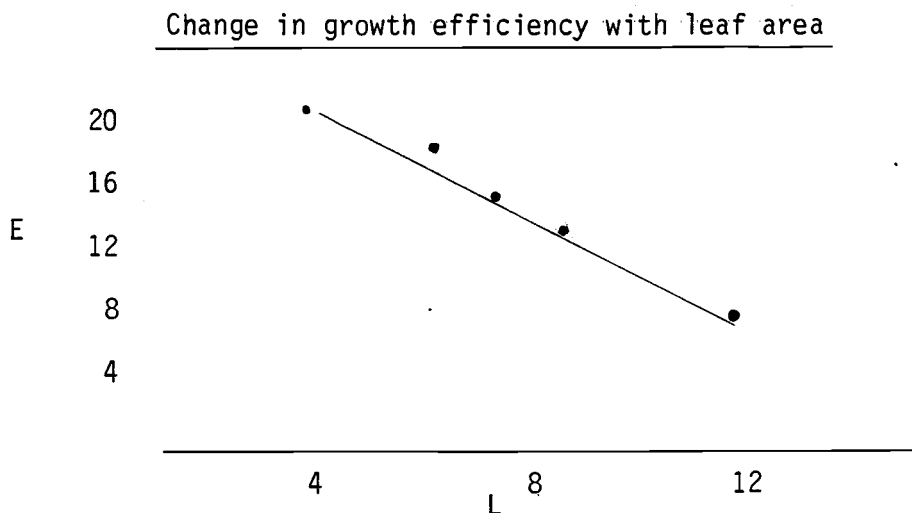
Interplanting alder with Douglas-fir has also been evaluated for its effect on the availability and cycling of nutrients, especially nitrogen (Gordon et al., 1979). Increased soil nitrogen availability with alder has been measured on poorer quality, nitrogen-deficient sites (Miller and Murray, 1977). Increasing the supply of nitrogen on these sites has been found to increase uptake as well, and result in higher foliar N concentrations (Turner, 1977). Stachurski and Zimka (1979) suggest that an increase in nitrogen released in litter-fall would also develop on sites where nitrogen nutrition was improved.

Changes in Douglas-fir phosphorus and sulfur nutrition on the alder plots are suspected from work by Binkley on Vancouver Island (1982). When nitrogen availability is increased with fertilizer or by nitrogen-fixing plants, other elements important to plant growth can become limiting (Turner et al., 1980). A balanced ratio of nutrients (like N, P, S) may be as important as individual concentration values. Optimum values for this ratio have been predicted by Ingestad (1969).

Sampling methods and sample analyses were chosen with the view of keeping the procedure simple. The study was designed to measure

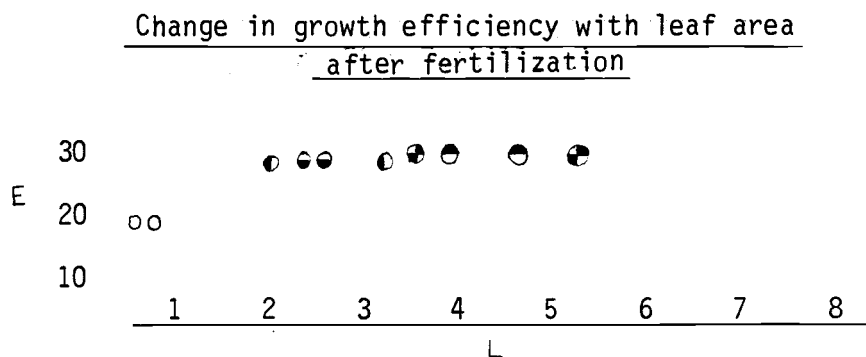
samples which were easily collected, quickly analyzed, and potentially useful in predicting changes in wood production efficiency.

Figure 1



As light decreases with increasing canopy leaf area index (L) growth efficiency (E), or wood production per m^2 of leaf area, is to decrease, as shown here, from Waring et al., 1981.

Figure 2



In this example, in a Norway spruce plantation, where increasing levels of N + P fertilizer were applied annually ($0 N_0 P_0$, $1 N_1 P_1$, $2 N_2 P_2$, $3 N_3 P_3$), growth efficiency (E) increased and was maintained as leaf area index (L) increased from 1 to 5.5. At higher values of L, E begins to decrease abruptly (after Albrektson et al., 1977, and from unpublished data of C.O. Tamm, U. of Uppsala, Sweden) (Also in Waring, 1981).

CHAPTER II

SITE DESCRIPTIONS

Sites were sampled at four locations in the Pacific Northwest where previous research had been done on Douglas-fir. This research included three studies involving the interplanting or establishment of alder with Douglas-fir. At the fourth site, the Douglas-fir had been thinned, or both thinned and fertilized with urea-N (Table I provides a summary of site descriptions).

The Cascade Head stand on the Oregon coast was established naturally on cleared and abandoned agricultural land in 1925. Several conifer species, including Douglas-fir, Sitka alder and western hemlock came in, along with red alder. Research plots were established in 1935-37 at which time the alder were removed to create a control plot. This area of the Coast Range is noted for its particularly high site quality for Douglas-fir timber production.

The Mt. Benson plots on Vancouver Island were planted with Douglas-fir in 1958, after logging and burning. Red and Sitka alder became established some time after plantation establishment. In contrast to the Oregon Coast stand, the site quality of this land is much lower (Binkley, 1982). The Wind River Experimental Forest plots in southern Washington are also located on poorer site quality land. This stand of Douglas-fir was planted after a wild fire in 1929. In 1933 red alder were interplanted in a 21 x 36 meter strip, originally

Table I

SITE	Site descriptions			
	ELEVATION (meters)	LATITUDE (north)	CLIMATE	SOILS AND PARENT MATERIAL
<u>Oregon Coast</u>				
Cascade Head Experimental Forest; near Otis, Oregon	180	45°3'	240 cm/yr average ppt; mean annual temp. 10°C	Typic Dystrandept; Astoria silty clay loam developed over interbedded basalt and tuffaceous siltstone parent material
<u>S. Washington Cascades</u>				
Wind River Experimental Forest; Planting Creek area near Carson, Washington	623	45°49'	229 cm/yr average ppt; mean annual temp. 9°C	Andic Haplumbrept; silty clay loam developed over andesite, basalt and breccia parent mat'l.
<u>Vancouver Island</u>				
MacMillan Bloedel Ltd. Tree Farm 19, Mt. Benson Vancouver Island, B.C.	510	50° 8'	200 cm/yr average ppt; mean annual temp ranges from 1-17°C	Typic Haplorthod; gravelly clay loam over uncompact basal till
<u>Oregon Cascades</u>				
HJ Andrews Experimental Forest; Blue River, Oregon	721	44°16'	215 cm/yr average ppt; mean annual temp. 8°C	Andic Haplumbrept; developed over andesite, breccia and volcanic ash

intended as a fire break. The site has since been the subject of interest for evaluating Douglas-fir/alder interactions (Miller and Murray, 1977).

The H. J. Andrews plots in the Oregon Cascades were planted with Douglas-fir in 1957 after logging and burning. The two treatment plots were thinned in 1977 to a prescribed 13 x 13 spacing, and one plot was hand-fertilized with urea-N (270 kg/ha) in 1978.

CHAPTER III

FIELD SAMPLING

During August and September of 1981, foliage, litter and soil samples were collected from randomly selected Douglas-fir trees on each plot. At plots where alder were present, the closest alder to the selected Douglas-fir was also sampled for foliage and litter. Douglas-fir diameters, sapwood radius and five year growth increment were measured.

At Cascade Head, on the Oregon coast, sample trees were selected from alternate sides of a 30-m transect through the plot center. At the Oregon Cascades site, a circular plot was established that included 15 Douglas-fir greater than 10 cm in diameter. Douglas-fir at the Wind River site that had been girdled by bears were avoided.

Soil was sampled within one meter of each selected Douglas-fir to a depth of 15 cm below the forest floor. This provided paired nutrient samples of the soil, foilage and litter for each Douglas-fir. On the Vancouver Island and Oregon Cascades sites, third year foliage was collected by hand from the third whorl of branches from the top. Alder were sampled at a similar height. Foliage was collected by shotgun from the same crown position at the other two sites. On Vancouver Island, first and current year conifer foliage was also collected (Table X).

Litter was sampled at the time of foliage collection on Vancouver Island and in the Oregon Cascades, by shaking the branches and collecting the brown senescent foliage which fell. At the Southern Washington Cascades and Oregon coast sites this Douglas-fir litter was collected in traps one-two weeks after the foliage. Alder litter was collected in the litter traps, along with the Douglas-fir litter (Southern Washington Cascades and Oregon Coast sites), except on Vancouver Island, where the alder litter was collected one month after the foliage.

CHAPTER IV

ANALYSES

Laboratory Analysis

Soil samples were air dried, sieved and subsampled for measurement of extractable, mineralizable and total nitrogen, fluoride-extractable phosphorus and total sulfur (Table VI). Mineralizable ammonium-N was determined after a seven-day incubation at 40° C (Waring and Bremner, 1964). The initial KCl-extractable ammonium measurement was made on un-incubated material. The total amount of nitrogen converted to NH_4^+ (total N) was analyzed with auto-analyzer techniques (Allen et al., 1974).

A separate 2.9 gram subsample of each soil was analyzed for available-P in a dilute acid fluoride extractant test (Jackson, 1958).

Total sulfur determination used an oxidation procedure from Tabatabai and Bremner (1970), as modified by the Soil Testing Laboratory, Oregon State University.

