AN ABSTRACT OF THE THESIS OF

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<u>Forest Science</u> presented on <u>July 7, 1983</u> .

Title: <u>Effects of Density Stress and Soil Productivity on Size,</u>

<u>Mortality and Nitrogen Fixation in Artificial Populations of</u>

<u>Seedling Red Alder (Alnus rubra Bong.)</u>

Abstract approved: Signature redacted for privacy.

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Red alder (<u>Alnus rubra</u> Bong.) seedlings were grown at three ini-
tial spacings (8 x 8 cm, 4 x 4 cm, and 2 x 2 cm) and on two soil types
(forest soil and river loam) under greenhouse and lath house con-
ditions for 525 growing days. There were seven harvest dates, com-
mencing at crown closure. Based on a 6% stratified (by size) random
sample, logarithmic regressions were used to estimate individual tree
biomass and structure at each harvest date. Acetylene reduction (a
measure of N_2 fixation capacity) was estimated as the mean sample tree
value per treatment combination for selected harvest dates. Average
tree size was consistently larger at wider than denser spacings and on
forest soil compared to river loam.

The -3/2 power rule, which imposes an upper limit on average
plant size ($\overline{S}$) as a function of actual stocking density (ρ), was
reformulated by examining the trend of the size to density ($\overline{S}-\rho$)
trajectory over the course of the experiment. A 5 parameter

non-linear model was used to estimate the self-thinning asymptote, relative density at crown closure plus shape and rate of change in the $(\overline{S}-\rho)$ trajectory. For average plant weight $(\overline{W})$ the self-thinning asymptote intercept and slope were 9.4×10^4 g/m^2 and 1.46, respectively. The crown closure line was parallel to the asymptote at a relative density of 0.31. The $(\overline{W}-\rho)$ trajectory was described by the same model regardless of initial spacing or soil type. This model was used to examine carbohydrate allocation and suggested the following priority: branches > stem $\geq$ leaves $\geq$ roots $\geq$ nodules, with decreasing density. The $(\overline{W}-\rho)$ time trajectory was examined using a logarithmic integral logistic equation which showed that intrinsic growth rate was higher on denser spacings and forest soils.

There were no soil type differences ($p < 0.01$) between acetylene reduction estimates. Values (μmoles C_2H_2/g nodule/hr) ranged from 297 at crown closure to 47 after 451 days. Highest values were for densest spacings at crown closure; this trend was reversed after 451 days. Acetylene reduction per tree was significantly higher ($p < 0.01$) in the wider spacings. Estimates of N_2 fixation (ranked by densest initial spacings) were 680, 638 and 454 kg/N_2/ha/6 months.

Effects of Density Stress and Soil Productivity on Size,
Mortality and Nitrogen Fixation in Artificial
Populations of Seedling Red Alder
(Alnus rubra Bong.)

by

Nicholas J. Smith

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed July 7, 1983

Commencement June 1984

ACKNOWLEDGEMENTS

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CHAPTER I. INTRODUCTION AND GENERAL METHODS

General Introduction

Intraspecific competition between two or more plants occurs when
one or more resources become scarce. Inter-plant interferences may
result in plastic changes in plant size or inelastic mortality respon-
ses (Harper 1979). The exact nature of density-dependent mortality is
little understood because it is etiologically difficult to attribute
fatality directly to any one plant or set of plants in a population.
For instance, while the primary cause of mortality may have been den-
sity-stress related, the actual cause of death could result from a
spectrum of secondary factors, such as disease, pest attack, or phy-
siological stress. Responses of monospecific plant populations to
density-stresses can be generalized and integrated at two levels: (1)
the average plant level (e.g., Reineke 1933, Yoda et al. 1963, White
and Harper 1970) or, (2) the population level (e.g., Koyama and Kira
1956, Hozumi 1975). Most research has been at the average plant level
because it is easier to investigate and, so far, has yielded more
fruitful results.

In particular, two apparently inviolable "laws" have been added
to population biology by analysis of average plant responses to
density:

(1) The reciprocal yield "law" (Shinozaki and Kira, 1956) states that over a range of densities, and providing initial density is maintained, average plant weight is eventually reciprocally related to density, i.e.,

$$\overline{w}_t = k_1 \rho^{-\theta_{1t}}, 0 \le \theta_{1t} \le 1$$

where $\overline{w}_t$ = average plant weight at time t

ρ = stocking density

k_1 = intercept

θ_{1t} = slope at time t

This equation says that the average weight is at first independent of density but plastically fills up available space as it grows--the lower the density the greater the space it may fill so that as time increases the exponent approaches 1.

