AN ABSTRACT OF THE THESIS OF

Bernard Thomas Bormann for the degree of Doctor of Philosophy

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Title: Stand Density in Young Red Alder Plantations: Production,

Photosynthate Partitioning, Nitrogen Fixation, and an Optimal

Spacing Model

Abstract approved: _Signature redacted for privacy._

John C. Gordon

Dimension analysis, acetylene reduction and canopy structure measurements were used to evaluate the relationship between density and dry weight production, nitrogen (N_2) fixation and photosynthate partitioning (as indicated by dimension analysis) in 5-year-old red alder (Alnus rubra Bong.) plantations established at three initial spacings. Density strongly affected most dry weight components and N_2 fixation. Low density stands (9 x 9 ft initial spacing) had the highest values per tree for all measured weight, volume, and surface area components and N_2 fixation. Mid-density stands (4 x 6 ft initial spacing) had the highest per unit area values for leaf weight, canopy volume, branch weight and surface area, root and stump weight, net branch production, aboveground net production and N_2 fixation. The highest density stands (2 x 4 ft initial spacing) had the highest values per unit area of the variables:wood volume, bole and total aboveground dry weight and net bole production. Nodule weight per unit area was approximately equal in the mid- and high-density stands averaging 146 kg/ha. Correlation coefficients for dimension analysis

were high (eg. leaf wt.: r = 0.952; branch wt.: r = 0.963; bole wt.: r = 0.995; root wt.: r = 0.971; nodule wt.: r = 0.931). Stand density, as an independent variable, improved the correlation coefficient for many of these equations, indicating that density strongly affected photosynthate partitioning.

The high correlation between per tree N_2 fixation and leaf weight (r = 0.892) supports the hypothesis of Gordon and Wheeler (1978). Leaf weight and N_2 fixation per unit area (averaging 2.15 metric tons/ha and 70 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively), however, were not highly correlated suggesting that less photosynthate was allocated to nodules in high density stands. Component net production to total aboveground net production ratios changed with density also suggesting that density strongly affects photosynthate allocation patterns. Crown structure related well to observed allocation patterns: a higher proportion of leaves close to the ground corresponded to higher N_2 fixation rates per tree.

An optimal spacing model is proposed that may eventually aid in economic evaluation of alder plantation designs and rotations. The model predicts optimal spacings for wood products (pulpwood, sawlogs) and uses variables that are physiologically tied to competition-linked processes (live-crown-ratio, crown volume and leaf density). Estimated spacing for sawlogs is similar to that predicted in the literature but projected pulpwood spacing appears too close. Assumed live-crown-ratio seems to have the greatest effect on projected spacing but crown shape and leaf density are also important. It may be possible to modify the model to produce estimates of alder yield

under management. Thus, it could aid in an economic evaluation of alder investment opportunities. Additional research, especially on live-crown-ratios, is needed before this model can be widely used.

Stand Density in Young Red Alder Plantations:

Production, Photosynthate Partitioning, Nitrogen Fixation, and

an Optimal Initial Spacing Model

by

Bernard Thomas Bormann

A THESIS

submitted to

Oregon State University

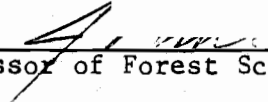in partial fulfillment of
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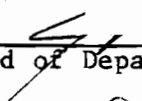Doctor of Philosophy

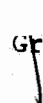Completed April 20, 1981

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ACKNOWLEDGMENTS

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STAND DENSITY IN YOUNG RED ALDER PLANTATIONS: PRODUCTION,

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CHAPTER I. EFFECT OF SPACING ON DRY WEIGHT, NET PRODUCTION,
NITROGEN FIXATION AND PHOTOSYNTHATE PARTITIONING
IN YOUNG RED ALDER PLANTATIONS

INTRODUCTION

Red alder (_Alnus rubra_ Bong.) is being considered for use in

intensive forest management in the Pacific Northwest primarily because

of its rapid growth and its ability to fix atmospheric dinitrogen

(N_2). These attributes are appealing in these days of rising N fer-

tilizer costs and interest rates and a projected downturn in timber

supply. Tarrant _et al_. (in preparation) state that alder-Douglas-fir

(_Pseudotsuga menziesii_ (Mirb.) Franco) crop rotation schemes are at

present less profitable than Douglas-fir monoculture with N fertilizer

but that a relatively small increase in alder yields could make crop

rotation as profitable as monoculture. Thus, ways to maximize alder

yield and N_2 fixation could raise alder management above the profit-

ability threshold.

Growth characteristics of red alder fit well with the ideal plant

specifications for maximum fiber yield (Gordon 1979). In fact, red

alder is thought to be one of the fastest growing species in the tem-

perate zone with one individual reported to have grown 9.75 m high and

15.5 cm dbh in 5 years from seed (Smith 1972). Biomass production in

naturally-established stands has been reported as high as 29 metric

tons/ha[1]. Although several allometric equations have been developed
for red alder (Zavitkovski and Stevens 1972; Smith[1]), growth charac-
teristics have not been fully analyzed and we know very little about
alder production in managed natural stands or plantations.

Red alder forms a symbiosis with an _Actinomycete_ (_Frankia_ sp.)
capable of N_2 fixation. Rates of N_2 fixation, like growth are high;
values reported from ecosystem N accretion studies in naturally-
established stands include 85 kg N ha^{-1}yr^{-1} (Cole et al. 1978), 100 kg
N ha^{-1}yr^{-1} (Bormann and DeBell in press) and 320 kg N ha^{-1}yr^{-1} (Newton
et al. 1968). Tripp et al. (1979), using acetylene reduction tech-
niques, estimated N_2 fixation to be 62 kg N ha^{-1}yr^{-1} in a red alder
plantation on coal spoils. Such rates rank high among in vivo
measurements of legume and non-legume species capable of symbiotic
N_2 fixation.

N_2 fixation is an energy expensive process with as many as 18.8 g
glucose needed to fix 1 g N (Gutschick 1978). Thus, a stand fixing
100 kg N ha^{-1}yr^{-1} would seem to sacrifice 1.9 metric tons ha^{-1}yr^{-1} of
potential dry weight yield. The analysis is complicated, however,
because additional nitrogen may cause additional dry weight production
through increases in leaf area and efficiency. Thus, the actual
sacrifice is probably less than the calculated one on most sites. The
energy cost of N_2 fixation, however, is a real factor in comparing the

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[1]N. J. Smith. 1977. Estimates of aboveground biomass, net primary
production and energy flows in 8 to 10 year old red alder (Alnus
rubra Bong.) ecosystems. Master's Thesis, Univ. of British Columbia.

dry weight yields of species capable of symbiotic N_2 fixation with those species which are not.

It is unclear how red alder can grow rapidly and at the same time fix large amounts of N_2. It is clear, however, from work with clonal material, that increased photosynthesis leads to greater nitrogenase activity in alder (Gordon and Wheeler 1978). This is supported by indirect evidence from legume studies where increased nitrogenase activity has been correlated with increased CO_2 concentration (Havelka and Hardy 1977), supplemental light (Lawn and Brun 1974) and grafting of 2 tops on 1 root (Streeter 1974); whereas darkening quickly led to reduced enzyme activity (Ching et al. 1975). Diurnal fluctuations in acetylene reduction corresponded to fluctuations in photosynthate production in greenhouse-grown alder seedlings (Wheeler and Lawrie 1976). In one of the very few studies relating nitrogen fixation to stand density, planting density of soybean was shown to strongly influence acetylene reduction (Hardy et al. 1972). The lowest densities showed the highest rates of acetylene reduction per plant and the maximum rate per hectare was observed at an intermediate density. Sprent and Bradford (1977) report a somewhat similar pattern for Vicia faba. Unfortunately, no data on dry weight production are included in these papers. To most effectively predict the response of N_2 fixation to stand density, the process of photosynthate allocation to nodules must be understood. Allocation patterns are undoubtedly affected by competition between individual plant parts. Classical growth analyses contend that growth, when defined as aboveground net dry weight production or leaf area index, will increase with increasing density

until a plateau is reached over a wide range of densities and then decrease only in very dense stands (mar Möller et al. 1954). Belowground production, N_2 fixation being of primary interest to us, is not thought to follow the aboveground net production response to density because of a reduction of photosynthate allocated to roots as density increases. Several hypotheses have been advanced to explain this poorly-observed phenomenon. Wareing and Patrick (1975) argue that lower leaves support root growth and that if there is strong competition between root and shoot, the shoot system has the advantage. Under "competitional stress," lower leaves are more shaded and thus less photosynthate should be transported downward. In small cottonwood trees, lower, older leaves translocate photosynthetically-fixed ^{14}C primarily downward (Larson and Gordon 1969). Thus, canopy structure may be linked to photosynthate allocation. It can also be argued that trees in dense stands have a reduced amount of foliage relative to their respiratory surface and thus have less photosynthate "left over" for use by the belowground system.

In the present study, growth and N_2 fixation were estimated in 5-year-old red alder plantations to analyze the effects of density on aboveground growth, N_2 fixation and structure of individuals (average tree basis) and the stand (per unit area basis). The relationship of photosynthesis (as estimated by dry weight production) and N_2 fixation (as estimated by acetylene reduction) was also explored to test hypothesis set forth by Gordon and Wheeler (1978) that N_2 fixation will be positively correlated with leaf area index in a field study. In addition, relationships between aboveground and belowground

dynamics were explored to obtain evidence for or against the possible effect of photosynthate partitioning between the root and shoot system on N_2 fixation.

MATERIALS AND METHODS

Study Site

A 30-acre tract in northwestern Oregon owned by International Paper Company was selected for this study because of the presence of a red alder spacing trial. The tract is located south of Rainier, Oregon, approximately 10 km southwest of the town of Apiary (T6N, R3W, Sec. 17) at about 550 m elevation. The area was previously covered by forest consisting primarily of Douglas-fir with some western hemlock and red alder, and is high site II (Douglas-fir) with north and east facing slopes ranging from 0-45%[1]. Soils in the alder spacing trials are of the Tolke Series: a stone-free, silt loam formed on mixed loess, volcanic ash, and colluvium overlying silt-stone. Portions of the tract were heavily infested with root rot (Phellinus sp.) and cooperative research between the U.S. Forest Service PNW, International Paper Co., Longview Fiber Co., Crown Zellerbach Corp., and Oregon State University is being conducted on this site to determine the effect of alder on Phellinus populations.

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[1]All information on the study site is from U.S. Forest Service PNW Study Plan No. EN 75-1, E. Hansen and E. E. Nelson. 1972. On file. Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon 97330.

As part of this study, the forest was cleared in 1973 and the slash was broadcast-burned in the spring of 1974. Red alder seedlings were planted in the winter 1974/75. In two areas of the 30-acre tract, spacing trials were established with a randomized block design in conjunction with the root rot study (U.S. Forest Service, Crown Zellerbach Corp., cooperators). Established alder spacings included 2 x 4', 4 x 4', 4 x 6', 6 x 6', and 9 x 9'. Due to high mortality in some plots, apparently caused by freeze damage, only the 2 x 4', 4 x 6' and 9 x 9'[1] spacing have adequate survival in replicate plots. Permanent measurement plots were established as part of this study.

Methodology

Dimension analysis. Dimension analysis techniques developed by Sprugel[2] were used to estimate aboveground and belowground biomass and aboveground productivity and structural characteristics during August, 1979. These involve relating easy- and difficult-to-measure parametes on sample trees using regression analysis. First, a stratified-random procedure, based on breast height diameter (dbh), was used to select 18 sample trees (one from each of the three diameter classes in each density replicate stand). Selected dbh's were based on preliminary survey and represented a "best estimate" of mean dbh plus and minus one standard deviation. Selected trees were

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[1]English units will be used to describe spacing dimensions since seedlings were planted in this fashion.

[2]D. Sprugel. 1973. Vegetation dynamics of wave-regenerated high-altitude fir forests. Ph.D. Thesis, Yale University. 287 p.

felled; five branches were randomly sampled (at intervals equal to crown length divided by six) to collect data on branch components and characteristics (Table I). Diameter at the base and distance from the terminal were measured on all remaining branches so that multiple regression equations using these variables as part of a set of predictor-variables could be used to estimate component weights and characteristics for the entire sample tree. The bole was cut into 50 cm sections and measurements were taken (Table I). Dimensional estimates based on branch equations were then combined with bole data to develop a new set of equations relating dbh to component weights and tree characteristics. Diameter at breast height was then measured on a large percentage of trees within each stand (9 x 9': 100%, n = 60; 4 x 6': 100%, n = 100; 2 x 4': 50%, n = 140), and entered into regression equations to estimate mean tree values of component weight and dimensional characteristics. Heights were measured on trees in the permanent measurement plots as well as on the dimension analysis sample trees.

Roots and nodules were excavated in entirety on eight of the 18 sampled trees. Fourteen additional trees, randomly selected in 1980, were also sampled for root and nodule biomass. Separate equations were developed relating dbh to root, nodule and stump weight.

Nitrogenase activity. The acetylene reduction technique of McNabb and Geist (1979) was used, in which acetylene is used as an internal standard and only one volumetric transfer of gas is made for each sample in the field. Once a month during 1979 growing season ten nodule samples were taken for acetylene-reduction measurements from at

TABLE I. MEASUREMENTS ON SAMPLE TREES.

Component	Variables
Branches	Diameter at the base
	Distance from the terminal
	Effective length
	Actual length
	Number of leaves
	Number of growth sites
	Leaf dry weight
	Current branch growth dry weight
	Old branch growth dry weight
	Branch surface area
Bole	Breast height diameter (dbh)
	Diameter at stump height
	Diameter in/outside bark every 50 cm up bole
	Radial increment every 50 cm
	Age every 50 cm
	Terminal length
	Total height
	Bole dry weight (total fresh weight and subsample dry weight)
Roots	Root dry weight
	Nodule dry weight

least two roots from each of two trees along a randomly located transect in each density replicate stand. Fifty ml glass incubation jars with rubber stoppers containing a 6 mm glass tube with a rubber septum were filled approximately one-third full with nodules, injected with acetylene (10% by volume), and allowed to incubate in the soil for one hour; sample sequencing was randomized. Gas samples were stored in vacutainers and analyzed several months later using a Hewlett Packard HP5830A gas chromatograph with a 6 mm Poropak N column and flame ionization detector. N_2 was used as the carrier gas. A conversion ratio of 3:1 (acetylene to N_2) was used to calculate specific activity of nitrogenase for N_2. Seasonal average specific activity values were multiplied by hours in the growing season and by average per tree and per unit area nodule weight obtained from the dimension analysis to estimate annual per tree and per unit area N_2 fixation rates.