In order to separate differences in foliar nutrient concentrations from seasonal fluctuations in leaf weight, the foliar and litter N, P and S values for this study were expressed per square meter of leaf area (Waring et al., 1980) (Table II). Table VIII lists the more conventional percent values. Projected leaf area was determined on oven-dried samples with a LICOR 3100 leaf area meter. Fresh foliage was subsampled before oven drying, and its leaf area

Table II

Douglas-fir foliage weight per unit leaf area, g/m^2

	Oregon Coast		S. Washington		Vancouver Island			Oregon Cascades		
	Conifer Only	Red Alder Mix	Conifer Only	Red Alder Mix	Conifer Only	Red Alder Mix	Sitka Alder Mix	Control	Thinned	Fertilized + Thinned
3 rd year* foliage	.036	.037	.016	.021	.024	.025	.020	.020	.020	.019
Litter	.031	.032	.017	.021	.019	.020	.019	.017	.021	.016

Table III

Growth efficiency

	Oregon Coast		S. Washington		Vancouver Island			Oregon Cascades		
	Conifer Only	Red Alder Mix	Conifer Only	Red Alder	Conifer Only	Red Alder	Sitka Alder	Control	Thinned	Fertilized + Thinned
g wood/m ² foliage/yr.	190	166	62	144	165	184	228	117	182	199

Table IV

Foliar and litter nutrient concentrations, and per cent retranslocation of nutrients on the
Oregon Coast, S. Washington Cascades and Vancouver Island sites

STAND	ELEMENT	CONIFER ONLY			RED ALDER/CONIFER MIX			SITKA ALDER/ CONIFER MIX		
		foliage g/m ²	litter g/m ²	% retrans location	foliage g/m ²	litter g/m ²	% retrans location	foliage g/m ²	litter g/m ²	% retrans location
<u>S. Washington Cascades</u>	N	1.64	1.31	21	3.07*	2.42	25.8			
	P	.59	.40	49	.38*	.27	32.3	no Sitka alder plot		
	S	.19	.08	52	.17	.15	27.2			
<u>Oregon Coast</u>	N	5.14	2.67	57*	5.54	.10	24.0			
	P	.77	.34	55*	.46*	.29	34.7	no Sitka alder plot		
	S	.25	.15	33	.17	1.9	29.5			
<u>Vancouver Is.</u>	N	2.98	1.49	45.2	6.03*	2.59	57.5	2.88	1.67	42
	P	1.04	.60	42	.29*	.60	24.6	.23*	.12	48
	S	.32	.26	31	.29	.24	38.1	.21	.19	33

*Indicates values significantly different from the control plot at $p \leq .05$

Table V

Foliar and litter nutrient concentrations, and per cent retranslocation of nutrients
on the Oregon Cascades site

STAND	CONTROL			THINNED			FERTILIZED AND THINNED		
	foliage g/m ²	litter g/m ²	% retrans location	foliage g/m ²	litter g/m ²	% retrans location	foliage g/m ²	litter g/m ²	% retrans location
<u>Oregon Cascades</u>									
ELEMENT									
N	2.62	1.49	57.2	2.77	1.11	57.5	2.87	1.15	59.0
P	.83	.70	18.2	.87	.76	13.0	.81	.77	13.0
S	.15	.14	25.8	.17	.13	28.3	.17	.14	21.1

Table VI

Soil N,P and S measurements for top 15 cm of mineral soil

	<u>Oregon Coast</u>		<u>S. Washington Cascades</u>		<u>Vancouver Island</u>			<u>Oregon Cascades</u>		
	Conifer	Conifer/ red alder	Conifer	Conifer/ red alder	Conifer	Conifer/ red alder	Conifer/ Sitka alder	Control	Thinned	Thinned and Fert.
Extractable N ppm	1.7	2.3	0.8	3.2*	2.0	3.1*	2.9	4.5	4.2	5.6
Mineralizable N	99.8	105.0	33.1	71.7*	35.7	61.0*	71.4*	68.0	54.0	52.0
Total N %	.55	.61	.16	.31*	.08	.29*	.24*	.23	.24	.21
F-Extractable P ppm	2.4	2.8	21.5	24.5	9.9	2.6*	15.4*	39.0	36.0	36.0
Total Sulfur ppm	<5	<5	5.8	5.7	5.5	6.8	9.9*	5.9	5.6	<5

* Indicates values which differ from the control plot value at a significance of $p \leq .05$

was compared to dried samples. Oven-drying caused a decrease of 8% in leaf surface area so measurements were adjusted to a fresh basis using this value.

Dried foliage was ground in a Wiley mill and digested using a micro-kjeldahl procedure (Black 1968). Digests were analyzed for nitrogen and phosphorus by autoanalysis (Allen et al., 1974). Total sulfur was determined by ashing a separate subsample in $Mg(NO_3)_2$, reacting the oxidized sulfur with $BaCl_2$, and measuring turbidity (Tabatabai and Bremner 1972).

Growth Efficiency Determination

Wood production efficiency was calculated as stem growth per unit of leaf area (Waring, Thies, Muscato, 1980)(Table III). Leaf area was calculated assuming a ratio of $.32m^2$ leaf area to one cm^2 sapwood area (Grier and Waring, 1974). An allometric equation developed by Gholz et al. (1979) was used to estimate stemwood biomass:

$$\ln(\text{stemwood biomass}) = 3.0396 - 2.5951 (\ln(\text{DBH}))$$

Statistical Analysis

Nutrient concentrations, ratios and per cent retranslocation (out of abscised foliage) were compared between plots on each site using a standard T test (Snedecor and Cochran, 1980). A significance level of $p \leq .05$ was accepted. Linear and non-linear regression analyses were performed to compare between different

nutrients, and between nutrients and stemwood production efficiency (growth efficiency), measured as the kilograms of wood produced per square meter of foliage per year. Significant correlation coefficients are reported within the text where appropriate.

CHAPTER V

RESULTS

Douglas-fir stemwood production (per m^2 foliage) in the presence of alder, and after thinning and fertilization was maintained at the same level or increased above the control plot. Leaf area of the individual Douglas-fir was also higher where stemwood production went up (Figure 3). Total stand leaf areas were higher on the alder plots, but the thinned, and fertilized and thinned stand leaf areas were insignificantly different from their controls.

Douglas-fir foliar nitrogen concentrations were higher in the presence of alder at the Southern Washington Cascades and the Vancouver Island sites. On the Oregon coastal site there was no significant difference in Douglas-fir foliar nitrogen between the alder conifer/alder and conifer only (control) plots. Among the three conifer/alder sites, Douglas-fir growing in pure conifer stands on the more infertile sites exhibited disproportionately high amounts of phosphorus to nitrogen (Table VII). This condition was reversed in Douglas-fir growing with alder. N:S ratios seemed unchanged between the pure conifer and mixed conifer/alder stands. The fertilized and thinned, thinned and control plots in the Oregon Cascades also reflected a significantly lower N:P ratio than the mixed alder/conifer plots, although between themselves they showed no significant differences.

Figure 3

Efficiency of wood production vs. total stand leaf area

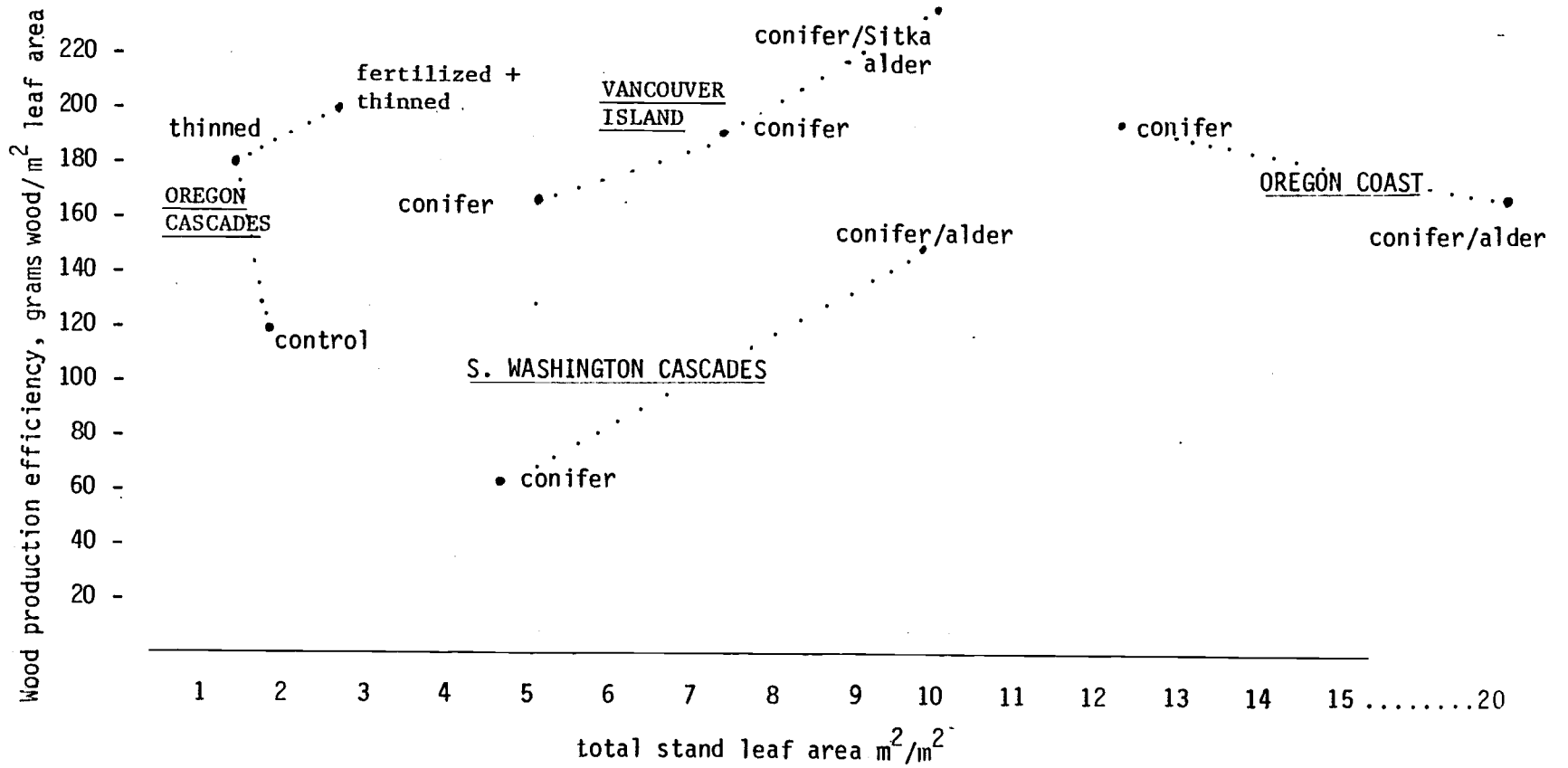


Table VII

Ratios of Douglas-fir foliage and litter nutrients

	OREGON COAST		S. WASH. CASCADES		VANCOUVER ISLAND			OREGON CASCADES		
	Conifer Conifer	Red Alder	Conifer	Red Alder	Conifer	Conifer Red Alder	Sitka Ald.	Control	Thinned	Thinned & Fert.
RATIO OF FOLIAR										
N:P:S	100:15:5	100:12:3	100:36:11	100:12:5*	100:35:11	100:5:5*	100:8:7*	100:27:6	100:31:6	100:28:6
RATIO OF LITTER										
N:P:S	100:13:6	100:9:6	100:36:6	100:11:6*	100:14:17	100:8:9*	100:7:11*	100:78:13	100:69:11	100:67:12

* Indicates N:P ratios only, that differ significantly from the control, or conifer only plot at $p \leq .05$

Table VIII

Foliar and litter nutrient concentrations, per cent values

	S. WASH. CASCADES		OREGON COAST		VANCOUVER ISLAND			OREGON CASCADES		
	Conifer Only	Conifer/Red Alder	Conifer Only	Conifer/Red Alder	Conifer Only	Conifer/Red Alder	Conifer/Sitka Alder	Control Plot	Thinned Plot	Thinned + Fertilized
Foliage										
N%	1.0	1.5	1.4	1.5	1.2	2.4	1.4	1.3	1.4	1.5
P%	.4	.2	.2	.1	.4	.1	.1	.4	.4	.4
S%	.1	.08	.07	.05	.13	.12	.12	.08	.09	.09
Litter										
N%	.77	1.15	.86	1.5	.78	1.3	.88	.88	.53	.72
P%	.2	.1	.2	.1	.3	.3	.1	.4	.4	.5
S%	.05	.08	.05	.06	.14	.12	.10	.07	.06	.09

Mineralizable soil nitrogen, like foliar nitrogen, was significantly higher in the presence of alder on the Vancouver Island and the Southern Washington Cascades sites, but not on the Oregon coast. Total nitrogen and KCl-extractable nitrogen paralleled the changes in mineralizable nitrogen, except at Vancouver Island. The Oregon Cascades Douglas-fir showed no differences with treatment in any of the three measurements of soil nitrogen (Table VI).