(2) The -3/2 power "law" of self-thinning (Yoda et al. 1963) states that in plant populations undergoing density-dependent mortality, surviving plants adjust to the increased space made available through death so that:

$$\overline{w} = k_2 \rho^{-\theta_{2t}}, 1 < \theta_{2t} \le 3/2$$

where symbols are as in the last equation. The slope of the line is steeper than under the reciprocal yield law. A reduction in initial density has to occur. The net effect is to produce larger average tree size. This effect increases with decreasing density. The intercept k_2 is thought to indicate efficiency of space occupancy (Harper

1979). The -3/2 power "law" gives a maximum upper limit to plant size and appears to remain independent of site type or age.

The reciprocal yield "law" applies only to the chronological relationship between average plant weight and stocking density. It holds only under specific circumstances, viz., that initial density is maintained. Exceptions to the rule have been reported (Hirano and Kira 1965) even under this condition.

The -3/2 power rule appears to operate almost universally on monospecific even-aged stands undergoing some form of systematic mortality, although there is some variability in the reported exponent of the power equation, e.g., 1.08 to 2.18 (White and Harper 1970). Gorham (1979) and White (1980), on examining a wide variety of published data, argued that a common -3/2 slope fits remarkably well and that, despite size differences, the intercept varies only between narrow logarithmic limits.[1] It has become apparent that, for any one species growing in conditions where light is not limiting, the maximum average plant weight is empirically approximated by a single -3/2 power law equation. Research has concentrated on the asymptote given by this line rather than the processes which give rise to it. Because of this, data which do not properly lie close to the -3/2 power "law" asymptote have often been included in its computation. Similarly, rejection of data from the calculation of the -3/2 power asymptote merely because they are not judged to be undergoing density-dependent

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[1]White (1980) found that $\log_{10}k_2$ from the logarithmic transformation of $\overline{W} = k_2\rho^{-3/2}$ varied from 3.5 to 4.4 or 3,000 to 25,000 g/m^2.

mortality (e.g., Mohler et al. 1978, Hutchings and Budd 1981)
seriously biases the results.

Biological reasons for a -3/2 power rule are unclear.
Derivations of allometric relationships (e.g., Yoda et al. 1963, Perry
unpublished) infer the process is a purely physical one, i.e., there
is a finite amount of average plant volume that can be packed in a
unit volume of space. For instance, if the number of plants per unit
area is ρ then the area each plant occupies is ρ^{-1}. The diameter of
occu pancy $(\overline{d})$ is equal to the square root of the area of occupancy,
or $\rho^{-1/2}$. Now, assuming that height of occupancy $(\overline{h})$ is proportional
to the diameter or $\rho^{-1/2}$, then the total volume $(\overline{V})$ the average plant
occupies is proportional to $\overline{d^2h}$ or $(\rho^{-1/2})^2 \cdot (\rho^{-1/2})$ or $\rho^{-3/2}$. It has
proven difficult to empirically test this derivation. Plants are
complex geometric shapes not easily described by simple linear dimen-
sions (White, 1981). In addition, verification has to be made with
data derived from plants which closely track the -3/2 power rule
asymptote.

The following two ideas thus formed the body and inspiration for
the research project. Firstly, that the -3/2 power rule asymptote
suggests a purely physical response of plant size to growing space.
Secondly, that analysis of the -3/2 power rule asymptote should
include consideration of plant-density responses both before and
during its operation.

I chose to test these ideas by growing red alder (Alnus rubra
Bong.) seedlings in a greenhouse at three initial densities and on two
soil types. Alder was a suitable candidate because of its rapid
juvenile growth and relative ease of culture. I wanted to examine the

responses of plant size and mortality to density up to and including
the self-thinning asymptote on two extremes of soil type that we might
expect to grow red alder stands. I further chose to restrict the phy-
sical growing space within which seedlings might potentially grow.
Clearly this experiment does not reflect natural conditions. It does,
however, mimic the conditions under which current theory suggests the
-3/2 power rule operates, so that the basic underlying processes
revealed should theoretically hold for natural stands.

The nitrogen fixing capabilities of red alder symbionts must,
because of their potential influence, be considered in this experi-
ment. The relationships of average plant and per unit area nitrogen
fixation to density and soil type were thus investigated. No other
study has looked in such detail at nitrogen fixation in alder
seedlings under these conditions.

In the interests of clarity I have divided the presentation of
this thesis into several sections. Where applicable, objectives are
given at the start of each section.