Leaf area and distribution of foliage in the canopy. Leaf area index (LAI) was estimated in 1978 using a line transect method in addition to being measured using the dimension analysis procedure in 1979. A line was attached to a pole and dropped, with the aid of a plumb-bob, and held over each of 20 randomly placed stakes within a randomly selected quadrat (with dimensions of 3.0 x 2.4 m, 3.7 x 1.8 m and 2.7 x 2.7 m in the 2 x 4', 4 x 6' and 9 x 9' spacings, respectively) in each density replicate stand. The average number of leaves that touched the line was used to estimate LAI. The transect line was marked every 0.5 m so that height interval could be tallied for each touching leaf.

RESULTS AND DISCUSSION

Dimension Analysis

Dimensional characteristics of red alder. Stand and average tree dimensions are strongly affected by stand density (Table II). Tree diameter, crown volume, live-crown-ratio, wood volume, branch surface area and number of growth sites are greatest in trees growing in the most open (9 x 9' initial spacing) stands. Mortality and per unit area values of wood volume, bole and total surface area and growth sites are greatest in the densest (2 x 4' initial spacing) stands. Intermediate density (4 x 6' initial spacing) stands had the highest canopy volume and per unit area branch surface area. Crown shape slope and leaf density were relatively unaffected by density.

Component and total dry weight. Dry weight of all average individual tree components and totals were highest in the most open (9 x 9') stands as expected. Leaf, branch, root and stump weight per unit area peaked in intermediate (4 x 6') stands, but bole, aboveground and total weight per unit area were greatest in the most dense (2 x 4') stands (Table III). The proportion of bole and branch dry weight to aboveground dry weight mirror one another as functions of density, both for individual trees and stand values (Figure 1). Nodule dry weight per unit area was similar in 2 x 4' and 4 x 6' stands, averaging 146 kg/ha but was much less in 9 x 9' stands (62 kg/ha).

TABLE II. AVERAGE TREE AND PER UNIT AREA TREE DIMENSIONS FOR STANDS OF THREE DIFFERENT INITIAL SPACINGS.

Tree Dimension	Average Tree Value			Per Unit Area (ha) Value		
	9 x 9 ft	4 x 6 ft	2 x 4 ft	9 x 9 ft	4 x 6 ft	2 x 4 ft
Density (trees/ha)	--	--	--	1,240	4,068	10,091
Mortality (%)	--	--	--	6.80	9.30	25.00
Growing space (m^2)	8.06	2.46	0.99	--	--	--
Diameter at breast height (cm)	5.42	4.55	3.40	--	--	--
Tree height (m)	5.44	6.11	5.50	--	--	--
Crown shape (intercept)[1]	0.335	0.424	0.193	--	--	--
Crown shape (slope)[1]	0.265	0.241	0.303	--	--	--
Crown, canopy volume (m^3)[2]	28.84	14.04	4.97	35,760	56,960	49,680
Leaf density (g/m^3)[3]	49.50	42.66	45.49	49.50	42.66	45.49
Live-crown ratio[4]	0.75	0.64	0.55	--	--	--
Wood volume (m^3)	0.0097	0.0067	0.0035	11.9	27.4	35.3
Branch surface area (m^2)	3.22	1.91	0.71	4,020	7,771	7,030
Bole surface area (m^2)	0.681	0.570	0.426	846	2,320	4,271
Total surface area (m^2)	3.90	2.48	1.13	4,866	10,091	11,304
Growth sites (#; # x 10^6)[5]	2,405	1,365	650	3.01	5.55	6.48

[1]As determined from a linear regression on branch effective length and distance from terminal.

[2]See Figure 12.

[3]Equals leaf weight (g) divided by crown volume (m^3).

[4]Determined as one minus (the height where 90% of leaves occur above this point divided by the stand average tree height; see Figure 8).

[5]Growth sites are buds that formed some vegetative growth during the season of measurement.

TABLE III. COMPONENT DRY WEIGHT ON AN AVERAGE TREE AND PER UNIT AREA BASIS.

Component Dry Weight	Average Tree Value			Per Unit Area (ha) Value		
(g/tree; metric tons/ha)	9 x 9 ft	4 x 6 ft	2 x 4 ft	9 x 9 ft	4 x 6 ft	2 x 4 ft
Leaf weight	1,430	595	224	1.79	2.43	2.23
Branch weight	5,561	2,612	945	6.97	10.63	9.82
Bole weight	3,965	2,763	1,428	4.96	11.24	14.25
Aboveground weight (total)	10,965	5,970	2,597	13.72	24.30	26.30
Root weight	919	533	133	1.15	2.17	1.29
Stump weight[1]	739	519	230	0.92	2.11	1.99
Nodule weight	49	36	15	0.06	0.15	0.15
Belowground weight (total)	1,707	1,088	378	2.13	4.43	3.43
Total weight	12,663	7,058	2,975	15.85	28.73	29.73

[1]Stump is defined as bole at mineral soil to 10 cm and includes first 10 cm of each root.
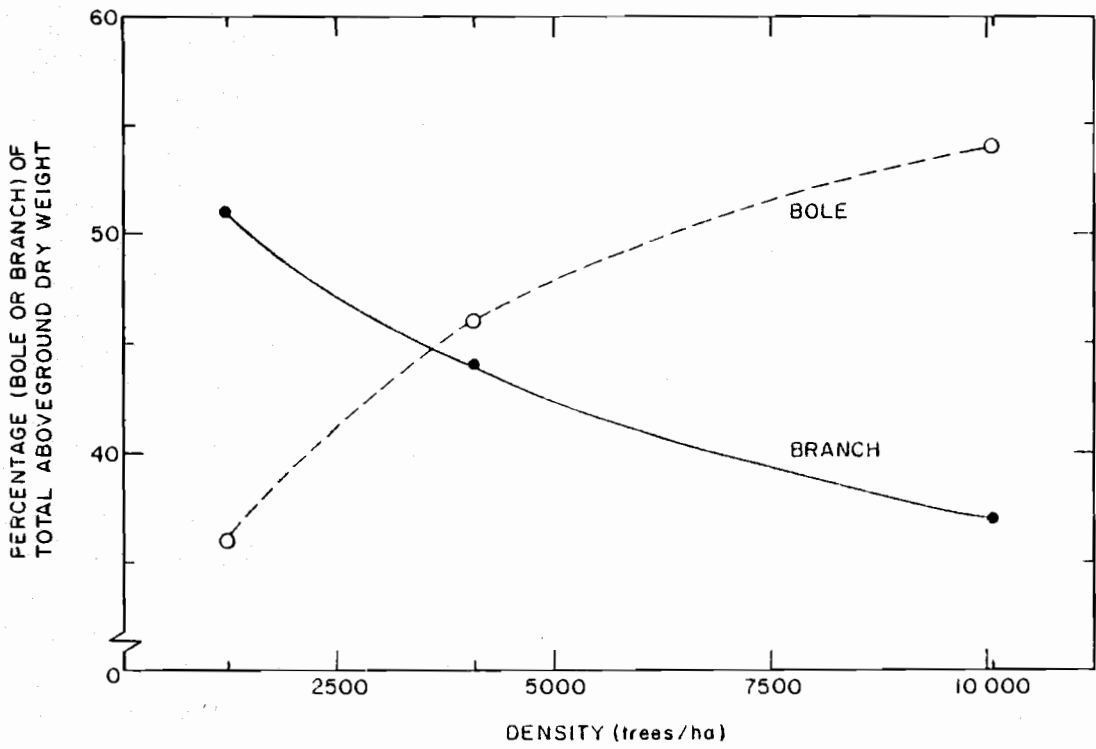
Figure 1. Bole and branch dry weight as a percentage of total aboveground dry weight.

These values for nodule biomass are much lower than the 444 kg/ha estimated by Akkermans[1] and other estimates of 450 kg/ha[2].

Net production and production indices. Branch and aboveground net production per unit area peaked in the intermediate density stands as did glucose-equivalent-N_2 fixation (Table IV). Net production of bole per unit area, however, was greatest in 2 x 4' stands. Aboveground net production and leaf weight per unit area appear to approximate the mar Möller et al. (1954) hypothesis of a range of stand densities over which net production doesn't vary (Figure 2). The slight drop-off of these variables in the high density stands may indicate that they fall in the excessive density range.

The maximum aboveground net production (13.3 metric tons$\cdot$ha$^{-1}\cdot$yr^{-1}) is low compared to natural alder stands measured by Smith[3] in British Columbia (29 metric tons$\cdot$ha$^{-1}\cdot$yr^{-1}) but mid-range compared with cool-temperate zone estimates of 9.0-15.0 metric tons$\cdot$ha$^{-1}\cdot$yr^{-1} (Westlake 1963) and 8.0-24.0 metric tons$\cdot$ha$^{-1}\cdot$yr^{-1} (Whittaker and Marks 1975). The low net production value relative to other alder estimates may indicate that this is a medium to poor alder site or that the seedlings are from an off-site source (freeze rings were commonly seen in first and second annual

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[1]A. D. L. Akkermans. 1971. Nitrogen fixation and nodulation of Alnus and Hippohae under natural conditions. Ph.D. Thesis, University of Leiden. 85 pp.

[2]B. T. Bormann. Unpublished data on file at the Forestry Research Laboratory, Oregon State University, Corvallis, Oregon.

[3]N. J. Smith. 1977. Op cit.

TABLE IV.   AVERAGE TREE AND PER UNIT AREA COMPONENT NET PRODUCTION AND PRODUCTION INDICES.

Component Net Production (g/tree; metric tons/ha)	Average Tree Value			Per Unit Area (ha) Value		
	9 x 9 ft	4 x 6 ft	2 x 4 ft	9 x 9 ft	4 x 6 ft	2 x 4 ft
Net branch production[1]	4,151	1,735	590	5.20	7.06	5.87
Net bole production	1,484	937	434	1.84	3.81	4.38
Aboveground net production (total)	7,063	3,732	1,254	8.83	13.30	12.48
Glucose-equivalent-N_2 fixation[2]	927	403	105	1.15	1.64	1.06
Total (- roots) net production[3]	7,990	3,675	1,359	9.98	14.94	13.54

Production Indices	9 x 9 ft	4 x 6 ft	2 x 4 ft
Leaf area index (m^2/m^2)[4]	2.25	3.06	2.81
Relative growth rate (%)[5]	64.50	54.80	48.30
Root-shoot ratio (%)	8.39	8.94	5.17
Foliar assimilation efficiency[6]	4.94	5.50	5.60
N_2 fixation efficiency ratio[7]	0.648	0.677	0.469

[1]Lateral branch production = old-growth branch weight x bole volume increment ratio.

[2]Assumes 18.8 g glucose needed to fix 1 g N (Gutschick 1978).

[3]Aboveground net production plus glucose-equivalent N_2 fixation.

[4]The conversion constant, 12.59 m^2/kg, from N. Smith Op cit. was used to calculate 1979 leaf area index from leaf weight per unit area (Table III).

[5]Aboveground net production divided by aboveground dry weight.

[6]Aboveground net production divided by leaf weight.

[7]Glucose-equivalent N_2 fixation divided by leaf weight.
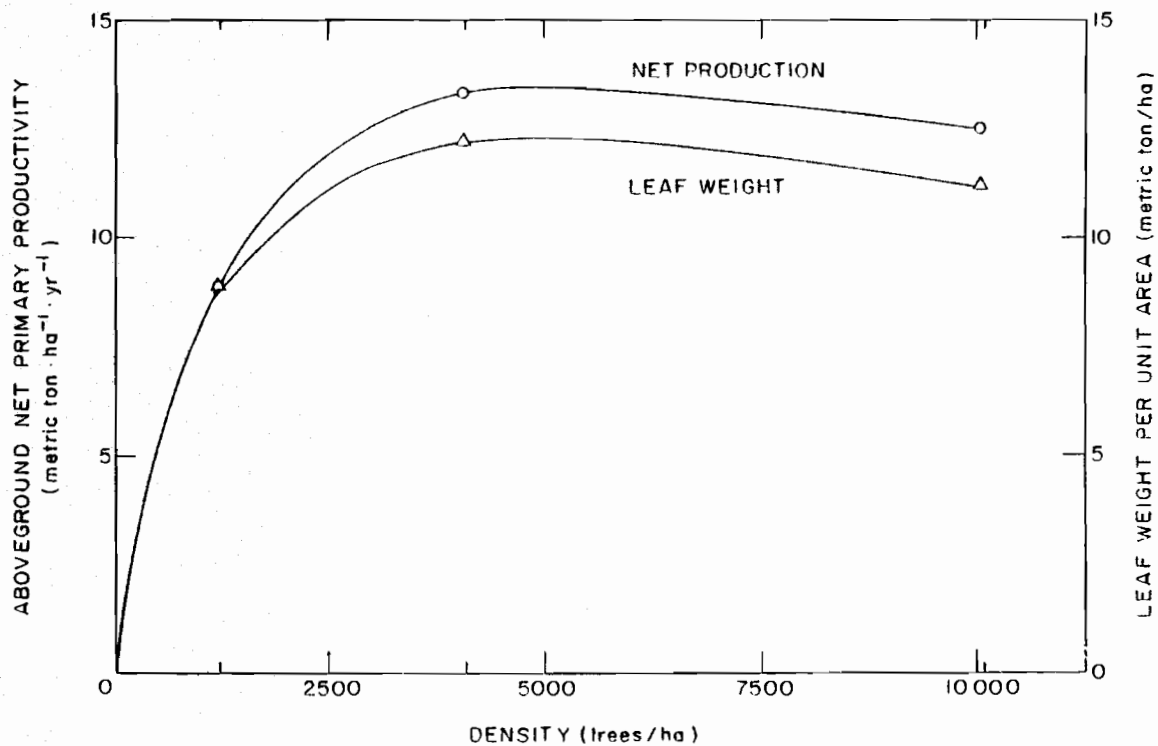
Figure 2. Aboveground net production and leaf weight per unit area as a function of density.

rings and aphids and a black leaf mold were abundant during the growing season). The relative growth rate is high in these stands, averaging 55.9%. This also may indicate that the trees have now become more adjusted to the site.