Extractable soil phosphorus did not vary greatly within sites, except on Vancouver Island, where the red alder/conifer mix Douglas-fir was significantly lower in phosphorus and the Sitka alder/conifer mix plot was higher in soil phosphorus than their control plot. The of soil P values on Vancouver Island and especially at the Oregon coast were much lower than on the southern Washington Cascades and the Oregon Cascades sites. Soil sulfur values were too low to be measured accurately on the Oregon coast site. Total sulfur tended to be lower with thinning and fertilizing treatments at the Oregon Cascades site, and was significantly higher in the presence of Sitka alder at Vancouver Island.

Regression analysis was performed between nitrogen, phosphorus and sulfur concentrations and ratios, and between these nutrient variables and wood production efficiency. Wood production/hectare increased with an increase in foliar N/hectare ($r=.94$) but it showed the same linear relationship with Douglas-fir leaf area/hectare ($r=.90$) (Figure 4). Wood production/m² increased with foliar N concentration up to a value of 3 g N/m², or 1.5% N. Above this the

Figure 4

Wood production/ha/yr vs. Douglas-fir foliar N/ha (x)
and wood production/ha/yr vs. Douglas-fir leaf area(.)

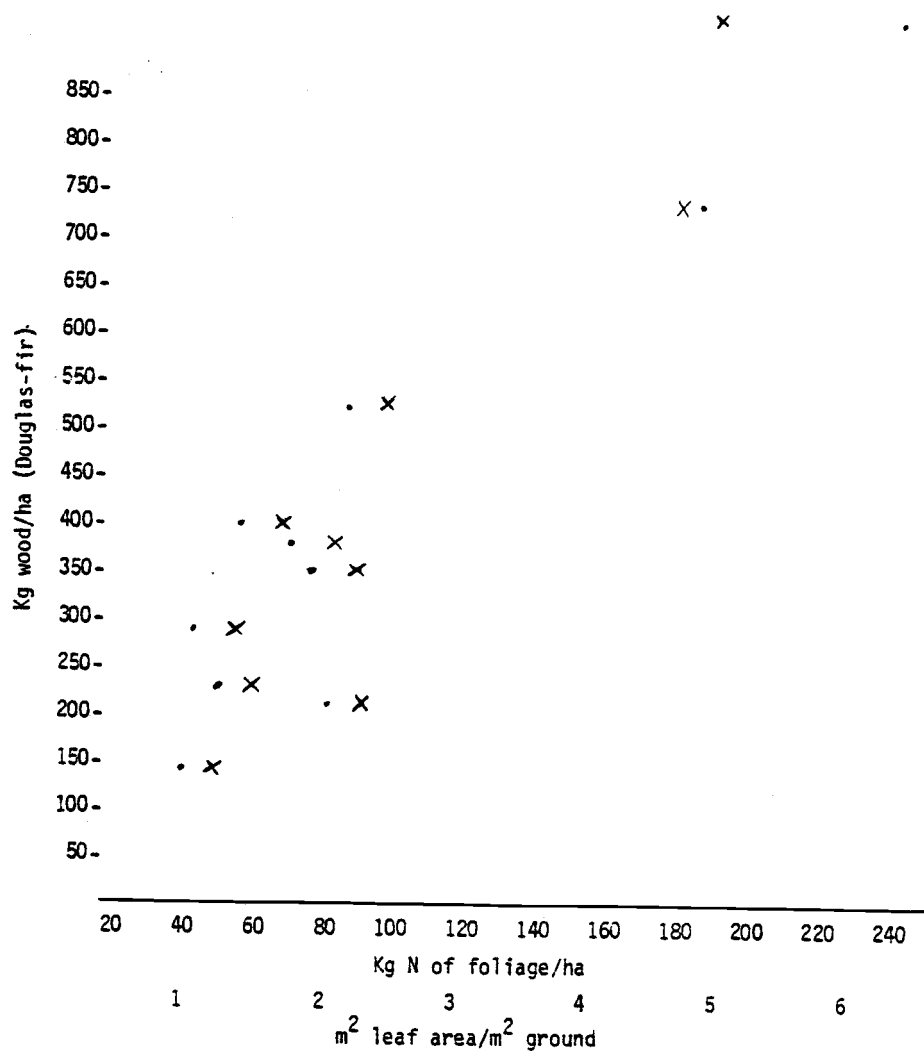
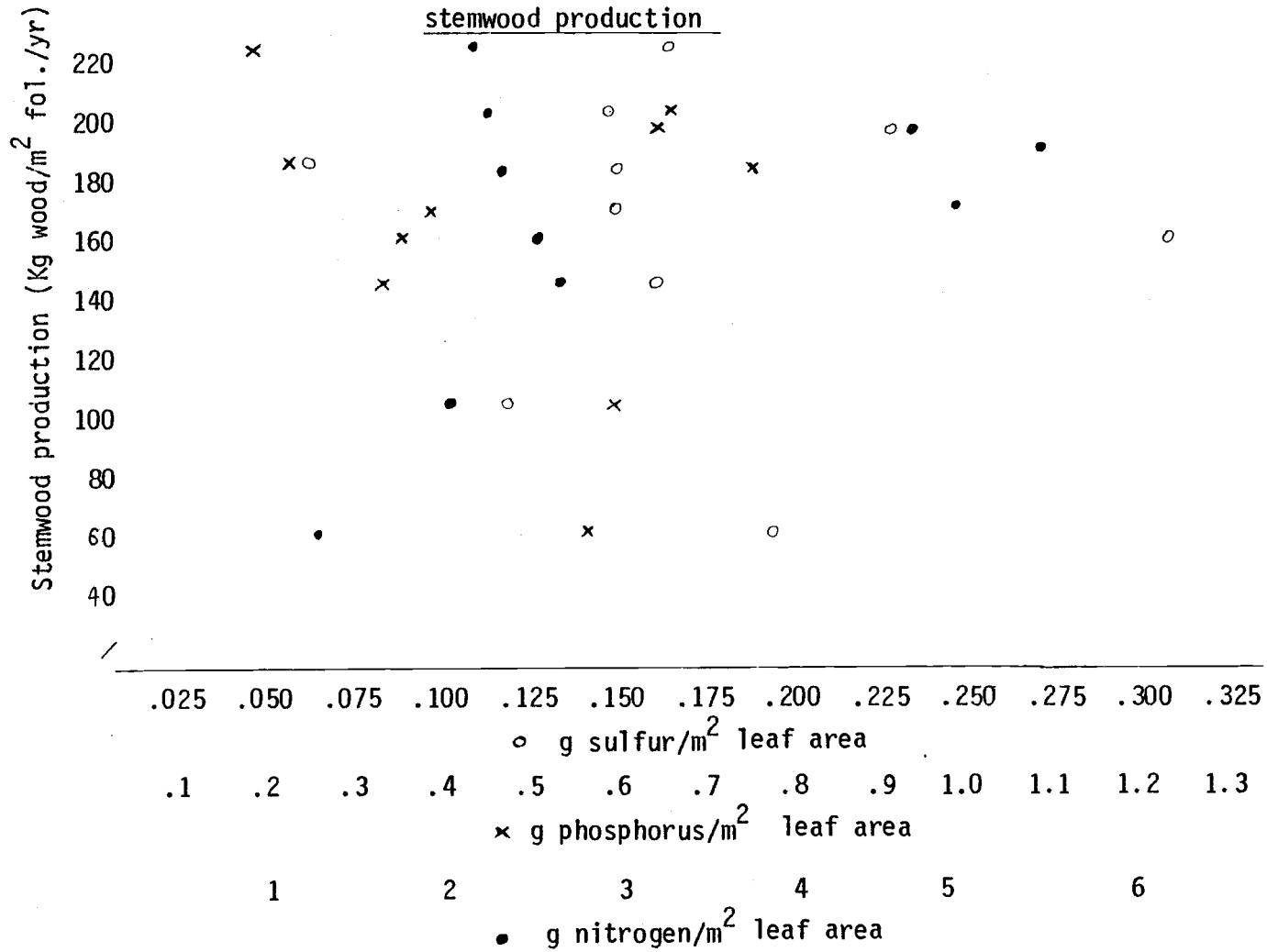


Figure 5

Foliar nitrogen, phosphorus and sulfur concentrations vs.
stemwood production



curve flattened (Figure 5) and increased foliar N corresponded with less change in wood production efficiency. This was also true for the relationship between N:P ratios and wood production efficiency. Foliar and total soil nitrogen correlation yielded a coefficient of .7. Plotting Oregon coast data alone, foliar nitrogen vs. percent nitrogen retranslocation ($r=.94$), and foliar phosphorus vs. percent phosphorus retranslocation ($r=.91$) yielded the highest correlation coefficients.

An additional linear regression was run to analyze wood production per unit of nitrogen in the foliage (nutrient use efficiency). Wood production per hectare increased linearly with increasing canopy nitrogen concentration, but wood production per unit of nitrogen in the foliage decreased as foliar nitrogen increased in concentration per m^2 and per hectare.

CHAPTER VI

DISCUSSION

Nutrient Analysis

Nutrient availability is one of several environmental factors that influence photosynthesis, and the subsequent allocation of photosynthate to growth functions and biomass accumulation. Nitrogen is an important component of the enzyme which catalyzes the incorporation of CO₂ into biomass. As such its availability could influence the photosynthetic capacity of the plant tissue. But this influence is integrated with other potentially limiting factors like light, moisture, temperature, etc., which together determine the 'balance' of conditions under which the plant must function.