General Methods

Seeds from two neighboring 25 yr old alder (<u>Alnus</u> <u>rubra</u> Bong.)
were collected in the fall of 1978 from MacDonald Forest, Oregon at c.
1,000 ft elevation. Cones were dried at c. 28°C for two days and
stored in a cool, dark place until the summer of 1980 when seeds from
both parent trees were separated from the cones and thoroughly mixed.
Stratification is not a prerequisite for successful germination of
this species (Radwan and DeBell 1981). These seeds were germinated in
plastic petri dishes on a sterile medium of filter paper and/or

perlite saturated with distilled water. After soaking for c. 1 h, all seeds were exposed to 1 hour of sunlight to ensure adequate U.V. light to stimulate germination. Petri-dishes were then placed in a germinating chamber, with 24°C days/20°C nights and a 16 hr photoperiod. Ten to twelve days later most seeds had germinated and developed sufficient roots for transplanting.

In the meantime boxes were constructed to receive the transplants. Three-eighths inch (9.5 mm) plywood was coated in bitumen based paint to retard fungal decay and fashioned into three box sizes with a basic depth of 16 cm: (1) 56 x 56 cm, (2) 28 x 28 cm, and (3) 14 x 14 cm. These were filled to within 1 cm of the lip of the boxes with either a forest soil collected from an alder site at Burnt Woods, in the central Coast Range Mountains of Oregon or a river loam collected from the Willamette Valley near Corvallis, Oregon (for a description of these soils at start and end of experiment see Table 1). Forty-nine seedlings were planted per box at the following square spacings: (1) 8 x 8 cm (156 trees per m^2), in the largest boxes; (2) 4 x 4 cm (625 trees per m^2) in the medium sized boxes; and (3) 2 x 2 cm (2500 trees per m^2) in the smallest boxes. There were a total of seven harvest dates, at three initial spacings on two soil types replicated three times.

The experimental design was a split-plot arrangement by date of a randomized complete block design with blocks as replicates (Appendix V). Thus, for each harvest date there were three grouped treatment units, one in each block. Each grouped treatment unit contained six treatment combinations (two soil types, three stocking densities). Blocks were situated according to the main environmental gradient in

Table 1. Soil conditions at start and end of experiment for seedling red alder growing at various levels of initial spacing and on two soil types.[1] Due to financial constraints extensive measurements were not made on the final soil conditions.

Harvest[2]	Soil type[3]	Spacing[4]	pH	% OM	CEC[5] (meq/100 g)	Total N[6] (%)	NO_3 (ppm)	P (ppm)	K (ppm)	Ca (meq/100 g)	B (ppm)
Start (day 0)	FS	All	5.4	7.2	24.4	0.23	46.7	85	410	8.7	0.68
Start (day 0)	L	All	6.2	1.2	17.0	0.06	4.9	12	98	11.2	0.17
7	FS	2				0.22	27.8				
7	L	2				0.06	0.6				
7	FS	4				0.16	39.1				
7	L	4				0.06	1.2				
7	FS	8				0.25	20.9				
7	L	8				0.05	1.8				

[1] All methods listed in Berg and Gardner (1978). Analyses performed at Oregon State Soils Testing Laboratory.
[2] 7th harvest = 525 days growth (see Table 2).
[3] FS = forest soil, L = loam.
[4] 8 = 8 x 8 cm, 4 = 4 x 4 cm, 2 = 2 x 2 cm initial spacing.
[5] CEC = cation exchange capacity.
[6] Total N microkjeldahl (does not include NO_3).

the greenhouse, one end of which faced south. Thus, block 1 was the most southerly located block. Block 2 (the middle block) was closest to the main cooling fan, while block 3 was shaded in late afternoon by nearby tree growth. Each grouped treatment unit was assigned randomly within each block. This position was maintained for the duration of the experiment, although each treatment combination was randomly relocated within each grouped treatment unit after each harvest date.

Each harvest date was planted on the same day. Planting was spread out over a three week period. Seedlings were watered thoroughly, sprayed with benomyl fungicide to reduce damping off problems once every three weeks. Pots were covered in aluminum foil for the first few weeks until judged sufficiently established. This reduced heat load and water loss. Soil field capacity was maintained throughout the experiment by watering in the evening and/or morning. All pots were flooded with a suspension of crushed nodules collected near the parent trees, c. 2 weeks and c. 6 months after planting. Two treatments were made to ensure inoculation. At the time of imputed crown closure[2], all pots were surrounded with 0.8 mm translucent polyethylene supported by 1/4 inch dowling rods. As trees grew, more material was added to ensure that physical growing space along the outside border was properly restricted.

Planting and harvesting dates are listed in Table 2. One harvest date was maintained solely for replacement purposes. A separate crown closure harvest[2] was begun in the greenhouse approximately 1 year later under almost identical conditions. It was decided that crown

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[2]Crown closure defined as point at which c. 90% of tree canopies overlap.

Table 2. Planting and harvesting dates for seedling red alder growing
at various initial spacings and on two soil types under
greenhouse and lath house conditions.