The root-shoot-ratio for these stands, averaging 7.5%, is low, lower than those reported for other early succession species[1]. This may be due to alder's ability to fix N_2 or to the late-summer (dry season) sampling date. The slight reduction in root-shoot-ratio in the 9 x 9' stands relative to 4 x 6' stands may indicate root competition with grasses, Pteridium aquilinum (L.) Kuhn and Ribes sanguinium Pursh.

Regression equations. Regression equations for dimension analyses have very high correlation coefficients and low p-values (Table V). These coefficients can be interpreted in the normal fashion because a limited range of tree sizes was sampled (three trees, approximately the mean dbh and plus and minus one standard deviation from the mean in each density-replicate stand). This is not the case in most dimension analysis studies (Whittaker and Woodwell 1968).

Multiple regression techniques were used to develop branch equations. Density and tree dbh were included in some or all branch equations to minimize unexplained variation in Y-values using the Cp criterion (Neter and Wasserman 1974). Density entered into all whole-tree equations except bole dry weight and volume and stump dry weight

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[1]P. L. Marks. 1971. Role of Prunus pensylvatica L. in the rapid revegetation of disturbed sites. Ph.D. Thesis. Yale University. 119 p.

TABLE V. REGRESSION EQUATIONS USED IN DIMENSION ANALYSIS.

Branch Equations	r	p <	n
ln(BR[1]new growth wt;g/BR)=4.822+0.6505(lnDBH)-0.4089(lnDEN)+2.504(lnDAB)-1.360(lnDFT)	0.7861	0.0001	90
ln(BR old growth wt;g/BR)=0.8682+1.560(lnDFT)+2.293(lnDAB)+0.00007212(DEN)	0.9396	0.0001	90
ln(leaf wt/BR)=5.151+2.867(lnDAB)-0.7019(lnDFT)-0.2683(lnDEN)	0.8040	0.0001	90
ln(growth sites/BR)=0.4762+1.829(lnDFT)+0.2260(lnDEN)+1.492(lnDAB)-0.8661(lnDBH)	0.9113	0.0001	90

Whole-Tree Equations			
ln(leaf wt/TR;g)=2.161+2.005(lnDBH)-0.4604(lnDEN)	0.9517	0.0001	18
ln(branch wt/TR;g)=6.573+2.709(lnDBH)-0.2854(lnDEN)	0.9628	0.0001	18
ln(branch lateral wt/TR;g)=-10.89+2.837(lnDBH)-0.0000765(DEN)	0.9283	0.0001	18
ln(branch extension wt/TR;g)=-3.081+1.998(lnDBH)-0.4865(lnDEN)	0.9485	0.0001	18
ln(bole wt/TR;g)=-6.418+2.137(lnDBH)	0.9954	0.0001	18
ln(net production bole/TR;g)=-5.874+2.083(lnDBH)-0.0000409(DEN)	0.9735	0.0001	18
ln(bole volume/TR;cc)=-5.450+2.305(lnDBH)	0.9953	0.0001	18
root weight/TR;g=579.6+31.44(DBH)^2-93.04(lnDEN)	0.9709	0.0001	22
stump weight/TR;g=-628.2+252.2(DBH)	0.8892	0.0001	22
nodule weight/TR;g=0.2484+9.321(DBH)-0.001689(DEN)	0.9313	0.0001	22
bole surface area/TR;cm^2=-1414+1260(DBH)	0.9846	0.0001	18
ln(branch surface area/TR;m^2)=6.646+2.193(lnDBH)-0.0000620(DEN)	0.9331	0.0001	18
ln(growth sites/TR;#)=-3.165+1.962(lnDBH)-0.2071(lnDEN)	0.8931	0.0001	18

[1]Abbreviations: BR   - branch
                 DBH - diameter at breast height (cm)
                 DEN - stand density (trees/ha)
                 DAB - diameter at base (cm) refers to branches
                 DET - distance from terminal (cm) refers to branches
                 TR   - tree

indicating that separate regression lines could be developed for each density when comparing dbh to all net production and some dry weight parameters. The usually large reduction in unexplained variation when density was included suggests that regression equations developed for each density would be statistically different if a sufficient number of samples had been collected. This further suggests that considerable caution should be used when applying dimension analysis techniques to physiological-level experiments in natural stands where density is highly variable and its effects are not quantified for individual sample trees.

Nitrogen fixation. Nitrogenase specific activity, averaging 14.07 μ moles $C_2H_2 \cdot g$ nodule dry weight$^{-1} \cdot hr^{-1}$ over the growing season, was negatively affected by increasing stand density (Figure 3). Differences were greatest during June and July when the highest rates were observed (Figure 4). N_2 fixation on a mean tree basis [specific activity (acetylene-reduction) x mean tree nodule weight x conversion constants] also decreased with increasing density. Density appears to affect average tree growth and N_2 fixation in a similar fashion. An increase in an individual's growing space leads to a greater leaf area and to a greater N_2 fixation rate. In fact, there is a strong linear relationship between leaf weight and N_2 fixation per tree (Figure 5), suggesting that photosynthesis is a major factor controlling N_2 fixation as suggested by Gordon and Wheeler (1976). To assess physiological interactions between photosynthesis and N_2 fixation, competition effects were incorporated by calculating estimates on a per unit area basis.
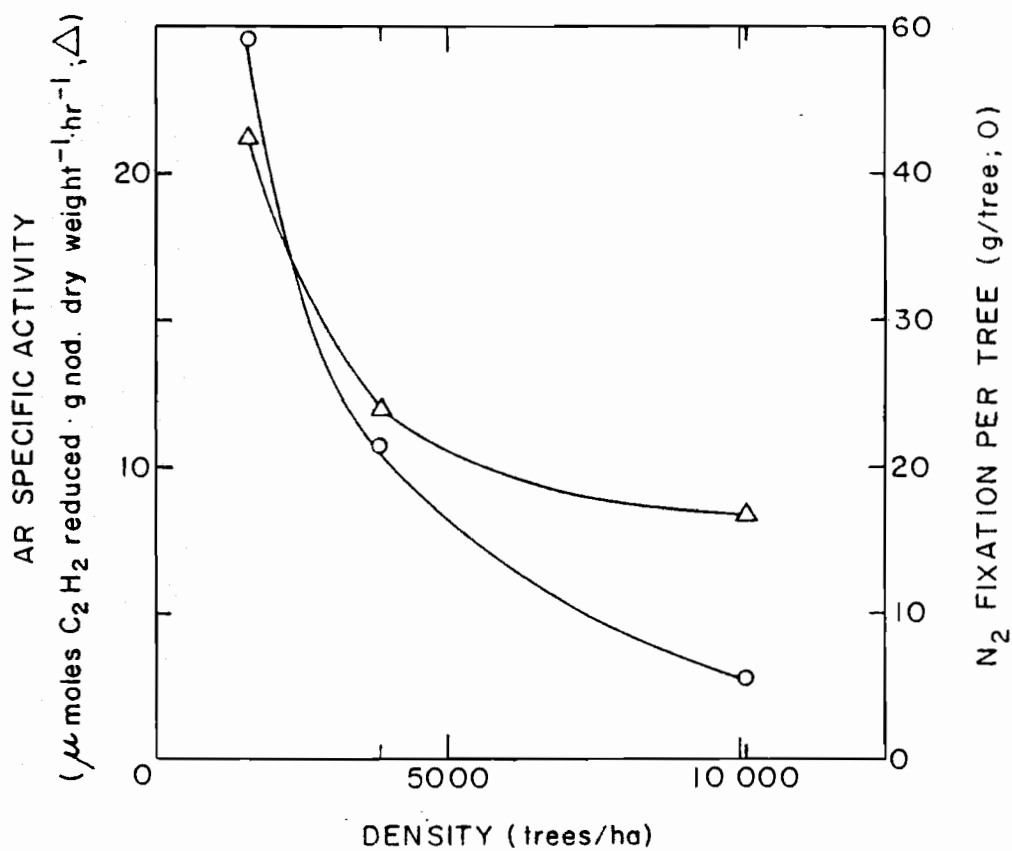
Figure 3. Nitrogenase specific activity (acetylene
reduction per gram nodule dry weight) and
N_2 fixation per tree as a function of
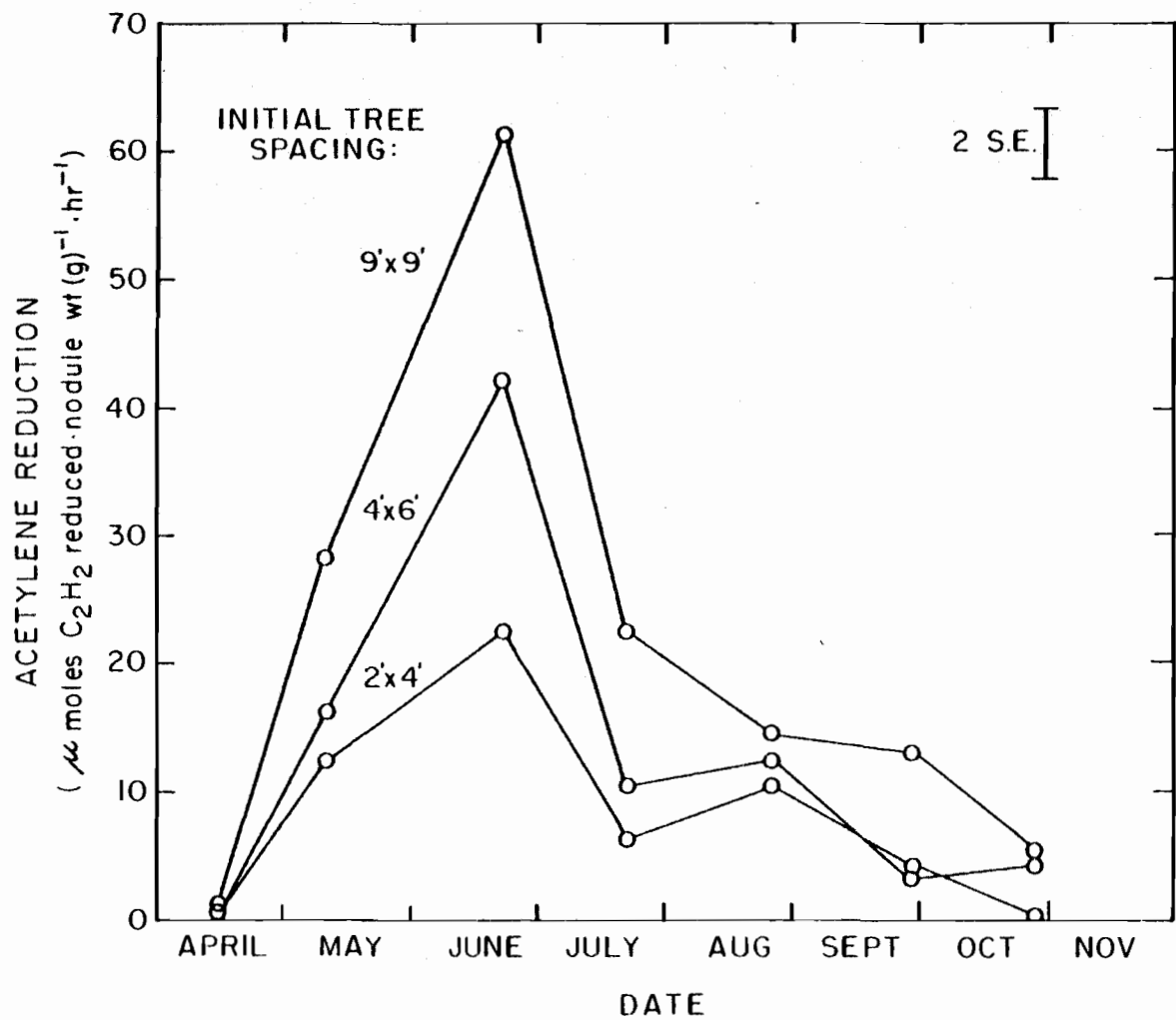density.