When one or more of these influencing factors is modified, the rate at which the plant photosynthesizes, and its pattern of photosynthate allocation are probably altered to a new 'balance' (Hall 1979). Monitoring the nutrient factors and how they change in a plant and its environment may provide insight into fluctuations in primary production, and ultimately, woody biomass accumulation.

The nutrient concentrations/ratios measured in this study reflect differences in site quality and location as well as differences in treatments between plots. The changes in N, P and S measured with treatment reflect whether nutrient deficiencies on a particular site

are of sufficient magnitude to allow a response to the treatment applied, in spite of other influencing factors (like time, light, moisture). This in turn affects whether these changes correlate with a new level of stemwood production.

nitrogen

Soil nitrogen was significantly higher where alder was introduced on the poorer quality sites. These are treatment plots which had significantly higher wood production efficiency than their controls. Response to fertilizer nitrogen was not evident as an increase in the concentration of soil N on the fertilized and thinned plot in the Oregon Cascades. However wood production efficiency was higher with this treatment. The soil nitrogen measurements made in this study then, do not by themselves consistently predict changes in wood production efficiency.

One limitation of the soil nitrogen results is that anaerobic incubation (mineralizable N) allows for measurement of ammonium nitrogen but not nitrate-nitrogen, another significant portion of the available nitrogen pool. The importance of this source of nitrogen can be different between sites, and possibly over time. Nitrate-nitrogen has been found to be particularly important on higher quality sites (Vogt and Edmonds, 1982).

Differences in foliar nitrogen concentrations between plots and between sites generally reflected differences in soil nitrogen. Significant differences in foliar nitrogen occurred between plots only

where a nitrogen limitation had been suspected, identified and amended by treatment, not where nitrogen concentrations were already very high. One exception to this was the lack of significantly higher foliar nitrogen values in the presence of Sitka alder on Vancouver Island (see Table IV). Binkley (1982) however, made the same measurements of foliar nitrogen on the same plots and got significantly higher values on the Douglas-fir-Sitka alder plot. Because he sampled in a different year, at a slightly different time of the year, his results probably reflect a somewhat different pool of foliar nutrients.

The relationship between foliar nutrient concentrations and wood production efficiency (Figure 5) is not linear. Wood production increases with an increase in foliar N to a certain concentration, then wood production efficiency seems to increase with relatively little change in nitrogen. This level of N-concentration in the foliage could be considered as a threshold above which the plant no longer increases its utilization (because of some other limitation?) Where nitrogen does increase above this level, wood production efficiency is not increased as significantly, if at all. Phosphorus and sulfur concentrations show a less recognizable pattern of change.

The amount of time which elapses between treatment application and sample collection may be an important factor in determining the ability of nutrient variables to show a response to site treatment. It may also affect different portions of the nutrient cycle in different ways. For example the amount of urea-N fertilizer (270 kg/ha)

applied on the Oregon Cascades fertilized and thinned plot might have long since been mineralized, released and recycled through the system, as has been seen elsewhere (Johnson, Edwards-Todd, 1980).

There is also evidence that the effects of nitrogen fertilizer on tree growth may outlast the initial change in soil nitrogen availability. Miller and Tarrant (1983) measured a long term (15 years) response to nitrogen fertilizer in terms of height and diameter growth of Douglas-fir. Their plots are located near the southern Washington conifer and alder/conifer stands sampled for this study. Neither the soil nor the foliage samples which I collected from either their control plots or the highest level of N fertilizer (420 kg/ha) showed any significant differences in nitrogen in 1981.

phosphorus

The metabolic demand for nitrogen is linked to similar demands for other elements in varying quantities. If increased nitrogen availability leads to changes in protein synthesis for example, this may affect phosphorus or sulfur demands. It is also possible that whatever effects nitrogen has on P or S foliar concentrations may persist after foliar-N levels have changed.

Differences in foliar phosphorus did not reflect the pattern of soil P values. Foliar phosphorus was significantly lower on all sites in the presence of alder. Other reports of a reduction in foliar phosphorus have been reported where foliar nitrogen was

elevated (van den Driessche, 1974), but differences in phosphorus measurements in my study occurred whether or not the alder plot currently showed a higher concentration of soil or foliar nitrogen than the control plot. If the P concentration was affected by nitrogen, then the effect persisted after foliar N values decreased.

There are other possible reasons for reduced foliar phosphorus values in the presence of alder. Alder may have either a set of enzymes more efficient at making phosphorus available (Ho, 1973), or a different set of mycorrhizal fungi (interacting with the nitrogen-fixing bacteria in the roots; Trappe, 1979), which allow the alder to compete more successfully for the limited phosphorus. Perhaps the alder are just another sink which merely increases stress on the system to provide phosphorus. The relative immobility of phosphorus in the soil may also limit the effectiveness of discrete samples to indicate what pool of phosphorus is being tapped by the tree roots.

Van den Driessche (1979), concluded that foliar analysis is most valuable on sites where a nutrient deficiency is present. Such sites would be those where nutrients are sufficiently limiting to override other factors which influence stemwood production. The comparison between plots and sites in this study supports this conclusion. Alternative sources of information, like wood, roots, bud material, etc., have been considered in other studies to avoid the problems of foliar analysis (van den Driessche, 1979). Sampling the phloem and soluble nitrogen concentration in root tissue are two alternatives

which could be used to indicate of total plant nutrition (Leaf, 1970; Smith et al., 1954). In this study, several different elements and their balance in the litter as well as the foliage are compared to gain additional insight into treatment responses that foliar concentration alone can't provide.

balanced nutrition

Interpreting plant nutrition from foliar concentration values is difficult because of the wide range of individual nutrient concentrations that appear to be 'acceptable' for growth (van den Driessche, 1982). The proportional concentration, or demand of one nutrient to another may provide a better indication of the presence of deficiency symptoms.

Specific optimum foliar nutrient ratios for several different tree species have been suggested by Ingestad (1966). His N:P:S ratios for Douglas-fir seedlings (100:20:8) provide some values for comparison with mature tree foliage. It is possible that such a balance of nutrients reflects the 'equilibrium' growing conditions under which the tree is photosynthesizing and allocating carbon compounds, and that a change in the balance indicates a change towards a new equilibrium. This would mean that a dynamic rather than a static balance occurs (Linder and Ingestad, 1977). The optimum ratio then could differ with time, and site. The effect of individual stand treatment on changing the balance however may be measurable and important.

The N:P ratios of the foliage and for the most part in the litter decreased significantly on the southern Washington and Vancouver Island sites (Table VII). On these sites the nitrogen concentration increased and the phosphorous concentration decreased sufficiently in the presence of alder to alter the ratio. The ratio of N:P on the fertile Oregon coast shows little change in the balance of nutrients. This is the same site where soil and foliar N do not show an influence of plot treatment, although foliar P was lower. N:P ratios seem to follow the same pattern of change as the foliar values alone (Figure 7). Wood production leveled off at a ratio of around four.

These results suggest that although individual nutrient concentrations may show change, the balance of several different nutrients may not be significantly altered (as in the case of the Oregon Coast site). If a balance of nutrient factors ultimately determines growth, then perhaps the balance should be monitored.

Litter measurements and the process of retranslocation before
leaf abscision

Litter is one of the links which complete the chain of ecosystem nutrient transfers. Many important nutrients are cycled primarily through abscised foliage. The concentration of nutrients in the litter may influence the rate at which decomposition occurs. It can also indicate the importance of the role that retranslocation plays in supplying nutrients for new growth.