Harvest date	[1]Soil type	[2]Spacing	Date planted	Date harvested	[3]Growing days	Location
1	FS	2	8/23/81	11/28/81	97	Greenhouse
1	L	2	8/24/81	12/7/82	105	Greenhouse
1	FS	4	8/23/81	1/14/82	144	Greenhouse
1	L	4	8/24/81	2/2/82	162	Greenhouse
1	FS	8	8/23/81	2/20/82	181	Greenhouse
1	L	8	8/24/81	2/28/82	188	Greenhouse
2	All	All	7/25/80	2/26/81	215	Greenhouse
3	All	All	7/26/80	5/7/81	284	Greenhouse
4	All	All	7/28/80	7/5/81	342	Greenhouse
5	All	All	7/29/80	9/6/81	405[4]	Greenhouse/ lath house
6	All	All	8/7/80	10/30/81	451[4]	Greenhouse/ lath house
7	All	All	8/8/80	4/14/82	525[4]	Greenhouse/ lath house/ greenhouse

[1]FS = forest soil, L = loam.

[2]Spacing: 2 = 2 x 2 cm, 4 = 4 x 4 cm, 8 = 8 x 8 cm initial spacing.

[3]The no. of growing days are computed as date planted to date har-
vested, except for harvest date 7 where plants were assumed not to be
actively growing from 11/17/81 to 2/17/82.

[4]Moved from greenhouse to lath house on 7/17/81.

[5]Moved from lath house back into greenhouse on 11/17/81.

closure was an important point at which to measure intraspecific competition. Thus, ontologically, the first four harvests (including crown closure) were made in the greenhouse. Greenhouse conditions were 25°C day (14-35°C range), 20°C nights (5-23°C range) with c. 4,800 lux supplemental fluorescent light 24 hrs per day. On July 17, 1981 all remaining pots were moved to a nearby lath house. (Because of the shape of the greenhouse, some of the grouped treatment units were beginning to touch the greenhouse roof.) Conditions in the lath house were natural except that the roof was covered in 0.8 mm polyethylene sheeting for water control purposes. Grouped treatment units were kept intact. Blocks were maintained but were situated along an E-W transect. On November 11, 1981 the remaining complete harvest date was moved back into the greenhouse by removing tables from the middle sections to ensure unimpeded growth. Previous artificial environmental conditions were resumed. Trees were stimulated to flush under these conditions. Time of flush was c. February 17, 1982. Thus the final harvest could be adjusted for days of growth. Interruptions in the continuity of the experiment do not materially affect the time-independent relationship between tree weight and stocking density.

During the experiment there were continuous outbreaks of powdery mildew (Uncinula sp.), mites (Tetranychus urticae Koch), white fly (Trialeurodes vaporarium Westwood) and aphids (Elatobium sp.). These were controlled using a 7-10 day spraying cycle of alternately: Orthene (acephate), Benlate (benomyl) and Vendex (fenbutatin-oxide). It proved impossible to eradicate the mite population so that the

miticide Vendex was occasionally switched with Kelthane (dicofol) to
prevent the development of pest resistance.

In addition, an outbreak of tent caterpillars (_Malacosoma_ sp.)
ravaged some pots before they were controlled using daily applications
of _Bacillus thuringiensis_ Balinger for 12 days. Any pot where plant
health was materially affected by pests was replaced using the backup
replicate. Because of the limited number of replacements per treat-
ment combination it was not always possible to replace damaged pots.[3]
There were thus a total of 118 harvested treatment combinations, where
126 were originally planned.

At each harvest data a maximum of 18 pots was destructively
sampled (two soil types, three initial densities, three replicates).
In each pot the exact location of surviving trees was recorded. Three
trees were randomly selected per pot (called the _sample-trees_), one
from each of three root-collar diameter (rcd) size classes per pot.
On these trees the following measurements were made: rcd, height,
crown length, crown width at each quarter crown length, number of
branches, branch diameter and branch length. Each width or diameter
measurement was made twice at right angles. Roots were carefully
removed and washed free from soil. All nodules were removed except
for those used for acetylene reduction analysis (the first, fourth,
fifth and sixth harvests - see Chapter V for documentation).
Similarly, all leaves were removed and a subsample of 9 to 12 leaves

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[3]A total of 8 treatment combinations were rejected and not replaced.
These were 3211, 2411, 3421, 3811, 2821, 2227, 3227, and 1416. Code:
1st digit = experimental block or replicate; 2nd digit = distance
between trees in cm at initial spacing; 3rd digit = soil type, i.e.,
1 = loam, 2 = forest soil; 4th digit = harvest date (Table 2).

were randomly selected across three leaf size classes (defined by leaf

length). These leaf subsamples were stored for a few days at 33°F

and/or directly photocopied, then measured for leaf area (one side

only) on a Lambda Instrument Licor Surface Area Meter Model 3100.