Figure 4. Seasonal pattern of nitrogenase specific activity (acetylene reduction) (S.E. based on ANOVA M.S.E.).
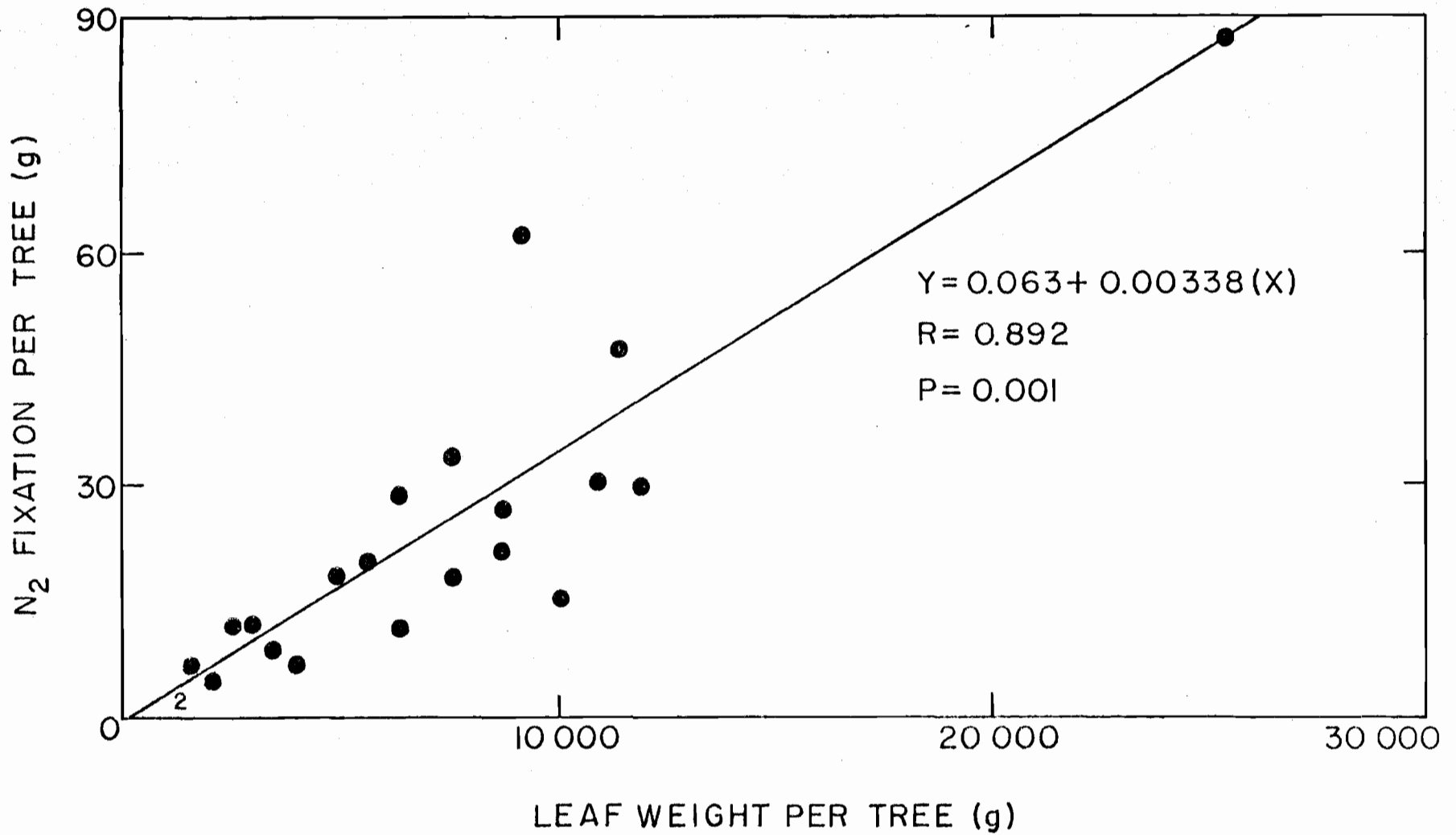
Figure 5.   The relationship between leaf weight and N_2 fixation per tree.

N_2 fixation per unit area averaged 70 kg $N \cdot ha^{-1} \cdot yr^{-1}$ for all stands. N_2 fixation in the mid-density (4 x 6') stands was 30-35% greater than either the low (9 x 9') or high (2 x 4') density stands indicating that as a function of density N_2 fixation peaks before total dry weight early on the aboveground net production and leaf weight per unit area plateaus (Figure 2, 6).

Interrelations of N_2 fixation and photosynthesis. The high density (2 x 4') stand N_2 fixation rate falls 28% below the point expected from the relationship between leaf weight per unit area and N_2 fixation in the 4 x 6' and 9 x 9' stands. The ratio of N_2 fixation to leaf weight (N_2 fixation efficiency ratio; Table IV) also demonstrates this drop off in the 2 x 4' stands. Aboveground net production closely follows leaf weight and thus the same relationship is observed. We suggest this difference is due to mechanisms of photosynthate partitioning between the root and shoot systems that favor shoots in dense stands.

Additional evidence for reduced allocation to the belowground system was observed in component net production to total aboveground net production ratios, leaf distribution patterns within the canopy and comparison of growth capacity and potential. When component net production is compared to total aboveground net production in stands of different densities, it becomes readily apparent that high density stands put a smaller proportion of their photosynthate into branch production because of reduced growing space and thus, most photosynthate goes toward bole production apparently at the expense of belowground components such as N_2 fixation (Table VI). The
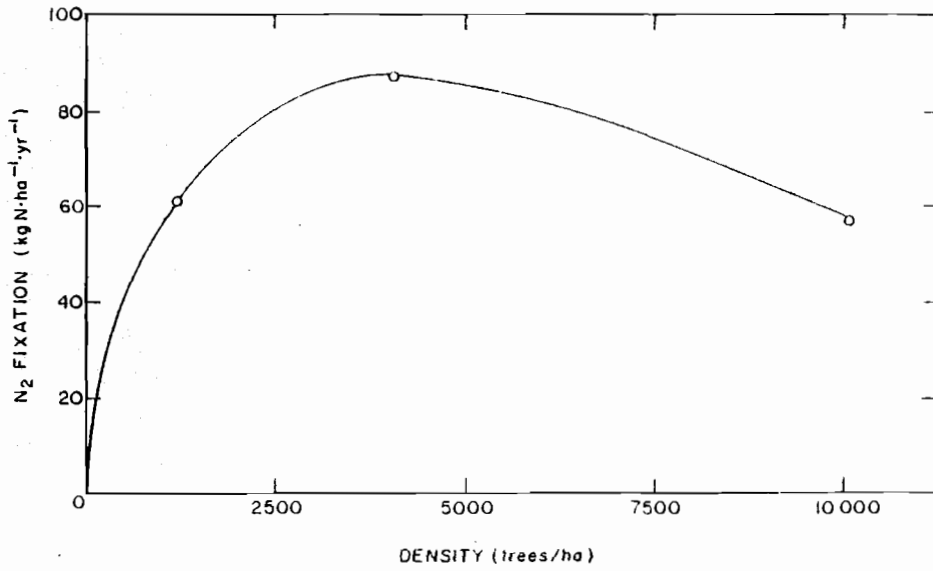
Figure 6. N_2 fixation per unit area as a function of
density.

TABLE VI. COMPONENT NET PRODUCTION TO TOTAL ABOVEGROUND NET PRODUC-
TION; % SLOPE INDICATES SINK PRIORITY (LOWEST % HAS THE
HIGHEST PRIORITY).

| Component Net Production | Percent of Total Aboveground Net Production[1] | | | % Slope[2] |
| | ---------Initial Spacing-------- | | | |
	9 x 9 ft	4 x 6 ft	2 x 4 ft	
Leaf weight	20.3	18.3	17.9	11.8
Branch extension	6.4	5.6	5.4	18.2
Branch lateral	52.5	47.4	41.6	20.8
N_2 fixation (glucose equivalent)[3]	13.0	12.3	8.5	34.6
Bole	20.8	28.6	35.1	40.7

[1]Equals component net production x 100 divided by aboveground net production.

[2]Equals maximum difference x 100 divided by maximum value.

[3]N_2 fixation (glucose equivalent) is not a component of aboveground net production but is included for comparitive purposes.

proportional distribution of photosynthate in mid-density stands (4 x 6') is nearer optimal at this age for belowground function while low density stands allocate a large proportion of photosynthate to branch production. The rate of change of these proportions with density should represent demand or "sink" ordering with greatest slope indicating a low demand priority (Figure 7). Such analyses suggest the order: leaves, branch extension growth, branch lateral growth, N_2 fixation, bole. Unfortunately, we did not measure net production of roots.

Leaf weight per unit area was not a good predictor of N_2 fixation. One possible reason for this lies in the distribution of foliage within the canopy (Figure 8). Clearly, the mean height of foliage aboveground increased with density. If the hypothesis of Wareing and Patrick (1975) and Larson and Gordon (1969), that lower leaves support root growth, is correct, crown shape and length may account for the observed photosynthate allocation patterns. Thus, the specific nitrogenase activity on a per unit area basis would be reduced in high density stands because of shedding of branches and foliage in the lower canopy which, in less dense stands, preferentially provide photosynthesis to roots.

Another means of estimating allocation patterns is to look at growth capacity and potential. Growth on a per unit area basis is limited by its capacity to capture light energy, best represented by leaf weight per unit area; while the ability to utilize photosynthate, or potential growth, can be represented by cambial surface area (we were only able to estimate bole and branch surface area and not that
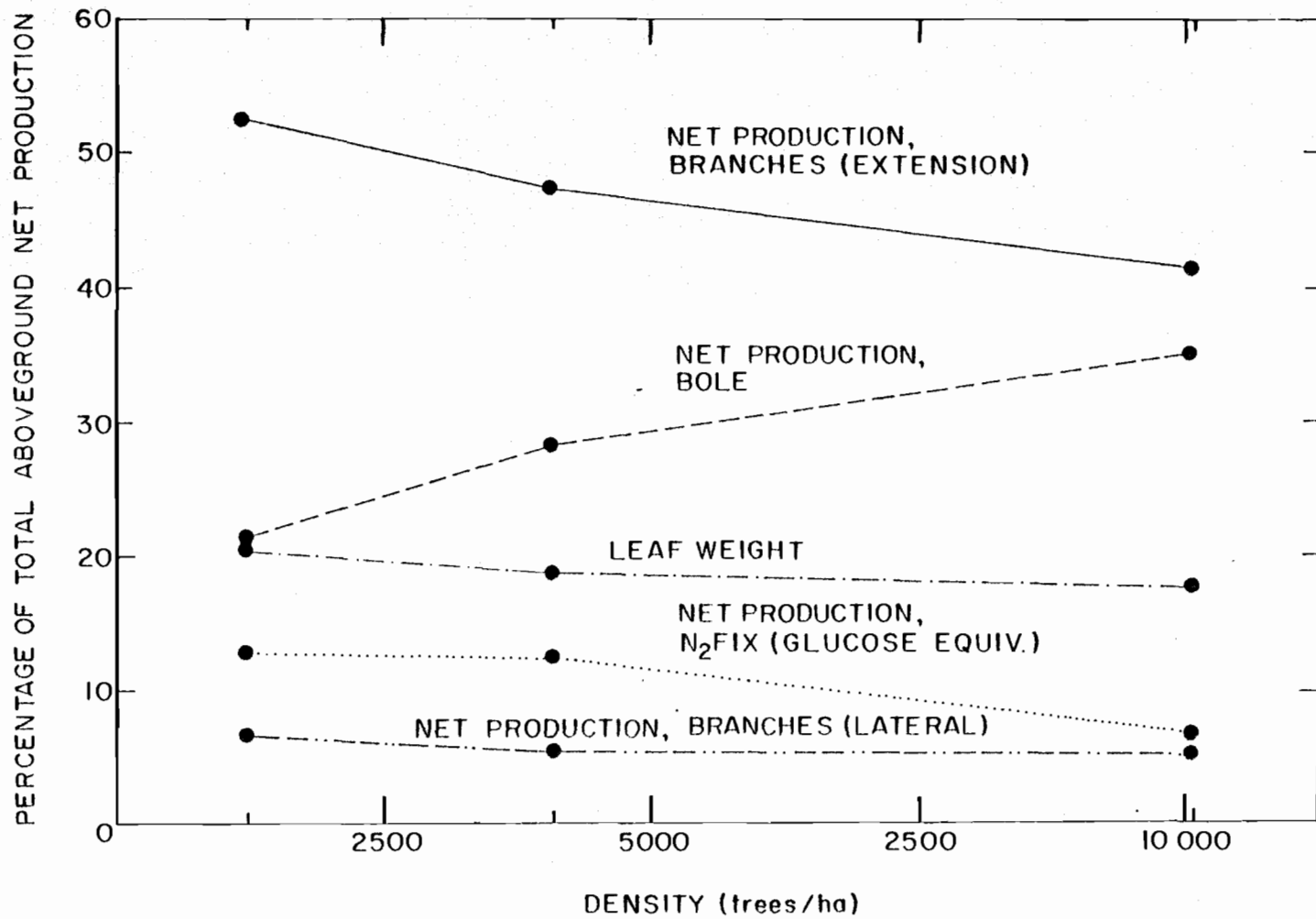
Figure 7.   Percentage of total aboveground net productivity (N_2 fixation is included for comparative purposes).
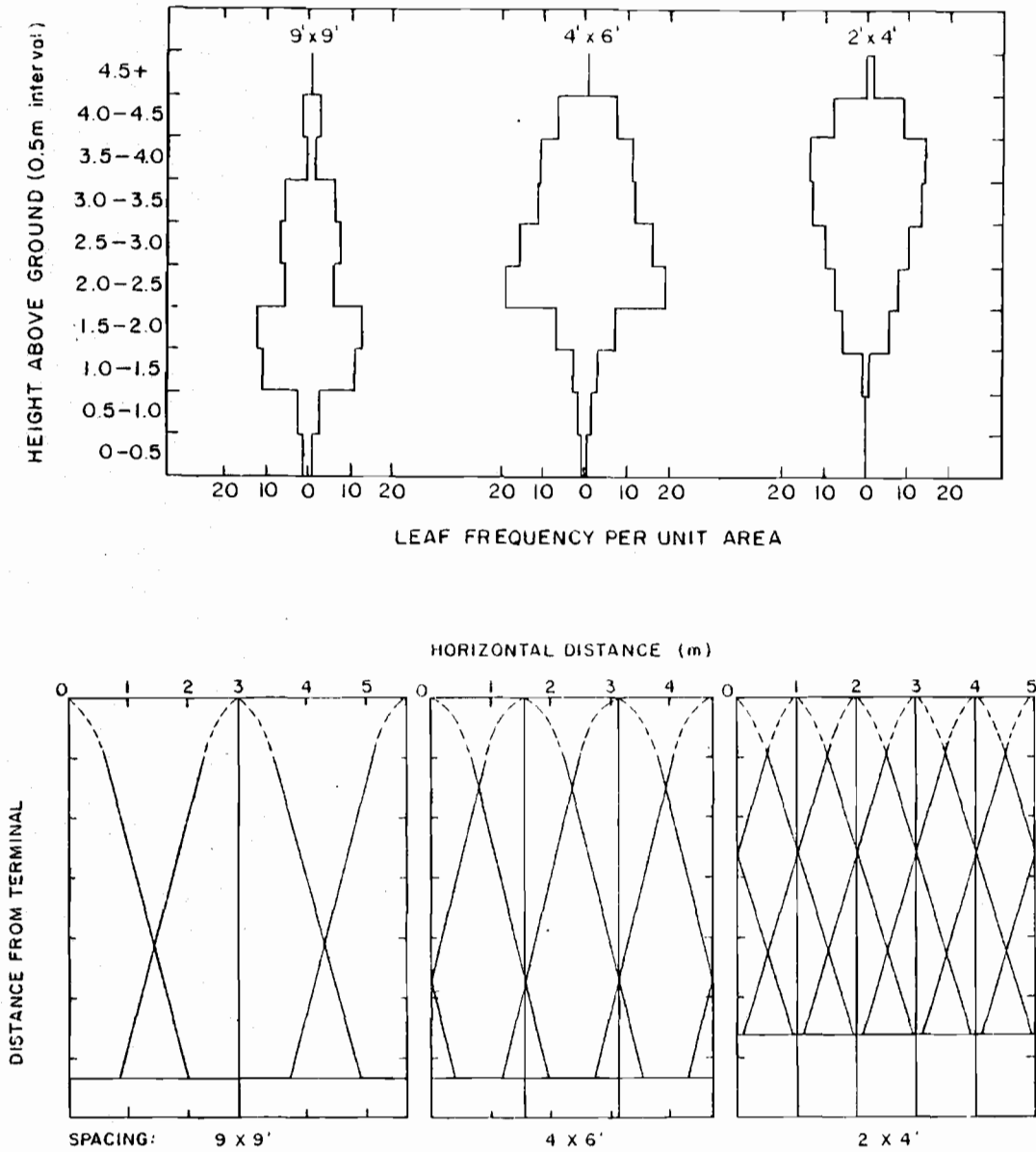
Figure 8. Leaf frequency aboveground (upper) and crown shape and degree of overlap (lower) as a function of initial spacing.