Figure 6

Foliage and litter nitrogen concentrations vs. stemwood production/m² foliage

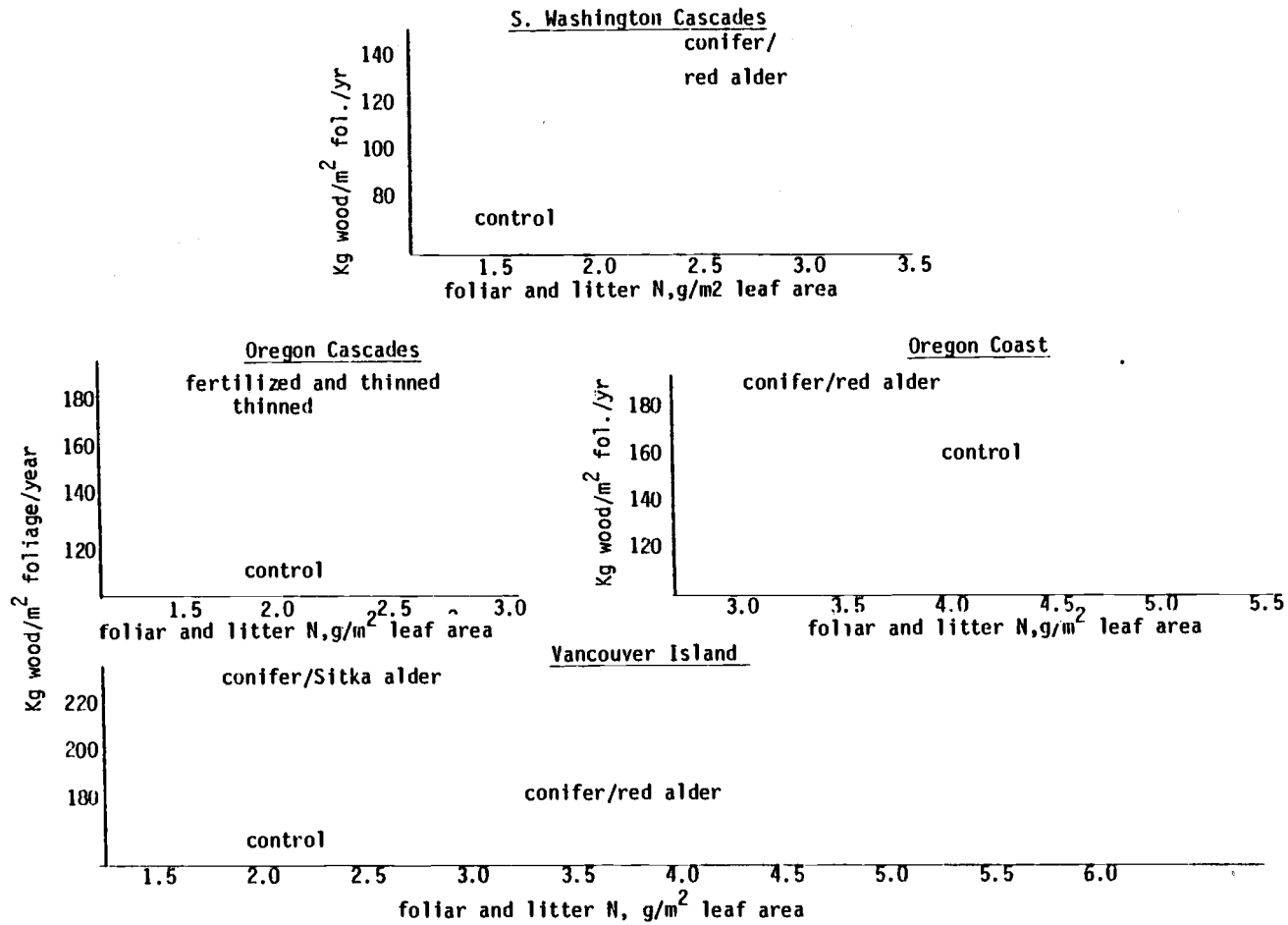
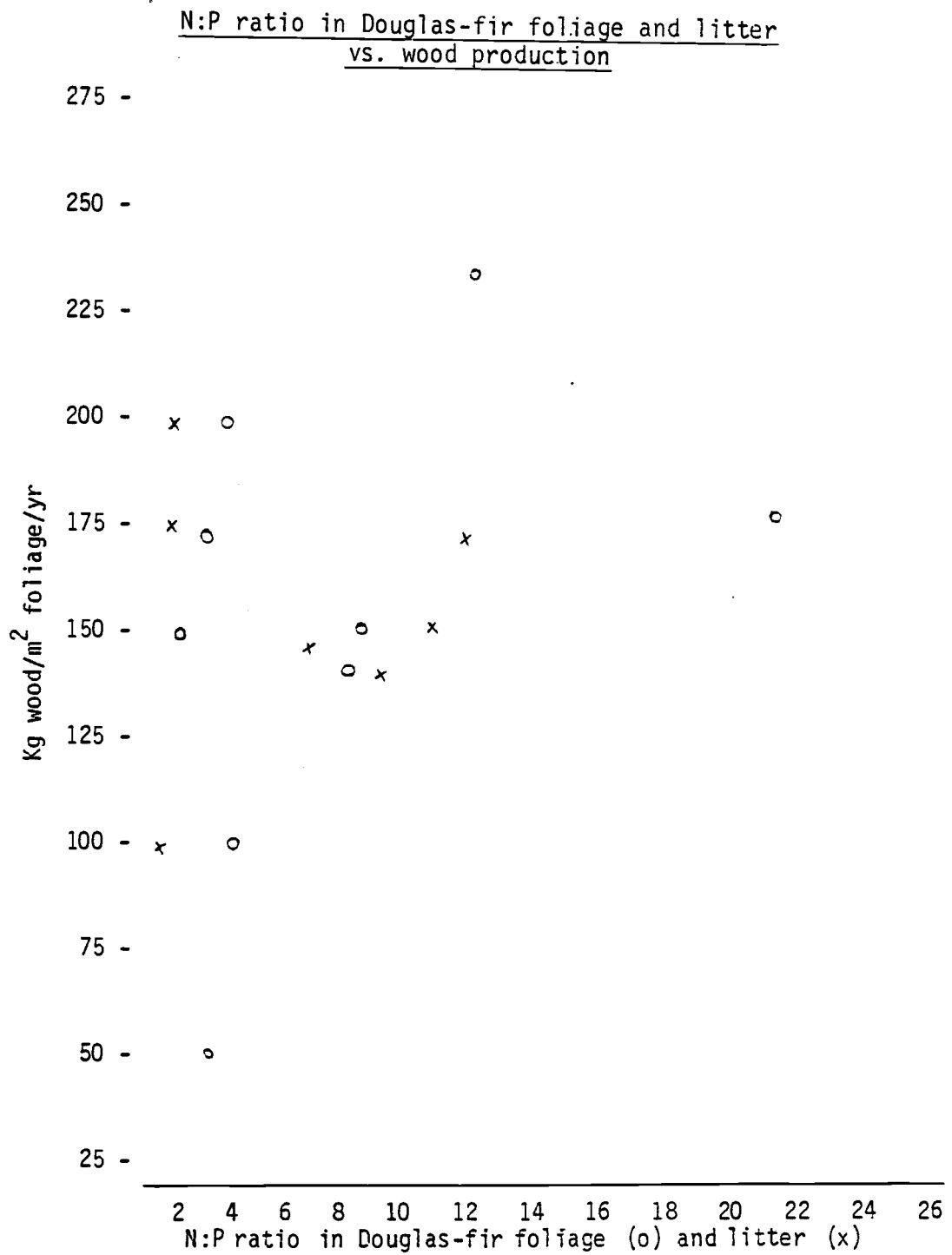


Figure 7



The pattern of changes, with treatment, of litter N, P and S values reflected the changes in foliar nutrient concentrations (Figure 6). Where higher foliar concentrations of N, P and S occurred, higher concentrations of N, P and S were left in the litter.

Nutrients retranslocated out of the foliage contribute importantly to the balance of nutrients in the litter. They are estimated in this data by the difference in nutrient concentration between fresh green and newly senesced foliage. Retranslocation of N and P decreased in the presence of red alder on the Oregon coast. On sites like Vancouver Island and the southern Washington Cascades, where a nitrogen deficiency was anticipated and amended, retranslocation was not significantly affected.

Two major theories have been proposed to interpret the significance and purpose of retranslocation. One hypothesis is that lower site fertility induces greater dependence on retranslocated nutrients. Thus foliage on nutrient deficient sites might resorb more before abscission, relative to a more nutrient rich site, or one supplied with additional nutrients (Stachurski and Zimka, 1975). This process may represent an energetically favorable alternative to absorbing more nitrogen through the roots. Barnes (1981) estimated the energetics of retranslocation, and concluded that it could 'cost' the tree more to take up soil NO_3^- than to pull it out of foliage before it is dropped. This would also seem to possess evolutionary advantage, with less chance of nutrients being leached out of a system already limited in resources. However, it might also tend to

perpetuate or intensify the level of nutrient deficiency on a site (Vitousek, 1982).

I did not find any significant differences in retranslocation when nitrogen concentrations were increased on a nitrogen-deficient site. The kind of response Stachurski and Zimka measured between their fertile and less fertile habitats may require more significant differences in nutrient availability than the treatments for this study were able to provide. They also measured two different sites, not the same site under different treatments.

Another hypothesis concerning retranslocation is that on sites of lower fertility, plants are adapted to low nutrient levels and thus have less flexibility to change strategies of nutrient acquisition. Chapin (1981), who defends this idea suggests that species adapted to low nutrient conditions have less fluctuation in their range of resorbence before leaf abscission. This would limit the ability of these plants to show 'immediate' changes in retranslocation when more nutrients are supplied.

The highly fertile site conditions on the Oregon coast, where nutrient retranslocation levels were different with treatment, could perhaps have been sufficient to evolve a more flexible and sensitive nutrient cycling system in the Douglas-fir. However the decrease in N and P retranslocation on the red alder plot occurred where foliar nitrogen values remained unchanged from the control and where foliar P concentrations had decreased. Although the fertility of the site may have increased the possibility of nutrient retranslocation, the

adaptation behind the changes is not clear. The amount of retranslocation of nutrients may depend on the relative mobility of different cell components, i.e., amino acids vs. cell wall protein. The level of mobile N, P or S in the older foliage could change over short periods of time and prevent the percent nutrient resorption value from being consistent. More consideration of the forms in which nutrients are present in the foliage may improve the sensitivity of foliage analysis, as well as that of the litter (van den Driessche, 1981).

Stachurski and Zimka, and Chapin all emphasize the effect that habitat fertility can have on the process of resorption. For my study, retranslocation measurements did not show a response to treatments which could be easily predicted on the basis of either proposed hypothesis. It could be that the treatments (the presence of alder, the level of N fertilization) were not intense enough to produce a response, or that there are other factors involved which were not considered. The ability of litter nutrient concentrations to provide useful information about nutrient cycling will become more evident as the edaphic factors which influence retranslocation are determined.

sampling

The difficulty of obtaining representative samples is a contributing factor to most environmental analyses. The techniques of analysis are sometimes limited in their usefulness because of this. The degree of variability found in forested ecosystems also reduces

the usefulness of foliar analysis in forestry as compared with the in agricultural systems where the technique was developed (Leyton, 1958).

In my study the three soil nitrogen analyses showed similar changes with treatment. One exception to this trend was the lack of significantly higher extractable nitrogen on the Sitka alder plot. Previous research has shown variable success in getting parallel responses from mineralizable, total and extractable soil nitrogen tests (Black, 1965). These tests sample portions of the same nitrogen pool, but how each portion is affected by different treatments may be site dependent. The nitrogen 'availability' index chosen, (mineralizable-N) which ignores the nitrate-N availability, and the pattern of sampling, which paired each soil sample with a Douglas-fir on each plot, could both introduce further sources of variability.

Foliar nutrition can also be difficult to analyze because of the bias introduced when selecting the foliage age, crown position, or season to sample (van den Driessche, 1978). Three-year-old foliage was sampled in the early fall for this study, to allow the effects of nutrient retranslocation before leaf abscission to be most evident. Comparison of the third year foliage results with one-year old and current foliage is possible for this study only with Vancouver Island samples (Table X). One-year-old foliage on this site responded similarly to three-year-old foliage by showing a significantly higher nitrogen concentration in the presence of both alder species. Phosphorus did not differ significantly in the first year foliage, but it

Summary Table IX

Showing treated plot measurements whose values significantly ($p < .05$) differed from their controls either higher (\uparrow) or lower (\downarrow)

SITE	SOIL N (mineraliz.)	FOLIAR N	LITTER N	FOLIAR P%	RETRANS. N P	N:P RATIO (foliage)	GROWTH EFFICIENCY
Oregon Coast conifer/red alder				\downarrow	\downarrow \downarrow		
S. Wash. Cascades conifer/red alder	\uparrow	\uparrow	\uparrow	\downarrow		\uparrow	\uparrow
Vancouver Island conifer/red alder	\uparrow	\uparrow	\uparrow	\downarrow		\uparrow	\uparrow
conifer/Sitka alder	\uparrow	*		\downarrow		\uparrow	\uparrow
Oregon Cascades thinned					\uparrow		\uparrow
thinned, fert.					\downarrow		\uparrow

*This same measurement made by Binkley (1982) showed a significant increase.