From this subsample a bulked leaf area:dry leaf weight conversion fac-

tor was determined for each sample-tree. Total roots, shoots,

branches, nodules and leaves were oven dried at 70°C for 48 hrs and

measured to the nearest 0.001 gram (0.0001 gram for nodules). Crown

volume and surface area of crown were estimated as two parabolic cones

(top and bottom) and two frustra of parabola (two middle sections).

Due to time constraints the remaining trees in the pot were

measured for only rcd and height, except for the first and seventh

harvest in which crown width and crown length were also measured. The

series of measurements made on the sample trees were estimated for the

remaining trees using regression mediated dimension analysis (see

Chapter III for details).

CHAPTER II. DEVELOPMENT OF ESTIMATING EQUATIONS FOR

SEEDLING RED ALDER

Introduction

The purpose of this section is to describe the genesis of the
estimating equations used later in the experiment. Because their
derivation is critical, I devote a whole section to this subject.

Objectives

(1) Determine estimating equations for red alder seedling
biomass and other related growth and structural variables.

(2) Use these equations to examine the effects of (1) soil type
and initial density on allometric relationships, and (2) allometric
variability with time.

Methods and Results

Chapter I, General Methods, describes in detail the harvest and
sample tree selection procedures. To recap, there were 7 harvest
dates. At each harvest date there were c. 18 pots (3 replicates, 3
density levels, 2 soil types). At least 3 trees were randomly
selected per pot. The selection was stratified across 3 root-collar
diameter size classes per pot. Every tree in the experiment was mini-
mally measured for root-collar diameter and height while many other
more inaccessible variables were measured on the sample trees (see
Table 3). Some samples were inadvertently damaged during harvesting

Table 3. List of measurements made on seedling red alder, units of measurement, and abbreviations.

Independent variables (all trees)	Dependent variables (sample trees)

Root collar diameter (RCD), mm.
Height (HT), cm
[1]Crown Width (CW), cm
[1]Crown Length (CL), cm
	Biomass (dry grams)
	  Stem (ST)
	  Root (RT)
	  Branches (BR)
	  Nodules (NOD)
	  Roots (RT)
	  Leaves (LVS)
	
	Other
	  Crown Surface Area (CSA), cm^2
	  Crown Volume (CV), cm^3
	  Leaf Area (LA), cm^2
	  Crown Width (CW), cm
	  Crown Length (CL), cm
	  Number of Branches (NOBR)
	  Branch Length (LBR), mm
	  Branch Diameter (DBR), mm
	  Number of Leaves (NOLVS)
	  [2]Acetylene reduction (ACT),
	    μmoles C_2H_2/g nodule/hr

[1]Measured on all trees for 1st and 7th harvests only.

[2]Measured on 1st, 4th, 5th, and 6th harvests only.

and storage. Several measurements on these trees (e.g., crown width, nodule weight) were not made.

I adopted the following analytical strategy: (1) develop estimating equations separately for each harvest date, and (2) find a common model <u>form</u> across all harvest dates that could be fit to each harvest date by examining data from the 1st, 3rd and 5th harvest subsamples. The 7th (final) harvest was not subsampled for biomass due to time constraints so that crown related variables were estimated from the 5th harvest (pre-leaf fall) while other variables were estimated from the 6th harvest (see Table 2 for harvest dates). Crown width and length were measured for all trees only at the 1st and 7th harvests.

Simple correlation coefficients between the variables in Table 3 are in Appendix I. Analysis of these data plus scattergrams indicated root-collar diameter squared times height (RSH) was the best overall candidate independent variable, except that crown width squared times crown length (CW2L) was most applicable for crown related variable estimation from the 5th to 7th harvest.

Using these two independent variables, all the dependent variables in Table 3 were estimated by three different potential linear regression model forms: (1) untransformed, (2) logarithmic (base e) and (3) weighted. The weighted and log transformation both correct for heteroskedasticity. The weighted transformation weights the sums of squares by the inverse squares of the independent variables, RSH and CW2L (Cunia 1964). This weighting approximately corrects for the actual increase in variance with increasing tree size. The three transformations were compared using Furnival's Index

of Fit (Furnival 1961) (which allows comparison of different transformations of the dependent variable), and the distribution of the model's residuals.