of roots) with the idea that the difference between the estimate of growth capacity and potential should represent "left-over" photosynthate that perhaps could be used for belowground functions. If the growth potential of the density where maximum potential is observed is set equal to one-half the growth capacity (units differ for capacity and potential as described above), then capacity minus potential equals 1.31, 1.44 and 1.12 for the 9 x 9', 4 x 6' and 2 x 4' stands, respectively. The similarity of this difference in 4 x 6' and 9 x 9' stands does not relate well to N_2 fixation per unit area estimates (4 x 6' is 30% greater than 9 x 9'; Table IV). Possible reasons for this discrepancy, in addition to possible differences in root surface area, are several. Differences in photosynthesis per unit leaf area or respiration per unit surface area could be linked to density, possibly through radiation or temperature effects.

An intriguing alternative reason was found when comparing leaf weight to nodule weight on individual trees (Figure 9). Trees in more open stands had a significantly lower nodule weight-leaf weight ratio. This suggests that the growth in nodule weight observed to occur during late fall and early spring may be better correlated with previous-year leaf weight since leaf weight is increasing at the greatest rate in the most open (9 x 9') stands. When a new nodule biomass was calculated for the 9 x 9' stands, using the mean nodule weight-leaf weight ratio for the 2 x 4' and 4 x 6' stands, N_2 fixation in the 9 x 9' stands surpasses that of the 4 x 6' stands. This time-lag phenomenon most likely applies to root production as well, further
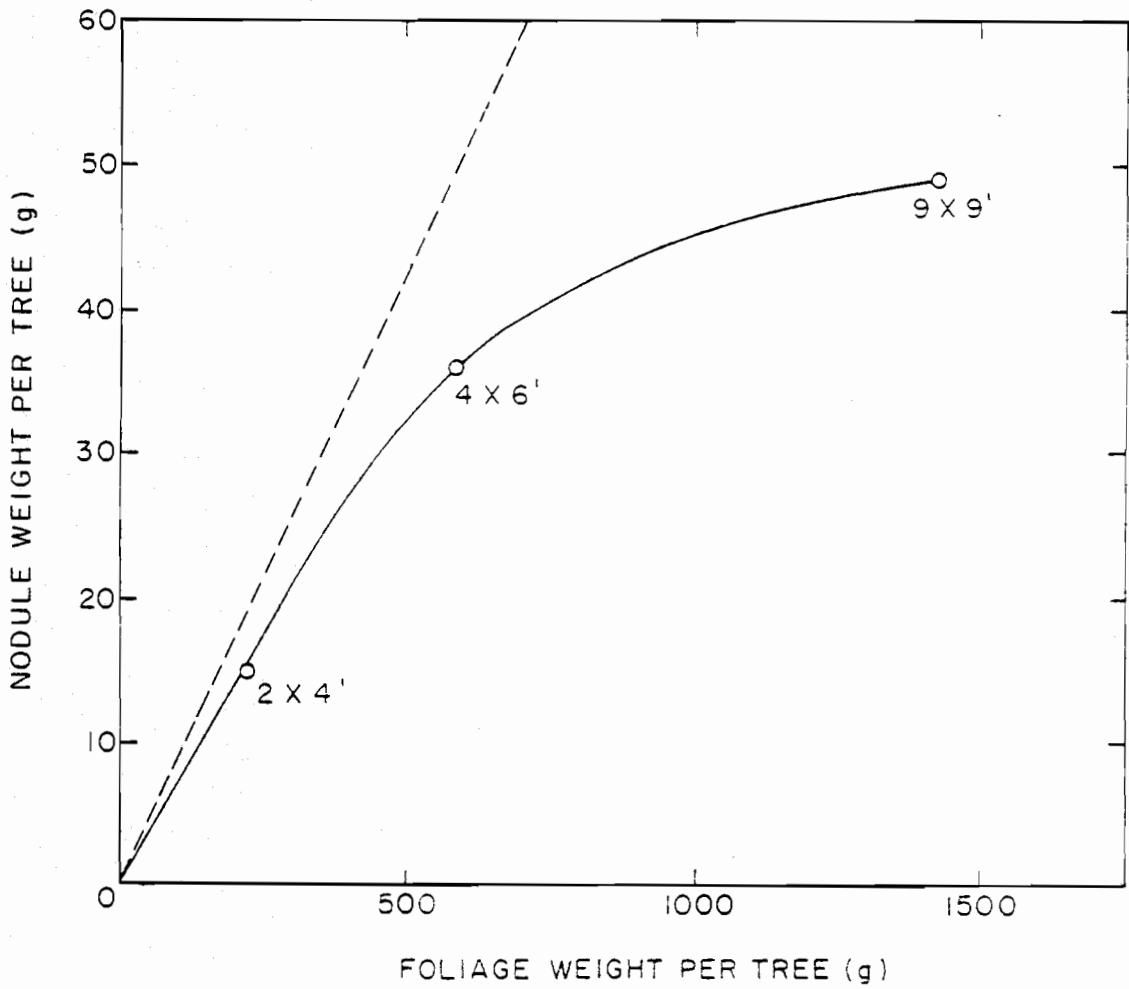
Figure 9. The relationship between leaf weight and nodule weight per tree for plantations (solid line) and natural stands (broken line) (D. Binkley, personal communication).

reducing the differences between growth capacity and potential in the 9 x 9' stands.

CONCLUSIONS

Although density effects on individual tree and stand values are closely linked, conclusions are presented for tree and stand values separately in the interest of clarity.

Individual Tree Behavior Under Varied Stand Density

1. Trees growing in the most open (9 x 9' stands) had, on average, the highest dry weight values for all components, including leaf, branch, bole, root and nodule weights.

2. Trees in the 9 x 9' stands also had the greatest dbh, crown volume, leaf density, live-crown-ratio, branch and total surface area and number of growth sites.

3. Branch, bole and total aboveground net production were greatest in 9 x 9' trees, least in 2 x 4' trees.

4. Leaf weight per tree did not relate linearly to nodule weight per tree. There appears to be a "time-lag" in nodule formation so that a better linear relationship exists between the current year's nodule weight and the preceding (as opposed to the current) year's leaf weight.

5. A greater leaf weight relative to nodule weight lead to a high nodule specific activity (21 μ moles $C_2H_2 \cdot g$ nod.$^{-1} \cdot hr^{-1}$) in 9 x 9' trees.

6. N_2 fixation per tree was greatest in 9 x 9' trees, least in 2 x 4' trees, corresponding to observed patterns in leaf weight per tree. This supports the hypothesis set forth by Gordon and Wheeler (1978) that leaf weight and N_2 fixation are highly correlated in field-grown alder.

7. Tree height and crown shape coefficients were the only variables that were not greatest in trees growing in the 9 x 9' stands. These appear to be relatively independent of stand density.

Stand Behavior Under Varied Stand Density

1. Stands were strongly influenced by density also, but mid- to low-density (4 x 6', 2 x 4') stands had the highest values, 9 x 9' stands had the lowest values.

2. 2 x 4' stands had the highest bole, aboveground and total dry weight per unit area, 4 x 6' stands had the greatest leaf, branch, root, stump and belowground weight per unit area.

3. Net branch and total aboveground production per unit area were greatest in 4 x 6' stands; net bole production was greatest in 2 x 4' stands.

4. Leaf weight and total aboveground net production were similarly affected by density with highest values in the 4 x 6' stands. This pattern approximates the mar Möller et al. hypothesis of a wide range of densities over which net production is unaffected by density.

5. N_2 fixation per unit area peaked sharply in the mid-density
   (4 x 6') stands at about 89 kg $N \cdot ha^{-1} \cdot yr^{-1}$, about 30 and 35%
   higher than 9 x 9' and 2 x 4' stands, respectively.

6. N_2 fixation in the densest stands (2 x 4') was 28% lower than
   predicted by a linear regression between leaf weight per unit
   area and N_2 fixation per unit area in 4 x 6' and 9 x 9' stands.
   This suggests that relatively less photosynthate is allocated to
   nodules and perhaps roots in dense stands.

7. Component to total net production ratios also suggest that
   density influences photosynthate allocation patterns. In high
   density (2 x 4') stands, bole production is favored over branch
   and belowground production while in low density (9 x 9') stands,
   high branch production is associated with lower than expected
   N_2 fixation. The photosynthate demand, or "sink," priority
   suggested by this analysis is leaves > branch extension growth >
   branch lateral growth > N_2 fixation > bole.

8. Leaf distribution also conforms well to predicted allocation
   patterns. The mean height of leaves above the ground increases
   with increasing density and thus less photosynthate was trans-
   ported to nodules in high density stands relative to 4 x 6'
   stands. This lends support to the idea that crown shape and
   length may strongly affect root growth.

Overall Conclusions

1. Density negatively correlated with all estimates of dry weight,
   net production and N_2 fixation in individual trees.

2. Alternatively, density is, in general, positively correlated with dry weight, net production and N_2 fixation per unit area.

Management Implications

1. Maximum stem growth per unit area is achieved in the densest stands (2 x 4' initial spacing). The density for optimal round-wood production, if defined as the lowest possible density with near-maximal bole production (i.e. near the beginning of the mar Möller et al. (1954) plateau), is reached in the 4 x 6' stands at this age.

2. Maximum N_2 fixation is also greatest in the intermediate density (4 x 6') stands. Thus, maximum N_2 fixation appears to occur at a density that is near optimal for short-rotation roundwood production.

3. Density of most natural stands is undoubtedly greater at the sampled age (5 years) than that found in the most dense (2 x 4') spacing. Because of the reduced growth in 2 x 4' stands relative to 4 x 6' stands, it follows that stands of greater density would be even less productive. Thus initial spacing control may help increase total yields in addition to production of individual trees and N_2 fixation.

CHAPTER II.   AN OPTIMAL SPACING MODEL FOR RED ALDER

INTRODUCTION

The use of nitrogen-fixing species in forestry has generated con-
siderable interest in recent years (Gordon et al. 1979). The most
important nitrogen-fixing tree that occurs naturally in the Pacific
Northwest is red alder (Alnus rubra Bong.). Forest management systems
involving mixed and rotational culture of red alder with Douglas-fir
(Pseudotsuga menziesii (Mirb.) Franco) have been suggested (Tarrant
and Trappe 1971; Gordon and Dawson 1979; Atkinson et al. 1979; Miller
and Murray 1979). One of the most promising hypothetical management
systems is rotation of alder and Douglas-fir, both species to be grown
for sawlog production (Atkinson et al. 1979). This system utilizes
the nitrogen-fixing ability of alder and its effects on subsequent
Douglas-fir growth and the profitability of sawlog production to maxi-
mize overall return on investment. A more recent economic analysis
has shown that primary emphasis should be placed on increasing alder
yields to surpass the profitability of continuous Douglas-fir mono-
culture fertilized with inorganic nitrogen (Tarrant et al. in
preparation). Even though alder-fir rotations are potentially more
profitable than currently used Douglas-fir monoculture, we have almost
no information on alder yields and N_2 fixation rates in managed
stands.

The effect of stocking control on wood yield has been studied
extensively. Increased density causes reduced cambial growth in the
lower stem (Koslowski 1971). In the view of mar Möller et al. (1954),

dry weight production increases with density reaching a plateau which is maintained over a wide range of densities, and finally decreases in excessively dense stands. The mar Möller hypothesis appears to hold true in young plantations of cottonwood (Heilman et al. 1972; Ek and Dawson 1976), sycamore (Wood et al. 1976) and loblolly pine (Harms and Langdon 1976).

The greatest value of individual trees is achieved at the lowest densities consistent with quality constraints (limbiness) because value of most species increases disproportionately with size. Maximum value per unit area is usually achieved at an intermediate density because sufficient numbers of trees per unit area are needed. Moderately low densities (near the beginning of the dry weight plateau) are usually most profitable for sawlog production. High logging costs, which generally increase exponentially with number of stems per unit area, also act to maximize value at intermediate densities. The effect of density on growth of red alder on an individual and stand basis needs to be assessed to enable estimates of densities and rotation lengths that will yield the greatest profit. The relative effectiveness of management techniques could easily tip the balance of profitability toward or away from alder; this question has prime importance and can't wait for culmination of pilot studies. Thus, a logically-derived growth model for managed alder stands could help to determine the feasibility of alder management.