Table X

Current and 1-yr-old Douglas-fir foliar nutrient concentrations from Vancouver Island

Element	Conifer Only		Red alder/Conifer Mix		Sitka al/ Conifer Mix	
	current foliage g/m ²	1-yr-old foliage g/m ²	current foliage g/m ²	1-yr-old foliage g/m ²	current foliage g/m ²	1-yr-old foliage g/m ²
N	4.1	3.2	5.8	4.1*	4.1	5.8*
P	.74	.41	.47*	.28	.42*	.45
S	.19	.32	.16	.28	.18	.21*

* Indicates values which differ significantly from the control plot at $p \leq .05$

was significantly lower in the current foliage on both alder plots. Sulfur was significantly lower on the Sitka plot in the one-year foliage. Different foliage ages appear to be more sensitive to changes in different nutrients, as other research indicates (Lavender and Carmichael, 1966).

summary table

Summary Table IX displays the major differences in nutrient concentrations and ratios which occurred with treatment over the sites. The pattern of differences show the influence of site quality and the effect of time. Only the Southern Washington and Vancouver Island sites show evidence of a significant change or improvement in the concentration and balance of nutrients in the presence of alder.

Trends in the entire data set suggest there are important relationships between these measurements and stemwood production. The amount of stemwood production shows response to changes in nutrient balance, but the level of nutrient deficiency, the intensity of treatment and the amount of time since application prevent some between-plot differences from being significant. At any one time our point estimates from parts of the nutrient cycle can provide only limited information. Identifying trends and thresholds of response are important, but this does not help create quick, predictive tests for identifying site response to silvicultural treatments.

Considering a balance of nutrients, rather than individual nutrient concentrations may represent a useful alternative by recog-

nizing the importance of nutrient interactions on plant nutrition. The litter values and their ability to reflect foliar changes may be another source of information, perhaps more easily sampled, and possibly better able to reflect a plant's efficiency at using nutrients (Vitousek, 1982).

Growth Efficiency

An estimate of the efficiency with which biomass is produced is used to indicate health or vigor of a tree. Growth efficiency can be measured on all or just one portion of the total biomass (i.e. stemwood). It can also be based on the 'cost' in terms of nutrient use (Vitousek, 1982) as well as the amount of foliage which is supported (Waring, 1980).

Brix (1981a) determined the influence of fertilization on stemwood biomass production, and divided the response to treatment into two influencing factors; efficiency of the foliage in producing photosynthate, and the amount of leaf area being supported to carry out photosynthesis. His research indicates that fertilization can cause an immediate increase in the efficiency of the leaves, but that the more significant long term benefit of the fertilization is through increased foliage. Increasing the foliage increases the amount of photosynthate which can be produced, and after other priority demands are met, this can lead to an increase in allocation to stemwood biomass.

Stemwood production per unit of leaf area (Waring, 1980) and the biomass production per unit of litter nutrient (Vitousek, 1982) are two additional methods of evaluating growth efficiency. Stemwood diameter is easily measured, and was used in this study to look at tree growth in response to site treatment. A modification of Vitousek's nutrient use efficiency index was also applied to these study sites to look at another aspect of nitrogen nutrition.

stemwood production efficiency

Forest management practices are intended to improve wood production. Increased stemwood growth is seen as an indication that other higher priority demands for photosynthate (maintenance, foliage production, etc.) are being met and thus the vigor of the tree is high (Waring et al., 1980). A higher Douglas-fir wood production efficiency was measured in the presence of alder on Vancouver Island and in southern Washington, (Figure 3) where soil nitrogen and foliar nitrogen were higher (except for the Sitka alder plot). Wood production was also higher with alder on the Oregon Cascades site, although differences in nutrient concentration were not significant. Stand canopy leaf area was also higher on these treatment plots (Table XI) so in spite of more shading, the Douglas-fir improved their wood production. On the Oregon Coast site wood production was not significantly changed with treatment in spite of higher total canopy leaf area. Increasing shade (increasing leaf area) on a site which

Table XI

Total stand and individual Douglas-fir leaf area

	<u>Individual Douglas-fir</u>	<u>Total Stand</u>
<u>Oregon Coast</u> ¹	m ²	m ² /m ²
Conifer only	122	12.0
Conifer/red alder	187*	20.0
<u>S. Washington Cascades</u>		
Conifer only	25	4.8
Conifer/red alder	75*	10.1
<u>Vancouver Island</u>		
Conifer only	32*	5.1
Conifer/red alder	13	7.4
Conifer/Sitka alder	36	9.9
<u>Oregon Cascades</u>		
Control plot	37	2.6
Thinned	40	1.5
Thinned & fert.	68*	2.0

* Indicates values which differ significantly from the control plot at $p \leq .05$

¹ On the Oregon coast site, there are several types of conifers present. Only Douglas-fir were cored for determination of sapwood area. In order to calculate a rough estimate of total canopy leaf area, the average sapwood area of the measured Douglas-fir was used, together with the stocking of each species. A different sapwood conversion ratio was determined for each individual tree species (Waring, 1980)

is fully occupied should result in a decrease in wood growth efficiency (Figure 1) (Waring, Newman and Bell, 1981). Evidence suggests, however, that improving another photosynthesis-related factor, such as light, moisture or nutrients (through fertilizing, thinning, or biological N-fixers) may allow the trees to allocate more photosynthate to wood production.

Stemwood production per square meter of foliage could increase either due to a change in the photosynthetic efficiency of the foliage, or to a change in the pattern of photosynthate allocation. Although the initial response to treatment may have been a change in foliar efficiency, as Brix (1981) points out, this is probably not the long term benefit. Increased nitrogen availability and uptake creates the potential for improving carbohydrate production in plants (through carboxylating enzymes), and a linear relationship is found between wood production and foliar nitrogen concentration on a per hectare basis (Figure 4). However this correlation is almost entirely accounted for by the equally linear relationship between stemwood production and leaf area per hectare (also Figure 4). Individual trees increased in leaf area with treatment (Table XI), and this increased the photosynthate production. On all sites except on the Oregon coast, this resulted in increased allocation to stemwood production, and a higher wood production/m² value (Figure 3). At the Oregon coast, although total canopy shade on the mixed conifer/alder plot was higher, Douglas-fir photosynthate allocation to stemwood was maintained.

Although leaf area accounts for the linearity of Figure 4 this does not prevent the foliar nitrogen concentration data from providing some information on stand response to treatment. Brix (1981), in a study which measured several levels of fertilization, estimated the percent of foliar nitrogen above which there is either no change, or a decrease in photosynthetic efficiency of Douglas-fir foliage. His value of about 1.73% nitrogen as an 'optimum' concentration for total biomass growth efficiency is slightly higher than the foliar nitrogen concentration (changed to a percent value) in this study, above which wood production efficiency appears to level off (Figure 5).

The Oregon Coast conifer-only plot foliar nitrogen was above what Brix suggests as 'optimum' (Figure 5) and the conifer-alder plot shows no significant change in foliar nitrogen, and no significant change in wood production efficiency. The Douglas-fir were not able to benefit from higher foliar nitrogen levels and although they increased their canopy leaf area.

On the Southern Washington Cascades site nitrogen in the foliage on the conifer-only plot was below the 'optimum' value of 1.73% maximum. The conifer-alder plot foliar nitrogen concentration was closer to this maximum, and it was significantly higher in wood production efficiency as well as leaf area. At Vancouver Island, the conifer-only plot nitrogen concentrations were closer to the hypothesized optimum. The Douglas-fir on the red alder-conifer plot, with significantly lower leaf area, seem to have used a portion of the increased nitrogen to increase stemwood production, but with

competition for light, water, etc., resources were probably too limited to increase it any more, in spite of the foliar nitrogen.

The Sitka alder plot, with higher Douglas-fir leaf area than the red alder plot, doesn't show a significant difference in foliar nitrogen from the control, but its wood production efficiency is significantly higher. Binkley (1982) measured higher wood production and higher foliar nitrogen values on this plot. As previously mentioned, he collected his foliage samples in a different year, at a slightly different time of the year, and in addition he used a slightly different digestion to determine nitrogen contents. Higher foliar nitrogen values would be expected on this site in the presence of Sitka alder, but as was previously discussed, the time elapsed since treatment can play an important part in determining whether nutrient levels reflect changes when sampled. If, as Binkley measured, these Douglas-fir did reach higher foliar nitrogen concentrations, with less crown competition from the Sitka alder (it has a more shrubby growth form than red alder), the fir may have been able to translate even a small change in nitrogen availability into increased allocation of photosynthate to the stem. The efficiency with which a tree makes use of its nutrients may be just as important as nutrient concentration, economically as well as physiologically, in determining the benefits of increasing nutrient availability to improve tree growth.

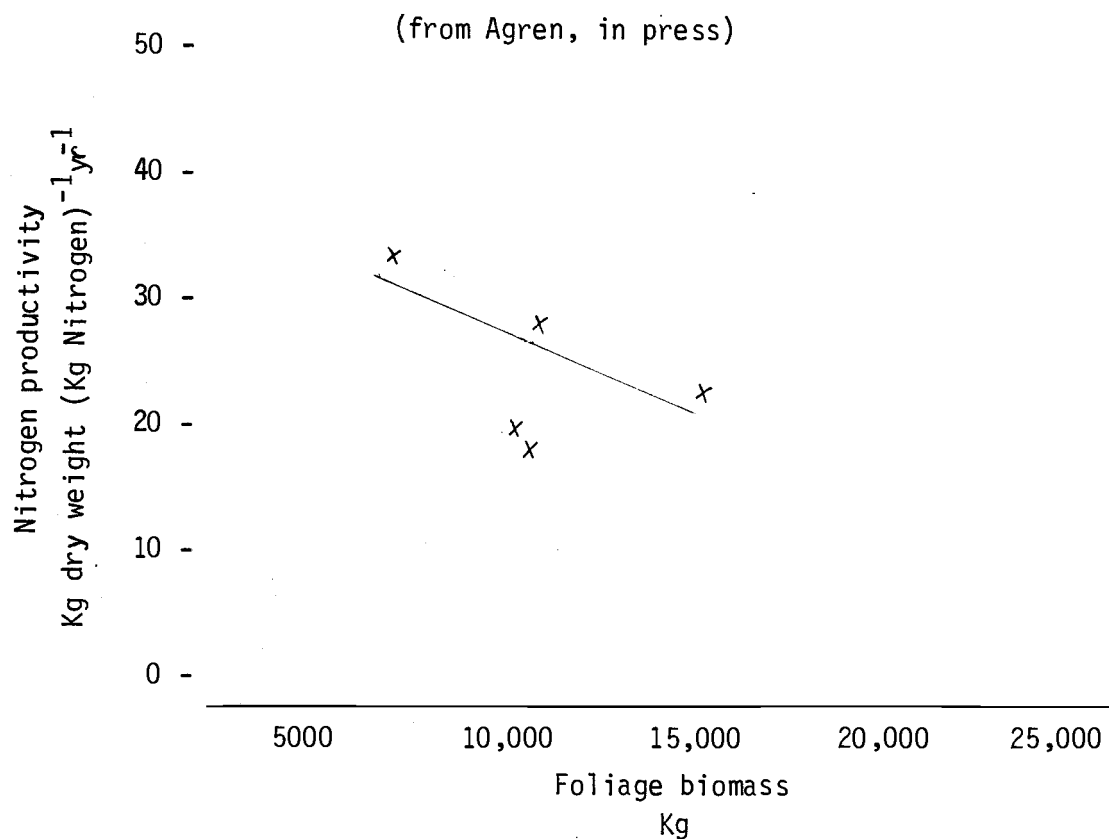
nutrient use efficiency

Another method of measuring efficiency of growth is through the pattern of nutrient use. This type of index has been calculated by Agren (1983) to help interpret responses to changes in nitrogen availability. His index looks at the amount of foliage biomass produced per unit of N in the foliage. He found that nitrogen use efficiency decreases as foliar biomass increases, and believes this is due to a reduction in irradiance as the canopy becomes more dense (Figure 8).