At each harvest, all sample trees were pooled and fitted using indicator variables to account for soil type and density levels, viz.

$$\hat{Y} = b_0 + b_1 X + b_2 Is + b_3 Id_4 + b_4 Id_8 + b_5 IsId_4 + b_6 IsId_8 \quad (1)$$
$$+ b_7 IsX + b_8 Id_4 X + b_9 Id_8 X + b_{10} IsId_4 X + b_{11} IsId_8 X$$

where $\hat{Y}$ = predicted dependent variable

X = independent variable

b_i = regression coefficients

Is = 1 if forest soil type, 0 if loam soil type

Id_4 = 1 if 4 x 4 cm initial spacing, 0 if else

Id_8 = 1 if 8 x 8 cm initial spacing, 0 if else

A combination of SIPS (Rowe and Brenne 1982) and SPSS (Nie et al. 1975) was used for examining and estimating these data. The model was fit with and without indicator variables. If addition of the indicator variables significantly ($p < 0.01$) contributed to the residual sums of squares, one by one the most insignificant indicator variables (largest relative confidence limits) were dropped from the model until all variables were significant ($t_{2\alpha} < 0.01$).

The significance of the intercept values for the weighted transformation was examined. Theoretically, they should be insignificant because the weighting procedure emphasizes the smaller trees. This should push the intercept towards the origin.

Weighted and logarithmic transformations corrected for heteroske-
dasticity and substantially reduced Furnival's Index (F.I.) in almost
all cases compared to untransformed equations (see Table 4).
Furnival's Index was usually slightly superior (i.e., smaller) for the
weighted transformation compared to the logarithmic transformation in
the first harvest, but this trend was reversed for the third and fifth
harvests. A combination of smaller F.I. and insignificant zero inter-
cept did not hold for weighted transformation regressions across har-
vest dates for any dependent variable. Similarly, weighted transfor-
mation regression residuals were not normally distributed whereas
those for logarithmic transformations were. Normality is a necessary
prerequisite for interval estimating or testing, i.e., rejection of
dummy parameters. Thus, log transformations were generally used
except where not significant or [2](n-k) < 10 (log bias extremely dif-
ficult to correct), when weighted transformation equations were used.

The final estimating equations are located in Table 5.
Corrections for logarithmic bias were based on the criteria of
Flewelling and Pienaar (1981). Normality should first be satisfied.
Then Baskerville's correction factor [4](θ = 1/2 MSE) was used where
[5](n-k) > 30 and [4]MSE $\leq$ .5. Where these two criteria were violated
Finney's correction factor (t_o) was generally used. The t_o values
were calculated from a graph presented in Flewelling and Pienaar
(1981). For log transformations, the dependent variable of branch
number was ln (branch no. + 1) to avoid taking logs of zeros.

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[4]MSE = mean squared error.

[5]n = no. of observations, k = no. of parameters.

Table 4. Statistical comparison of potential estimating equations from selected harvest dates for seedling red alder.

Dependent variable	Transformation	1st Harvest				3rd Harvest				5th Harvest			
		FI	R^2	No.	Int.	FI	R^2	No.	Int.	FI	R^2	No.	Int.
Stem	Ln	.02	.96	58		.44	.88	74		.59	.93	66	
	Wt	.01	.92		**	1.26	.04		NS	.81	.51		**
	Untr	.06	.98			1.03	.99			4.29	.98		
Branches	Ln	.08	.85	6		.90	.78	37		1.35	.67	66	
	Wt	$.33 \times 10^{-5}$	.97		NS	NS	NS			.15	.08		NS
	Untr	.03	.47			.72	.98			2.79	.84		
Root	Ln	.03	.76	6		.90	.78	37		1.35	.67	66	
	Wt	.01	.64		**	1.28	.12		**	.62	.49		**
	Untr	.83	.69			.30	.99			3.36	.94		
Crown surface area	Ln	111.0	.93	46		896.8	.96	58		1095.3	.94	49	
	Wt	101.7	.97		NS	897.1	.72		**	959.0	.3		**
	Untr	357.4	.89			3771.9	.88			6536.7	.79		
Crown volume	Ln	201.0	.94	46		5661.2	.96	37		3929.7	.97	49	
	Wt	1964.5	.92		NS	NS	NS			NS	NS		
	Untr	1.4×10^6	.95			5.37×10^4	.88			1.12×10^5	.71		
Branch diameter	Ln	NS	NS	6		1.96	.84	74		10.12	.75	31	
	Wt	NS	NS			1.72	.97		**	1.48	.98		**
	Untr	NS	NS			2.12	.84			5.13	.50		
Branch no.	Ln	1.22	.76	21		1.09	.73	74		1.67	.78	66	
	Wt	1.31	.79		NS	1.04	.05		NS	.38	.97		**
	Untr	NS	NS			3.64	.76			4.0	.83		
Leaves	Ln	.07	.91	58		.66	.87	63		.29	.94	66	
	WT	.01	.54		**	NS	NS			.69	.34		**
	Untr	.22	.75			2.22	.88			3.61	.90		