MATERIALS AND METHODS

An optimum spacing model is proposed that does not utilize growth information from yield tables derived for unmanaged stands other than tree height which is thought to be relatively independent of density. The degree of competition within a stand is accounted for in the model through the inclusion of leaf weight per unit area, optimal live-crown-ratio and canopy volume as a function of crown shape and density.

The model, outlined in Figure 10, utilizes an estimate of crown length at harvest for optimal production of specified wood products (i.e. sawlogs, pulpwood, etc.), a mathematical model predicting canopy volume as a function of crown shape and spacing and maximum leaf weight per unit area for the specified site.

Optimum crown length at harvest is estimated by multiplying the optimum live-crown-ratio for production of specified products by the percentage reduction in maximum production at harvest age and tree height from unmanaged stand yield tables (Worthington et al. 1960). The percent reduction in maximum production at harvest age may be fairly constant, reflecting an efficient balance between utilization of productive periods of growth and the need for shortest possible rotation length, an economic constraint. The commonly used technique of estimating optimal rotation length to be the age where current annual increment and mean annual increment lines cross (Figure 11) suggests that current annual increment at harvest age is about 75% of maximum current annual increment (Daniel et al. 1979). It is assumed
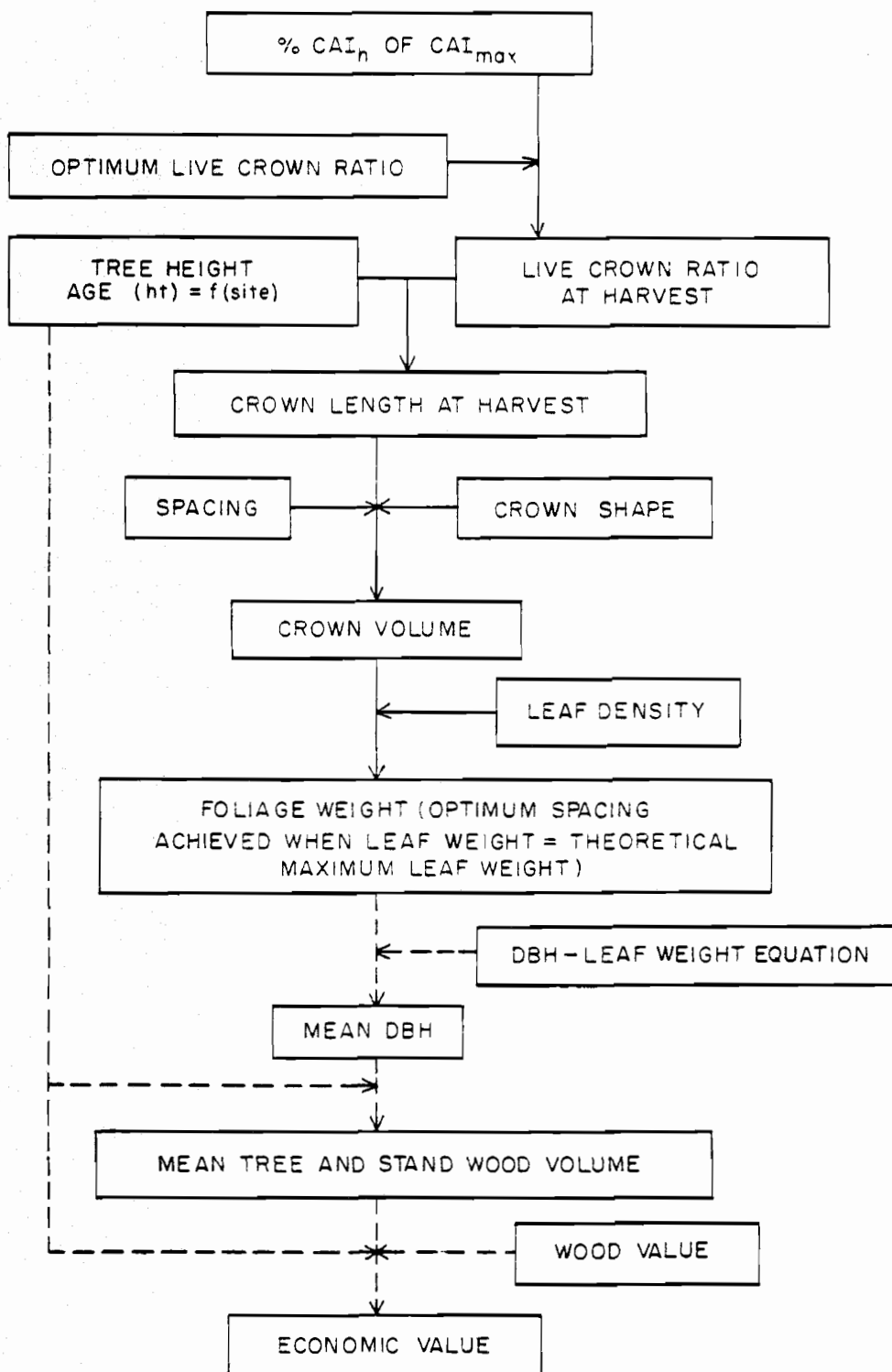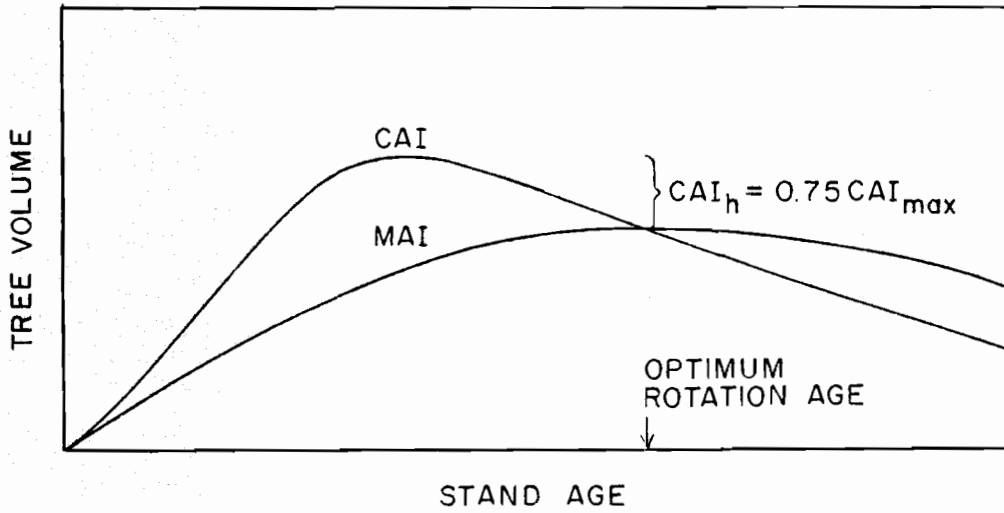
Figure 10. Optimal spacing model flow chart.

Figure 11. Current and mean annual volume increment as a
function of stand age (after Daniel et al.
1979).

that live-crown-ratio will decrease proportionately with current annual increment. Age is purposely left out of this part of the model to avoid use of yield estimates from unmanaged-stands. Live-crown-ratio controls, to a large degree, photosynthate allocation to various components. Through the inclusion of estimated optimal live-crown-ratios for various products, optimal production of various produces are specified in the model. At present, this may be the weakest link in this model but with further work, this approach may represent the best physiological approach to optimization of spacing for specific desired wood products. Furthermore, existing data on live-crown-ratios from other species may be applicable.

Once optimal crown length at harvest is calculated in this fashion, a mathematical model is used to predict canopy volume based on spacing and crown shape. A maximum of three component volumes are calculated to estimate total tree and canopy volume (Figure 12).

Leaf density is multiplied by canopy volume to estimate total leaf weight per unit area for the specified crown length and spacing. Optimal spacing is proposed to be the spacing that produces a leaf weight per unit area that is equal to the maximal site leaf weight per unit area. In conifers, an optimal site needle weight per unit area may be more appropriate; alder does not appear to develop excess leaf weight due to a strong tendency to loose leaves in response to adverse environmental conditions such as drought.

If a dbh-leaf weight per tree equation for larger alder trees were available, it could be used to predict mean tree dbh which could be combined with tree height to estimate wood volume per tree and per

PARABOLIC VOLUME $= \left\{ \dfrac{\pi \left(\frac{sd}{2} \right)^2}{2} \right\} \times L_{xsecx}$

AREA $= \pi \left(\dfrac{sd}{2} \right)^2$

$L_{xsecx} \longrightarrow$

VOLUME $= \left\{ \dfrac{\pi \left(\frac{sd}{2} \right)^2 + \left(sd \right)^2}{2} \right\} \times \left(L_{diagx} - L_{xsex} \right)$

AREA $= \left(sd \right)^2$

$L_{diagx} \longrightarrow$

VOLUME $= \left(sd \right)^2 \times \left(L_{max} - L_{diagx} \right)$
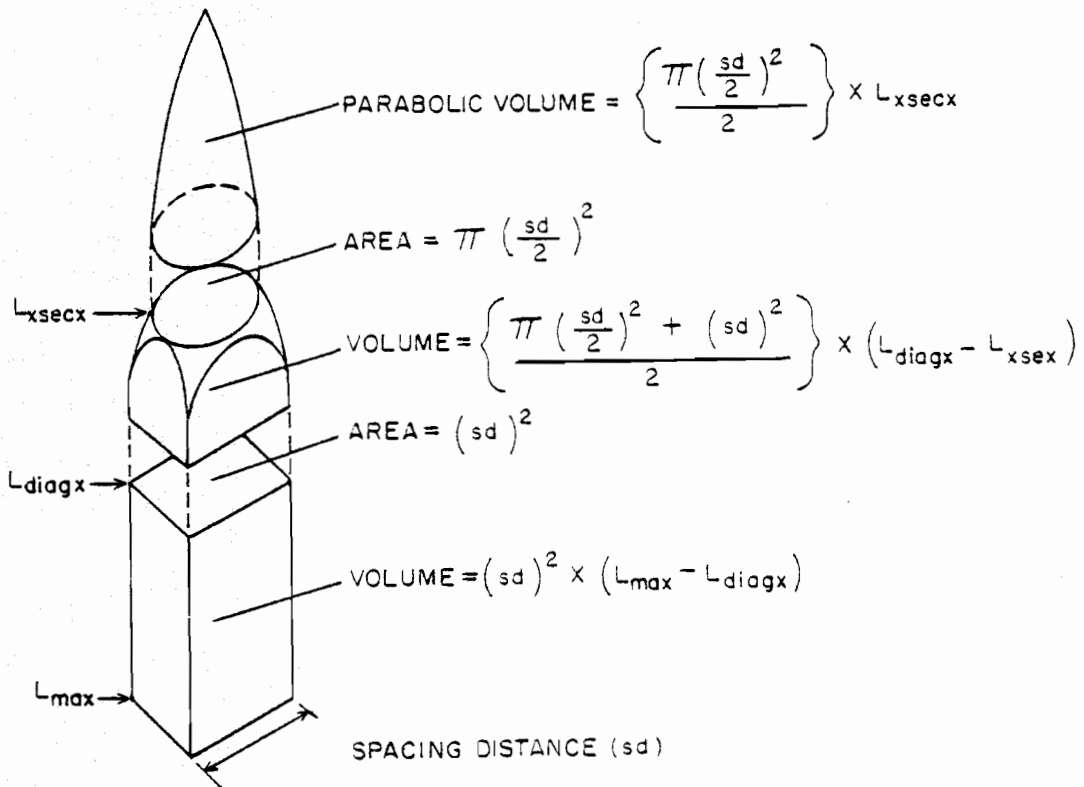
$L_{max} \longrightarrow$

SPACING DISTANCE (sd)

Figure 12. Calculation of crown volume as a composite solid (L_{xsec} is distance from terminal where crown shape lines first tough – see Figure 8; L_{diagx} is distance from terminal where crown diameter equals spl $\times \sqrt{2}$; L_{max} equals crown length at harvest).

unit area enabling an economic evaluation. Such equations exist for young trees (Table V; Smith[1]) but extrapolation errors for large trees potentially are too great to justify their use here.

ASSUMPTIONS

Production of specified wood products at harvest age is assumed to be constant at 75% of maximum production (Figure 11). As a first approximation optimal live-crown-ratio was assumed to be about 0.60 for sawlogs, 0.80 for biomass production. These were varied, however, for different tree heights. Crown shape was determined to be relatively independent of density (Table II) although crown length was highly dependent on density. The 9 x 9' spacing shape (b_0 = 0.3348, b_1 = 0.2649) was thought to be most appropriate but b_1 was varied (b_1 = 0.2, 0.25, 0.3) to see what effect shape had on optimal spacing. Leaf density was fairly constant between densities (Table II) averaging 45.9 g/m^3. It too was varied (30, 40, 50, 60 g/m^3) to test for its effect on estimated optimal spacing. Maximum leaf weight per unit area for this site is 3.00 metric tons/ha (Appendix 1).

RESULTS AND DISCUSSION

Model output is shown in Table VII. Clearly, as optimal live-crown-ratio and L max are increased, optimal spacing increases. Higher leaf densities and a greater slope of the crown shape line also increase optimal spacing as expected. Model output for several cases

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[1]N. J. Smith. 1977. Op cit.