Vitousek (1982) also created a productivity, or an efficiency index based on several different nutrients, including nitrogen. He suggests that the nutritional status of the litter may be a better indicator of growth efficiency than the foliage, since it represents the amount of nutrients which are 'lost' from the tree. His data for dry weight of litterfall was plotted against the concentration of nitrogen in the litter to yield a positive linear correlation; (Figure 9), showing that, similar to Agren's results with foliage, more litter dry mass is produced when the dry weight/unit of N is low (Figure 10).

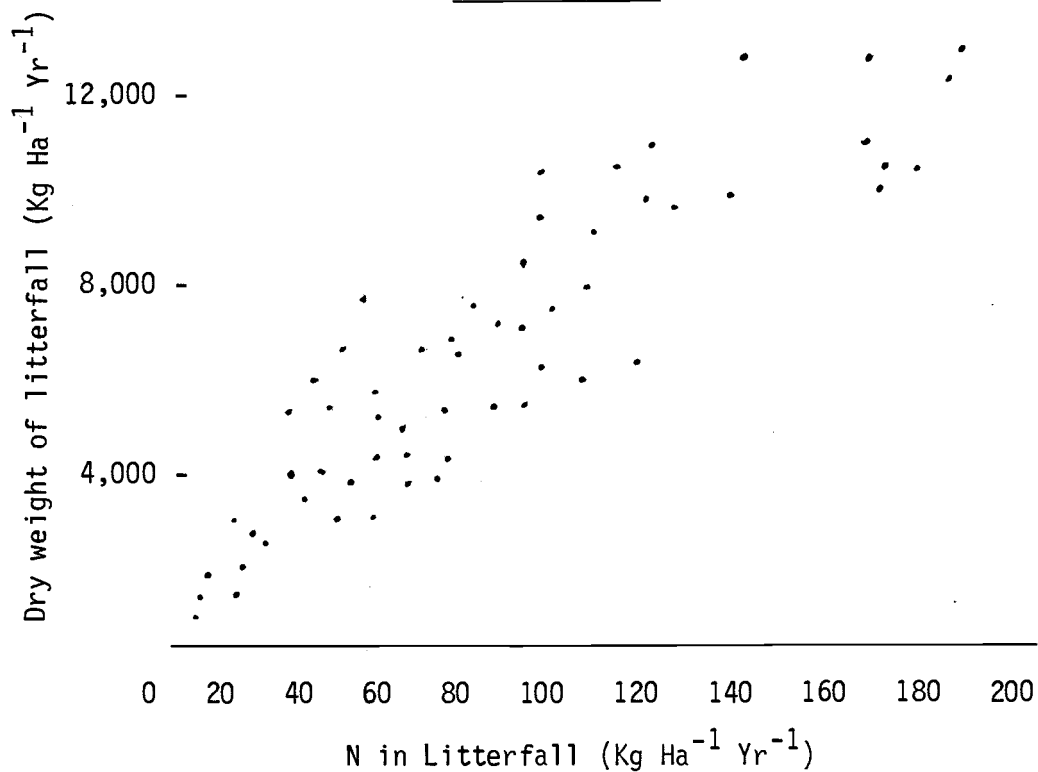
For this study a nitrogen use efficiency index was estimated based on the amount of N 'used' (present in the foliage) to produce a unit of stemwood biomass. My data in Figure 11 shows the somewhat negative correlation between the amount of nitrogen per m^2 of foliage, and the wood produced per unit of nitrogen in the foliage.

Figure 8

Nitrogen productivity vs. foliar biomass

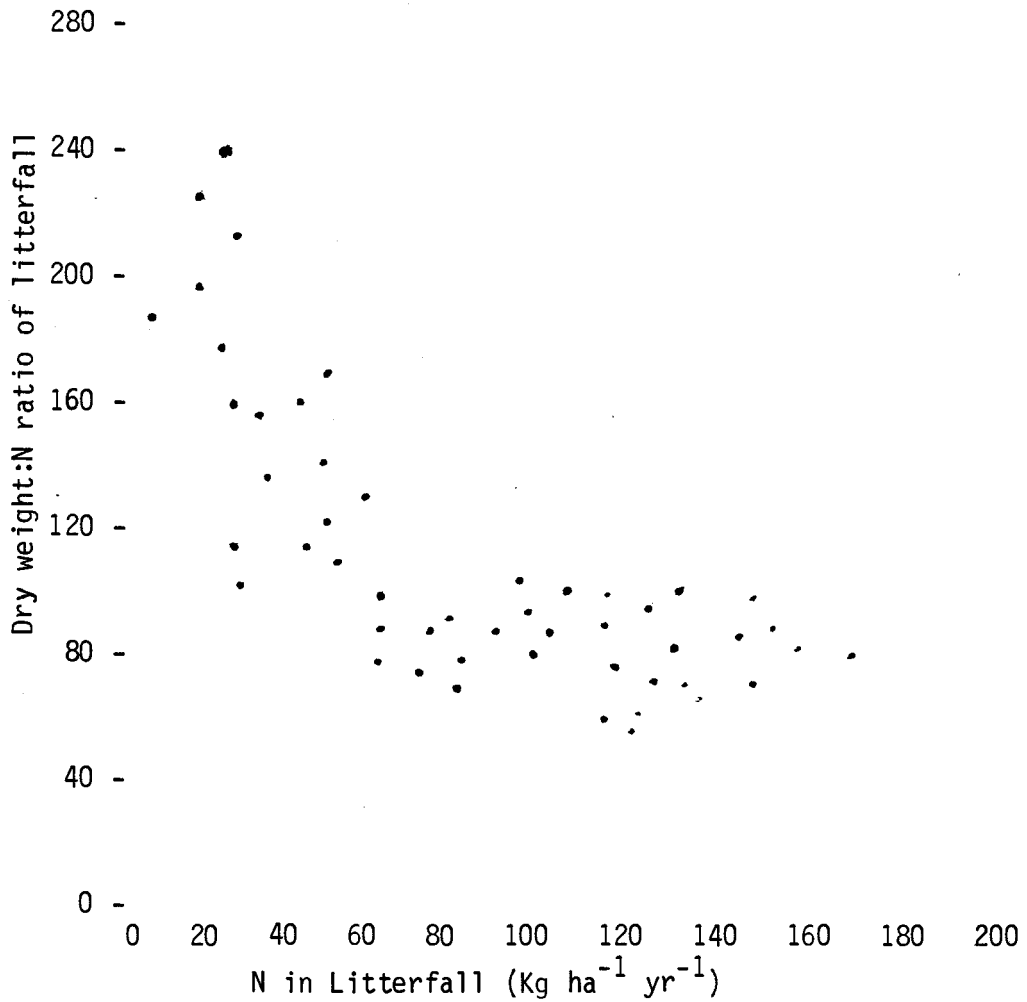
Agren (in press) calculated nitrogen productivity as the amount of wood produced per unit of N in the wood per year. His data, collected from different sites, show a decrease in nitrogen productivity as foliar biomass increases.

Figure 9
Vitousek's data showing
litterfall dry weight per year vs. nitrogen content
of litterfall



Vitousek (1982) plotted litterfall data from a series of coniferous, temperate, deciduous, evergreen and mediterranean type forest ecosystems. Also included are data points from temperate zone sites dominated by symbiotic nitrogen fixers.

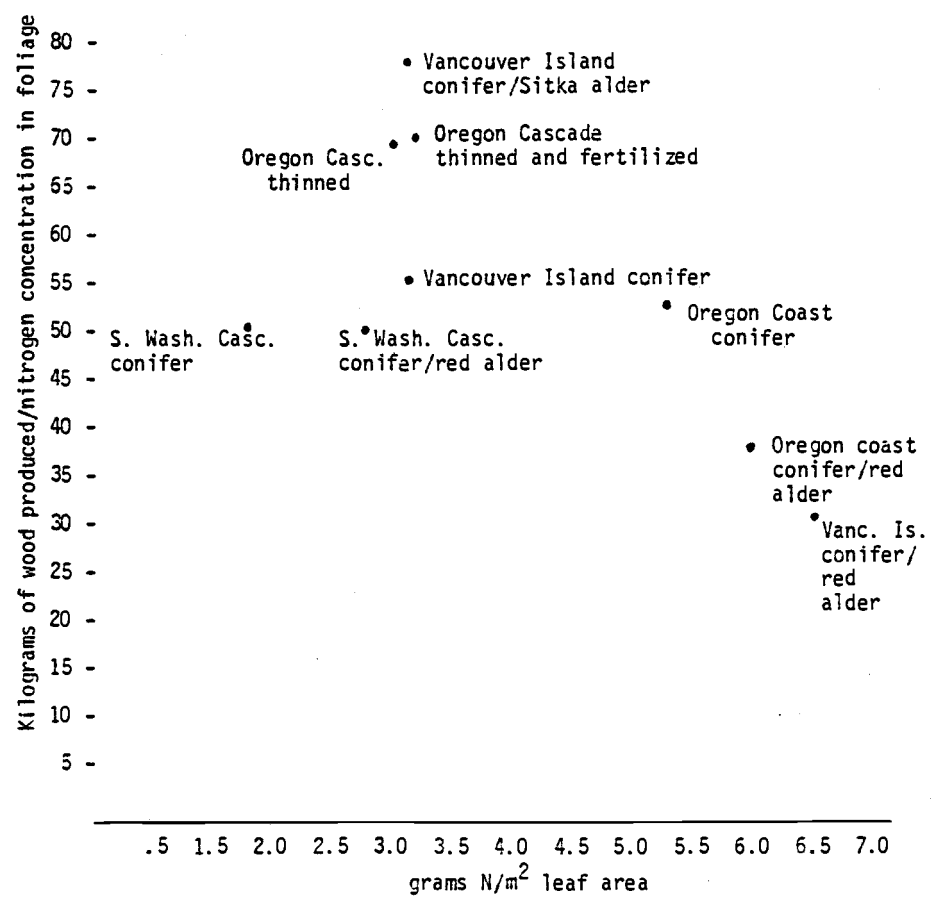
Figure 10
Vitousek's data showing
the relationship between the amount of nitrogen in the litterfall
and the dry mass to nitrogen ratio of that litterfall



Vitousek (1982) also determined a nutrient use efficiency index based on the dry weight of litter produced per unit of nitrogen in the litter. Data points as in Figure 9.