Table 4 (continued)

Dependent variable	Transformation	1st Harvest				3rd Harvest				5th Harvest			
		FI	R^2	No.	Int.	FI	R^2	No.	Int.	FI	R^2	No.	Int.
Nodules	Ln	.008	.60	58		.04	.80	74		.07	.92	62	
	Wt	.001	.54		**	NS	NS			.56	.18		**
	Untr	.002	.75			.13	.89			.39	.89		
Crown length	Ln	3.76	.60	58		.27	.87	74		15.04	.87	65	
	Wt	3.38	.15		**	37.76	.76		**	113.93	.75		**
	Untr	8.52	.51			20.75	.84			29.99	.85		
Leaf area	Ln	25.59	.88	58		207.48	.87	63		91.18	.94	66	
	Wt	11.34	.77		*	NS	NS			515.67	.27		**
	Untr	93.17	.70			711.48	.88			804.0	.88		
Branch length	Ln	.69	.91	6		7.84	.50	37		7.95	.73	30	
	Wt	1.00	.89		*	5.79	.43		**	1.53	.99		**
	Untr	1.22	.89			11.51	.47			8.66	.46		
No. leaves	Ln	3.80	.81	58		4.47	.87	63		1.19	.95	66	
	Wt	5.98	.58		**	25.17	.15		*	2.88	.26		**
	Untr	8.46	.70			26.58	.64			19.27	.67		
Crown width	Ln	2.54	.84	58		4.98	.91	58		1.12	.89	49	
	Wt	9.90	.90		**	13.48	.89		**	3.91	.75		**
	Untr	4.8	.90			8.89	.90			11.71	.86		

Table 4 (continued)

Dependent variable	Transformation	1st Harvest				4th Harvest				6th Harvest			
		FI	R^2	No.	Int.	FI	R^2	No.	Int.	FI	R^2	No.	Int.
Acetylene reduction	Ln	136.4	.50	39		NS	NS			13.9	.49	47	
	Wt	1169.6	.98		**	669.0	.47	45	*	70.2	.88		*
	Untr	188.6	.50			NS	NS			26.7	.43		

Codes: $\underline{Ln}$ = $\log_e$ transformation, $\underline{Wt}$ = weighted transformation, $\underline{Untr}$ = untransformed, $\underline{F.I.}$ = Furnival's Index, $\underline{R^2}$ = multiple coefficient of determination, $\underline{No.}$ = number of observations, $\underline{Int}$ = significance of intercept for weighted regression: NS = not significant, * = significant $p < 0.05$, ** = significant $p < 0.01$.

The regression equations found in Table 5 were used to estimate the various dependent variables for all living trees harvested to give the results presented in the next section (Chapter III).

Discussion

Analysis of the significant indicator variables (Table 5) illustrates the allometric relationship between the 15 dependent variables and the independent variables, RSH or CW2L, as they varied with soil type, harvest date and over time. Table 6 lists the positive or negative effects of the indicator variables and which dependent variables were most affected.

Table 6 shows that, in general, wider spacings on forest soils increased the slope values but lowered the intercepts. This was because trees were generally larger at wider spacings, and on the forest soil. Under these conditions the smaller trees were the more suppressed ones, whereas on the loam and denser spaced treatments trees of the same size were less suppressed.

More dummy variables tended to be included with increased time as differences in spacing and soil type were made manifest. The 4th harvest was an exception. Growth was most luxuriant at this time and may have tended to mask any soil or spacing differences.

The dependent variables most affected by soil or spacing were generally related to crown geometry (e.g., CSA, CV, NOLVS, NOBR). This suggests that allometric instability is likely to occur in crown geometry concurrent with allometric stability in tree biomass.

Table 5. Listing of estimating equations for seedling red alder.