TABLE VII. ESTIMATED OPTIMAL SPACING DISTANCE (M); INPUT VARIABLES ARE: LEAF DENSITY (LDEN), CROWN LENGTH AT HARVEST (LMAX), OPTIMAL LIVE-CROWN-RATIO (LCR_{opt}), TREE HEIGHT AT HARVEST AND CROWN SLOPE.

| Input Variables (25 m) | | | Estimated Optimal Spacing Distance (m) | | | |
LDEN (g/m^3)	LMAX (m)	LCR opt[1]	0.20	0.25	0.30	mean
30	5.0	0.27	< 0.1	< 0.1	< 0.1	< 0.10
	7.5	0.40	< 0.1	< 0.1	< 0.1	< 0.10
	10.0	0.53	0.5	0.5	0.5	0.50
	12.5	0.67	2.1	2.6	3.0	2.57
	15.0	0.80	3.5	4.5	5.0	4.33
40	5.0	0.27	< 0.1	< 0.1	< 0.1	< 0.10
	7.5	0.40	0.6	0.6	0.6	0.60
	10.0	0.53	2.2	2.5	3.0	2.57
	12.5	0.67	3.7	4.5	5.3	4.50
	15.0	0.80	5.3	6.4	7.8	6.50
50	5.0	0.27	< 0.1	< 0.1	< 0.1	< 0.10
	7.5	0.40	1.5	1.8	2.0	1.77
	10.0	0.53	3.0	3.6	4.3	3.63
	12.5	0.67	4.8	5.8	6.9	5.83
	15.0	0.80	6.5	8.0	9.5	8.00
60	5.0	0.27	0.6	0.6	0.6	0.60
	7.5	0.40	2.2	2.5	2.9	2.53
	10.0	0.53	3.8	4.5	5.3	4.53
	12.5	0.67	5.6	6.8	8.1	6.83
	15.0	0.80	7.2	9.0	10.5	13.37
LDEN mean	5.0	0.27	0.16	0.16	0.16	0.16
	7.5	0.40	1.08	1.23	1.38	1.23
	10.0	0.53	2.78	3.28	3.28	2.81
	12.5	0.67	4.05	4.93	5.83	4.94
	15.0	0.80	5.63	6.98	8.20	6.94
$\bar{\bar{X}}$	10.0	0.53	2.66	3.22	3.77	3.22

[1]LCR_{opt} (at height = 25 m) = LMAX divided by [0.75 (see Figure 11) x 25 m].

are shown in Figure 13. The linear initial portion of the curves indicate no interaction between trees. The inflection zone represents initial interaction of crowns leading into more intensive competition. Note the theoretical maximum leaf weight per unit area. Optimal live-crown-ratios that produce curves that do not intersect the maximum leaf weight per unit area in a medium range of densities are subject to error and predicted spacings are either high or low corresponding to excessively high or low live-crown-ratios, respectively. This may help to explain some of the excessively wide and close spacings predicted in Table VII. Wide spacings may be predicted when using average leaf densities because of self-shading in the interior of leaf crowns. Perhaps the most difficult estimate is that of determining optimal live-crown-ratio. The optimal live-crown-ratio for pulpwood production should be the live-crown-ratio of a spacing that produces maximum net bole production per unit area. This was determined to be 0.55 (Table II). Sawlog live-crown-ratio is much more difficult to estimate but an approximation is to define optimum live-crown ratio for sawlogs to be the live-crown-ratio of a stand which has the maximum product of net bole production and dbh. This product was calculated to be 10.0 for 9 x 9' stands, 17.3 for 4 x 6' stands and 14.9 for 2 x 4' stands. Thus, the live-crown-ratio for sawlogs would best be represented by that in the 4 x 6' stands (0.64). Live-crown-ratio for biomass production would best be represented by live-crown-ratio of the stand with maximum aboveground net production per unit area also the 4 x 6' stands (0.64) although a 100% live-crown-ratio seems more appropriate, intuitively.
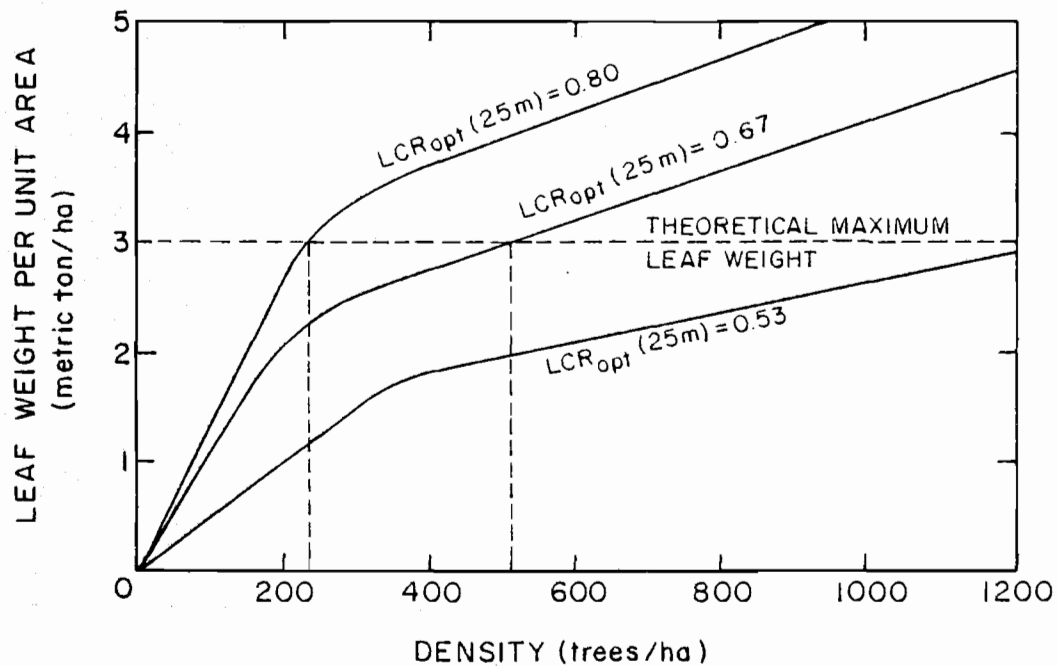
Figure 13. Sample model output [$LCR_{opt}(25 \text{ m})$] is optimal
live-crown-ratio for a 25 m tree; see Appendix I
for calculation of theoretical maximum leaf
weight.

Specific estimates for pulpwood production can be made on these stands that are close to half the rotation age and thus the optimal spacing should be near maximum net bole production. Using the 2 x 4' crown slope of 0.3 m/m and the closest leaf density (50 g/m^3) and a 15 m (49 ft) harvest height, optimal spacing is projected to be 1.05 x 1.05 m (Figure 14). This is much closer than the spacing estimated by DeBell et al. (1978) of 2.7 x 2.7 m for pulpwood rotations. The reason for this discrepancy is unclear.

If we use the dbh x net bole production index for estimating sawlog spacing distance, the best estimate of live-crown-ratio comes from the 4 x 6' crown shape (slope = 0.30) and a leaf density of 40 g/m^3. Thus, optimal spacing is predicted to be 4.5 x 4.5 m (Figure 14). This is nearly identical to the spacing estimated by Atkinson et al. (1979), Tarrant et al. (in preparation) and DeBell et al. (1978).

CONCLUSIONS

This model is a first attempt at using variables closely tied to competition: live-crown-ratio, canopy volume and leaf weight per unit area. Many of the assumptions need further testing, however. It remains to be seen whether optimal live-crown-ratio will be practical to use because of the high sensitivity the model has to it and because it may be difficult to measure. Once measured, however, it may prove reasonable to assume it to be a constant for specific products from a given species. Additional crown shape measurements are needed to con- firm that density has little effect on shape and to determine shape of larger crowns. Additional measurements are also needed on leaf
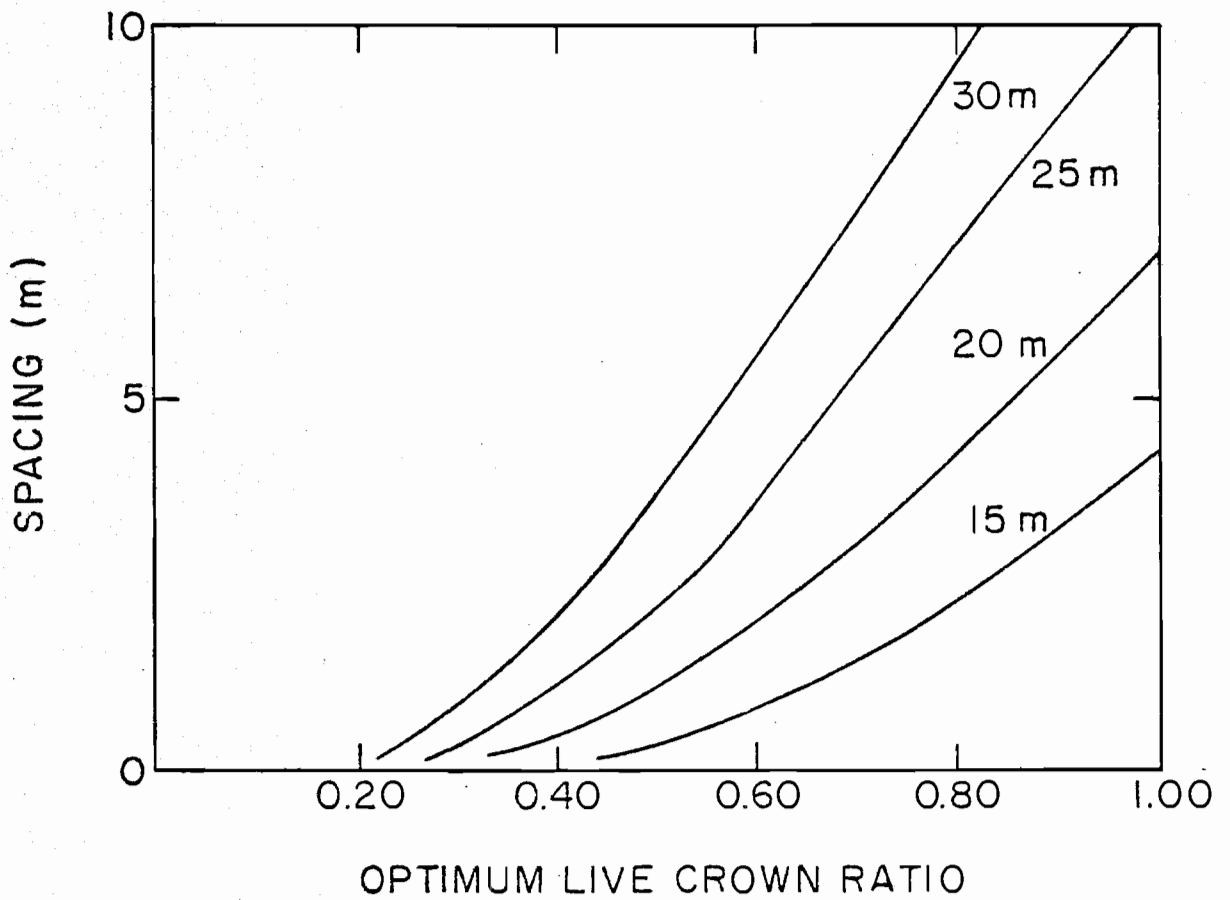
Figure 14. Square spacing distance as predicted by optimal
live-crown-ratio for tree heights (30, 25, 20, 15 m).

density. Verification of the proportionality of live-crown-ratio to current annual increment and the percent reduction in current annual increment from maximum to harvest levels are also needed. The model may eventually be useful to estimate possible genetic gains from manipulation of crown shape, volume and leaf density. Also, after basic relationships are established, all components of the model could be estimated from aerial photographs, since age is not needed. This may also prove useful where cambial growth rings are difficult to interpret, or absent, as in tropical planations. Additional work relating dbh or sapwood area to leaf weight per tree on large trees may enable us to estimate mean dbh and wood volume to aid in economic evaluations.

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APPENDICES

APPENDIX I: SEASONAL ADJUSTMENT IN LEAF WEIGHT PER UNIT AREA

A method was developed to document changes in leaf weight per
unit area with season because it was thought that the mid-August
sampling period of the dimension analysis might not be representative
of the whole season. Ladders were erected by a tree selected to be
near the mean dbh of the stand and the number of leaves per growth
site (a growth site is a current twig developed from a previously set
bud) was measured monthly on each density replicate stand. To relate
leaf weight to number, the average weight per unit number of leaves
was measured by sampling branches from the stands in June and calcu-
lated from the dimension analysis estimates for August. A straight
line was developed relating weight of leaves per unit number and date.
This was multiplied by the number of leaves per growth site for each
sampling date and the number of growth sites per unit area (developed
from the dimension analysis and assumed to be constant for each stand)
to yield a leaf weight per unit area estimate. The leaf weight per
unit area estimate from the dimension analysis was based on five
branches from each of 18 trees and is thought to be a better estimate.
Thus, all points on the seasonal curve were adjusted the difference
between the seasonal curve estimate for the time the dimension analy-
sis was conducted and the dimension analysis value.