Figure 11

Stemwood production per unit of N in the foliage
vs. nitrogen in Douglas-fir foliage per m²



The trees which increase their canopy leaf area with more nitrogen in this leaf area produce more wood (Figure 4), more wood per unit leaf area (Figure 3) but some produce less wood per unit of N (Figure 11). The plots which increased their foliar nitrogen concentration beyond what was probably necessary for photosynthetic efficiency show a smaller nutrient use efficiency index value, or a smaller increase (Oregon Coast). Where site treatment increased foliar nitrogen to near 'optimum' values, the use efficiency index was elevated (S. Washington Cascades).

Agren points out that at the low and high nitrogen concentrations, his nitrogen productivity index can assume a constant value. There no doubt are limits to the range of conditions over which any of these productivity indices is sensitive. They all provide information for interpreting responses to changes in nitrogen availability in terms of tree growth. The form of the productivity index used in this study is simple and has been kept simple to keep it as a convenient tool rather than a cumbersome analysis. The precision of the information it provides is limited by the laboratory techniques, variable sampling media and assumed mathematical relationships on which it is based. Further research will determine whether this approach will be applicable under other environmental conditions, with other nutrients and other tree species.

CHAPTER VII

SUMMARY AND CONCLUSION

Many factors influence the amount of stemwood growth which occurs in trees. Availability of nutrients is important, but its effect on plant growth cannot be entirely separated from moisture, temperature and light conditions. Stemwood growth may be further influenced by the ability of the plant to satisfy other growth and maintenance demands, or sinks with greater priority.

A direct relationship between changes in nutrient content/uptake and stemwood growth is more evident on sites where nutrients are more limiting than moisture, light, etc. Time and intensity of site treatment can also influence the ability of plant nutrient analyses to reflect a particular growth pattern.

The balance of several nutrients represents an alternative to single element determinations. It can allow the possibility of nutrient interaction to be detected, and acknowledges the importance of more than just one element to plant growth. Litter nutrient concentrations may represent another sensitive indication of plant nutrition. But the relative priority of nutrient deficiencies over other influencing factors on different sites remains a controlling factor on plant growth response, and limits the ability of nutrient variables (concentrations, ratios) to predict or diagnose site response to treatment. Identifying the right time to sample, and the

most appropriate plant tissue to analyze may improve results, but these decisions depend on the type of site treatment and site quality involved.

Calculating leaf area on the basis of sapwood area (as done by Waring, et al., 1980) acknowledges the relationship between conducting, active stemwood tissue, and the leaves which depend on the nutrients, water, etc. which this tissue supplies. The amount of leaf area supported in turn, then plays a major role in determining the supply of photosynthate allocated to plant growth, including stemwood production. The efficiency with which leaves produce photosynthate may be increased with certain silvicultural treatments, but the major long term effect is probably to increase the amount of leaf area and the amount of stemwood growth which is supported.

The ability of trees to translate improved nutrient availability into greater leaf area is then complicated by the other site-dependent factors, like light and moisture. Because of this it can be difficult to evaluate the effect of site treatments on stemwood production efficiency per unit leaf area. An alternative efficiency index may be to look at the amount of nutrients used to produce the woody biomass. A particular site treatment may increase nutrient utilization to a greater extent than it increases stemwood production, or the reverse may be true. This is an important consideration when evaluating the costs and benefits of certain silvicultural practices.

BIBLIOGRAPHY

- Agren, G. Nitrogen productivity of some conifers. Paper accepted by Canadian Journal of Forest Research.
- Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical analysis of ecological materials. John Wiley and Sons, N.Y., N.Y. 564 pp.
- Barnes, R. L. 1981. An allocation and optimization approach to tree growth modeling; concepts and application to nitrogen economy. Unpublished manuscript prepared for seminar; Center for Quantitative Science in Forestry, Fisheries and Wildlife. University of Washington, Seattle, Washington.
- Binkley, D. 1982. Case studies of red alder and sitka alder in Douglas-fir plantations: nitrogen fixation and ecosystem production. PhD Thesis, Oregon State University. 114 pp.
- Binkley, D., P. Matson, and J. D. Lousier. 1982. An evaluation of the effects of red alder and Sitka alder on availability of nitrogen, phosphorus and sulfur. MacMillan Bloedel, Ltd. Nanaimo, B.C.
- Black, C. A. 1965. Methods of soil analysis: Part 2, Chemical and microbiological properties. American Society of Agronomy, Inc., publisher. Madison, Wisconsin, USA.
- Brix, H. 1981a. Effects of nitrogen fertilizer source and application rates on foliar nitrogen concentration, photosynthesis and growth of Douglas-fir. Can. J. For. Res. Vol. 11 pp 77.
- Brix, H. 1981b. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can J. For. Res. Vol. II, pp. 502-511.
- Chapin, F. S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.
- Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Res. paper 41, Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, OR.
- Gordon, J. C., C. T. Wheeler and D. A. Perry. 1979. Symbiotic N-fixation in the management of temperate forests: proceedings of a workshop held April 2-5. Forest Research Laboratory, Oregon State University, Corvallis, Oregon. 501 pp.

- Grier, C. C., and R. H. Waring. 1974. Conifer foliage mass related to sapwood area. *For. Sci.* 20:205-206.
- Ingestad, T. 1966. Experiments on constant internal nutrient concentration. *Proc. XVII Int. Hort. Congr.* Aug. 1966.
- Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 770pp.
- Johnson, D. W., N. T. Edwards, and D. E. Todd. 1980. Nitrogen mineralization, immobilization and nitrification following urea fertilization of a forest soil under field and laboratory conditions. *Soil. Sci. Soc. Am. J.*, Vol. 44.
- Keeney, D. 1980. Prediction of soil nitrogen availability in forest ecosystems; a literature review. *For. Sci.*, Vol. 36; 1. 159-171 pp.
- Lavender, D. P. and R. L. Carmichael. 1966. Effect of three variables on mineral concentration in Douglas-fir needles. *For. Sci.* 12(4):441-446.
- Leaf, A. L. 1973. Plant analysis as an aid in fertilizing forests. In: Soil testing and plant analyses. Ed.: L. M. Walsh and J. D. Benton. pp. 427-454. *Soil Sci. Soc. of Am., Inc. Madison, Wisc., USA*.
- Leyton, L. 1958. The relationship between the growth and mineral nutrition of conifers. pp. 323-345. In: The physiology of forest trees. Ed.: K. V. Thimmann. Ronald Press, N. Y.
- Linder, S. and T. Ingestad. 1977. Ecophysiological experiments under limiting and non-limiting conditions of mineral nutrition in field and laboratory. In: A centennial celebration of C.P. Thunberg's visit to Japan, pp. 69-76. Tokyo.
- Miller, H. G., J. D. Miller, and J. M. Cooper. 1981. Optimum foliar nitrogen concentration in pine and its change with stand age. *Can. J. For. Res.*, Vol. 11:765-777.
- Miller, J. D., and D. Murray. 1977. The effects of red alder on growth of Douglas-fir. In: Utilization and management of alder Proceedings of a symposium held at Ocean Shores, WA, D. G. Brigs, D. S. DeBell, and W. A. Atkinson, compilers.
- Miller, R. and R. Tarrant. 1983. Long term growth response to ammonium nitrate fertilizer. *For. Sci.*, Vol. 29 (1), p. 127-137.

- Newman, K. 1979. Sapwood basal area as an estimator of individual tree growth. M.S. thesis, School of Forestry, Oregon State University, Corvallis, Oregon, U.S., 65 p.
- Smith, P. F., W. Reuther, A. W. Specht, and G. Henelar. 1958. Effect of differential N, K and Mg supply to young Valencia orange trees in sand culture on mineral composition, especially of leaves and fibrous roots. *Plant Physiol.* 29(1):349-351.
- Snedecor, G. W., and W. G. Cochran. 1980. Statistical Methods. Iowa State University Press. Ames, Iowa, U.S.A.
- Stachurski, A. and J. R. Zimka. 1975. Methods of studying forest ecosystems: leaf area, leaf production and withdrawal of nutrients from leaves of trees. *Ekologia Polska* 23 (4) pp. 637-648.
- Tabatabai, M. A. and J. M. Bremner. 1972. Distribution of total available sulfur in selected soils and soil profiles. *Agron. J.* 64:40-44.
- Trappe, J. M. 1979. Mycorrhiza-nodule host interrelationship in symbiotic nitrogen fixation: a quest in need of questers. In: *Symbiotic nitrogen-fixation in the management of temperate forests: proceedings of a workshop held April 2-5*. Forest Research Laboratory, Oregon State University, Corvallis, OR, 501 p.
- Turner, J. 1977. Effect of nitrogen availability on N-cycling in a Douglas-fir stand. *For. Sci.*, Vol. 23(3), pp. 307-316.
- Turner, J., D. W. Johnson and M. J. Lambert. 19 . Sulfur cycling in a Douglas-fir forest and its modification by nitrogen application *Acta Oecologica Pecol. Plant.*, Vol. 1 (15), No. 1, pp. 27-35.
- van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. *Bot. Rev.* July-Sept. 1974, Vol. 40 (3), pp.347-394.
- van den Driessche, R. 19 . Estimating potential response to fertilizer based on tree tissue and litter analysis. In: *Forest fertilization conference and symposium*. S. P. Gessell, R. M. Kenady, and W. A. Atkinson, editors.
- Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. *Am. Naturalist* Vol. 119 (4), pp. 553-572.

- Vogt, D. and R. L. Edmonds. 1982. Nitrate and ammonium levels in relation to site quality in Douglas-fir soil and litter. N.W. Science 56 (2), pp. 83-89.
- Waring, R. H., W. G. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci., Vol. 26 (1), pp. 112-117.
- Waring, R. H., K. Newman and J. Bell. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. Forestry, Vol. 54 (2), pp. 129-137.