Leaf weight (metric tons/ha) appears to peak in June and decline
almost linearly into August and September (Figure Al). The estimated
peak leaf weight is 1.71, 1.53 and 1.62 times larger than that
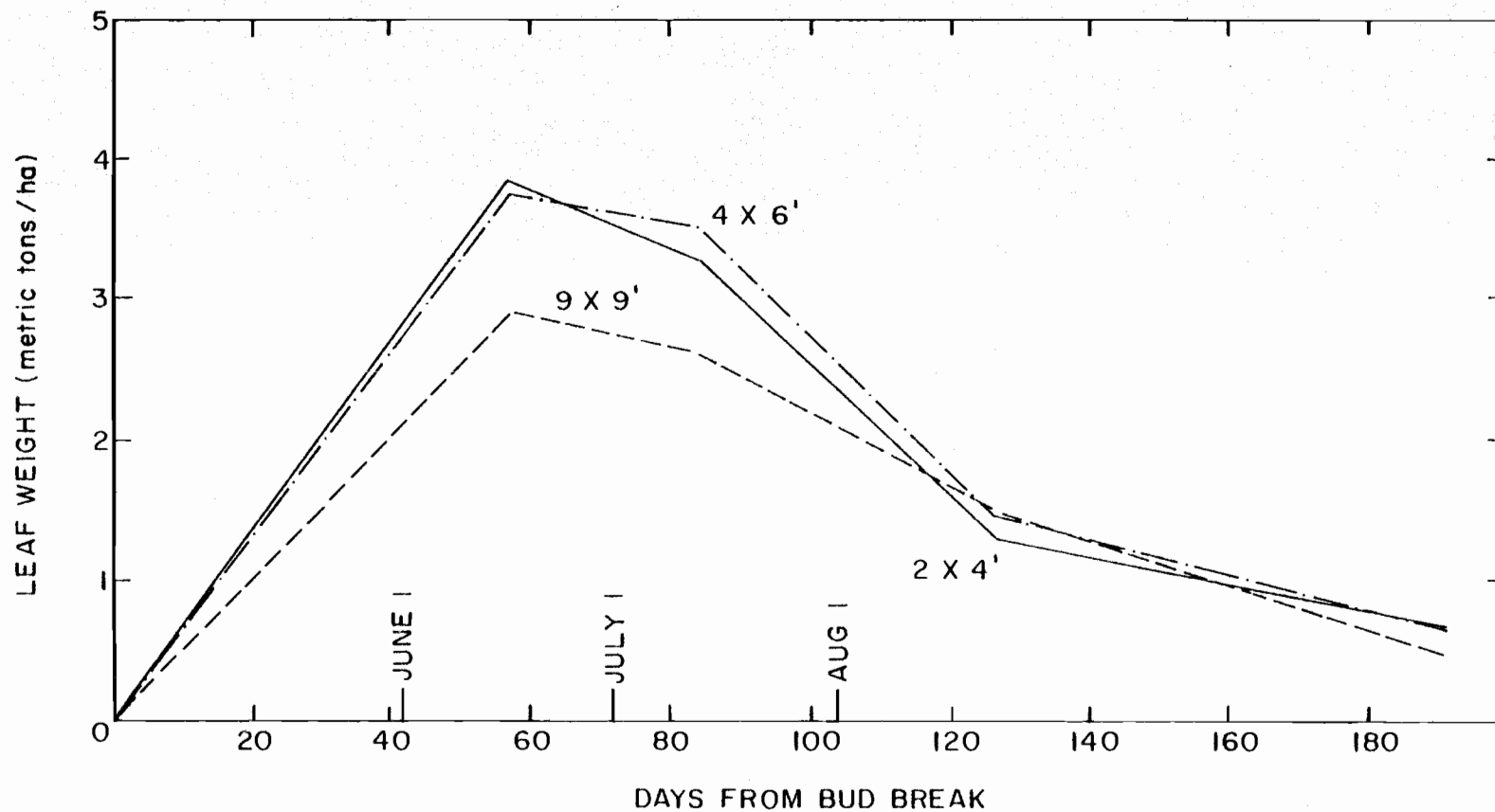measured in the dimension analysis in the 9 x 9', 4 x 6' and 2 x 4'

Figure A1. Seasonal pattern in estimated leaf weight per unit area.

stands, respectively. The average leaf weight for June, July and

August is 2.33, 2.89 and 2.80 metric tons/ha for the 9 x 9', 4 x 6'

and 2 x 4' stands, respectively.

APPENDIX II: NODULE BIOMASS BASED ON SOIL CORES

A 9.6 cm diameter tube sampler was used to estimate nodule biomass to a 20 cm mineral soil depth in 1978. Cores were taken adjacent to 20 randomly placed stakes in the leaf transect plots in each density replicate stand. These plots were small: 8.4 m^2 in 9 x 9' initial spacing stands, 8.9 m^2 in 4 x 6' stands and 7.4 m^2 in 2 x 4' stands, however, plots were randomly selected from each stand. Nodules were carefully separated from soil cores, washed, oven-dried at 70°C and weighed.

Variability of estimated nodule biomass is large, but means approximate those of the dimension analysis approach (Figure A2). For these stands, estimates produced in the dimension analysis are thought to be more accurate because of the large weight of nodules sampled and the high correlation coefficient of the derived equation.

The negative aspects of the dimension analysis approach are that some nodules are not collected, and that large amounts of time are needed. A soil core or soil-pit method[1] would be preferable in a stand with large trees. Soil coring has the drawback that nodules near the base of trees or large roots or deep in the soil would not be sampled. Note, however, in this study that soil core estimates are slightly higher than those from the dimension analysis.

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[1]B. T. Bormann. Unpublished method, on file at the Forestry Research Laboratory, Oregon State University, Corvallis, Oregon.
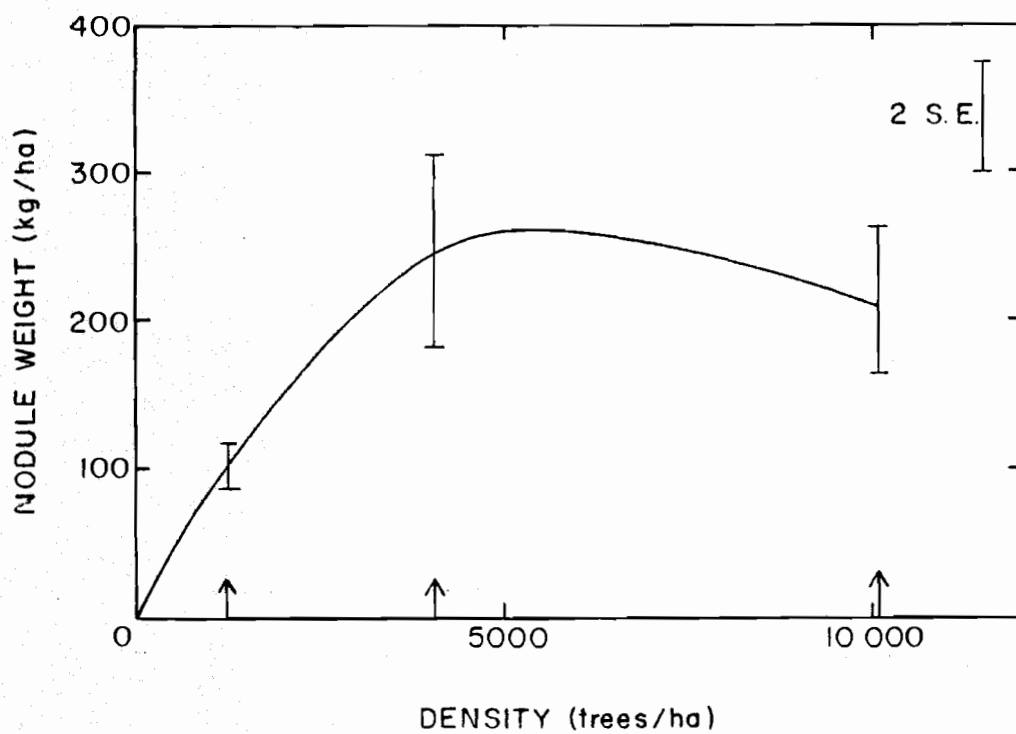
Figure A2. Nodule weight per unit area as estimated by a soil
core method.

APPENDIX III: NUTRIENT RELATIONS

All leaf and branch subsamples, a disk subsample of the bole and

several entire roots from each dimension analysis tree were ground to

a powder (to pass a 40-mesh sieve) with a Wiley mill and/or Waring

blender for nutrient analyses. Samples were analyzed for total N

(Kjeldahl) in branches, bole and roots and for N, P, S and Mn in

foliage[1].

N concentration in leaves, branches and roots was highest in the

most open (9 x 9') stands corresponding to maximal per tree

N_2 fixation rates in these stands while bole percent N was highest in

the most dense (2 x 4') stands reflecting small bole size (Table AI).

N weight in leaves, branches, and roots, however, peaked in the mid-

density (4 x 6') stands corresponding to maximum N_2 fixation and

aboveground net production per unit area observed in these stands

(Figure A3). A high per unit area bole weight and bole percent N in

the most dense stands lead to a very high bole weight per unit area.

This was mostly responsible for maximal total tree N weight per unit

area in 2 x 4' stands.

Maximum concentration of phosphorus (P) and manganese (Mn), like

N, were observed in trees in the most open (9 x 9') stands. Sulfur(s)

concentration, however, was highest in the most dense stands (Figure

A4). Per unit area weight of P followed the same pattern in response

to density as N with maximum weight in the mid-density stands. N to

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[1]OSU-PNW Cooperative Analytical Laboratory, Manual of Procedures.

TABLE AI. NUTRIENT RELATIONS AS INFLUENCED BY STAND DENSITY.

	Concentration (%)			Weight (kg/ha)		
	9 x 9 ft	4 x 6 ft	2 x 4 ft	9 x 9 ft	4 x 6 ft	2 x 4 ft
N foliage	3.027	2.971	2.891	54.2	72.2	64.5
N branches	0.911	0.854	0.786	63.5	90.8	77.2
N bole	0.420	0.355	0.526	19.7	39.9	75.0
N roots	0.938	0.918	0.894	10.8	19.9	11.5
Total N	--	--	--	148	223	228
P foliage	0.211	0.229	0.217	3.79	5.54	4.83
S foliage	0.012	0.009	0.019	0.207	0.223	0.404
Mn foliage	0.0022	0.0016	0.0013	0.039	0.038	0.028
N:P (N = 100; P = x)	--	--	--	6.99	7.67	7.49
N:S (N = 100; S = x)	--	--	--	0.38	0.31	0.63

The table header spans: "Initial Spacing" over both Concentration (%) and Weight (kg/ha) groups.
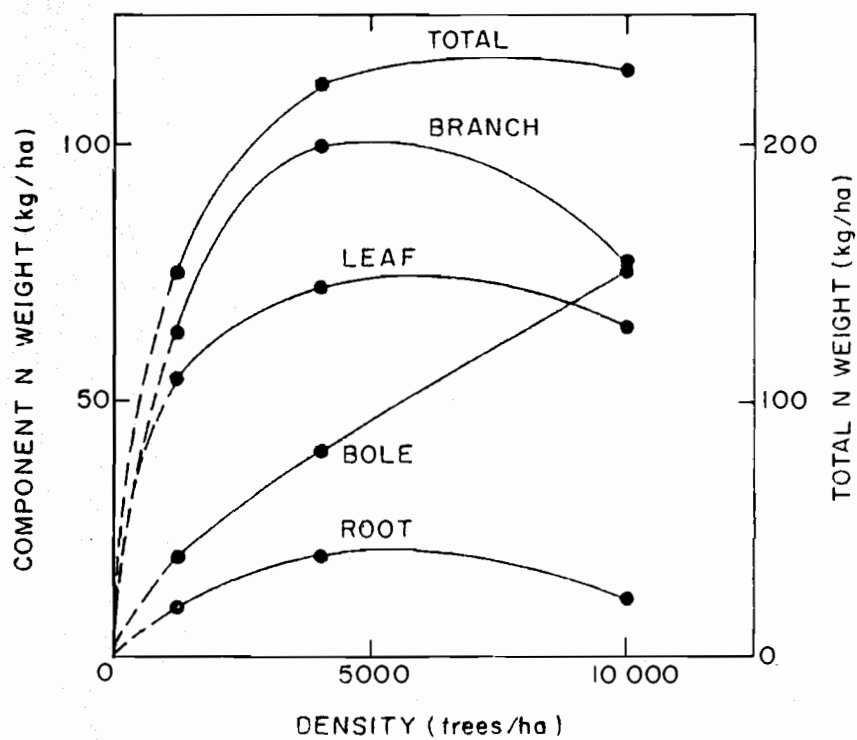
Figure A3. Component N weight as a function of
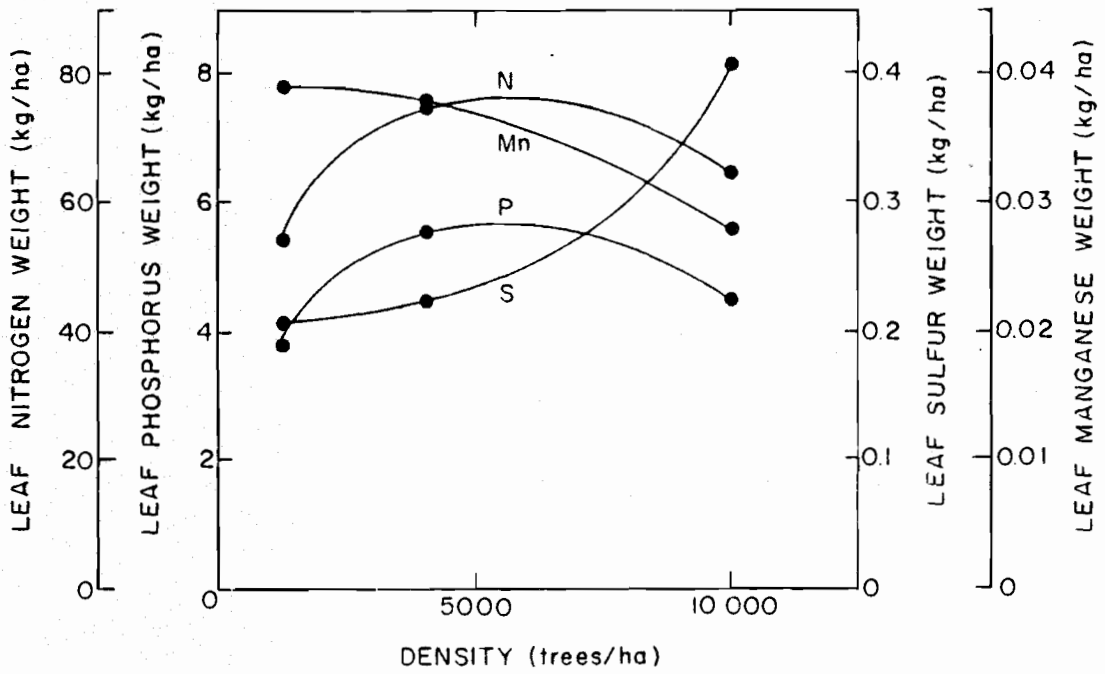stand density.

Figure A4. Foliar nutrient weights (kg/ha) as a function of stand density.

P ratios were fairly constant and high averaging 100:7.4. Ingestad (1980) reported an optimum foliar ratio of 100:16 for growth chamber-grown Alnus incana (Moench) seedlings. Perhaps there is a P deficiency on these sites. Foliar S weight per unit area was maximum in the most dense stands and N:S ratios fluctuated widely in an unexplained fashion.