	t_o	No.	$\bar{R}^2$	MSE
ln (ST)				
1st H = -5.65578 + .739928 (lnRSH)		58	.95	.1418
2nd H = -5.99546 + .838349 (lnRSH)		56	.91	.2559
3rd H = -6.48845 + .905096 (lnRSH)		74	.94	.2073
4th H = -5.40897 + .933785 (lnRSH)		64	.95	.2248
5th H = -6.07806 + .902127 (lnRSH)		66	.94	.1190
6th H = -6.1579 + .919903 (lnRSH) − 1.52276 (X2) − 2.0745 (X5) + .212202 (X10)		53	.95	.2142
7th H = 5th H				
ln (BR)				
1st H* = -.0246834 + .00123208 (RSH)*		6	.52	$.6826 \times 10^{-6}$
2nd H = -15.3781 + 1.63204 (lnRSH)		14	.78	.4846
3rd H = -4.04924 + .565874 (lnRSH)		35	.78	.1636
4th H = -10.1561 + 1.11506 (lnRSH)	.970	45	.68	1.5299
5th H = -1.50198 + .307183 (lnRSH)		66	.67	.4086
6th H = 2.65059 + .433888 (lnRSH)	.991	53	.64	.5845
7th H = -7.84365 + .764997 (lnCW2L)	.998	31	.86	.5486
ln (RT)				
1st H = -5.45564 + .601388 (lnRSH)	.994	58	.76	.6249
2nd H = -6.05578 + .760223 (lnRSH)		56	.84	.4039
3rd H = -5.81964 + .660612 (lnRSH) + .280549 (X2) + .394144 (X4) − 1.99615 (X5) + .269911 (X10)		74	.89	.2440
4th H = -6.47686 + .817153 (lnRSH)		63	.92	.2971
5th H = -6.75082 + .869378 (lnRSH)		66	.94	.4056
6th H = -6.56122 + .868119 (lnRSH)		53	.90	.4651
7th H = 6th H				
ln (CSA)				
1st H = 3.10177 + .658977 (lnRSH)		46	.93	.1821
2nd H = 3.3459 + .587817 (lnRSH)		28	.89	.1184
3rd H = 3.0887 + .649698 (lnRSH) − 1.01755 (X3) − 1.62064 (X4) + .1456 (X8) + .214244 (X9)		58	.96	.0824
4th H = 2.04351 + .776047 (lnRSH)		55	.91	.2532
5th H = .852718 + .811734 (lnRSH)		49	.94	.2620
6th H = -.170308 + .894474 (lnRSH) + .565708 (X4)		53	.88	.3141
7th H = 1.71376 + .624524 (lnCW2L)		49	.99	.1409

Table 5 (continued)

	t_o	No.	$\overline{R}^2$	MSE
ln (CV)				
1st H = 2.01137 + 1.0144 (lnRSH)		46	.94	.3723
2nd H = 2.05867 + .968702 (lnRSH)	.980	28	.82	.8737
− 8.13997 (X4) + .848518 (X9)				
3rd H = 1.08534 + 1.1273 (lnRSH)		58	.95	.1923
4th H = .430237 + 1.16317 (lnRSH)	.993	55	.90	.6093
5th H = −1.24982 + 1.18676 (lnRSH)		49	.97	.3551
+ .567988 (X3) − .718403 (X5)				
+ .0906.34 (X9) − .157195 (X11)				
6th H = .997506 + .935611 (lnRSH)	.990	54	.89	.6584
− 5.64856 (X2) + .598297 (X4)				
7th H = −.0381297 + .933645 (lnCW2L)		49	.99	.1410
ln (CW)				
1st H = 1.03763 + .298117 (lnRSH) also		46	.84	.0877
measured directly on all trees				
2nd H = .804459 + .288293 (lnRSH)		28	.86	.0509
3rd H = .17227 + .394107 (lnRSH)		58	.91	.0497
4th H = −.256261 + .420779 (lnRSH)		55	.86	.1209
5th H = −.236655 + .387768 (lnRSH)		49	.89	.1540
− 1.57814 (X4) − .03859 (X7)				
+ .001279 (X8) + .162867 (X9)				
6th H = −1.64093 + .504245 (lnRSH)		39	.77	.1196
7th H = measured directly on all trees				
ln (CL)				
1st H = .68318 + .461526 (lnRSH) also		57	.88	.1511
measured directly on all trees				
2nd H = 1.3886 + .328706 (lnRSH)		38	.83	.0771
− .708538 (X4)				
3rd H = 1.28998 + .366363 (lnRSH)		74	.87	.0717
4th H = 1.28998 + .366363 (lnRSH)	.994	64	.90	.5338
5th H = −.219910 + .479264 (lnRSH)		65	.87	.3129
6th H = .668616 + .403959 (lnRSH)		65	.78	.1393
7th H = measured directly on all trees				
ln (LBR)				
1st H* = 5.74488 + .00293864 (RSH)*		6	.89	$.4624 \times 10^{-6}$
2nd H = −.173095 + .356407 (lnRSH)		37	.58	.1932
3rd H = −.173095 + .356407 (lnRSH)		37	.58	.1932
4th H = .448962 + .266405 (lnRSH)		46	.70	.1306
5th H = −.959727 + .393125 (lnRSH)		30	.73	.1498
− 4.4310 (X6) − .414614 (X11)				
6th H = .303033 + .271762 (lnRSH)		50	.71	.2197
7th H = .0327412 + .257404 (lnCW2L)	30	.78	.1252	
− .120141 (V2) + 2.91498 (V5)				
− .228262 (V10)				

Table 5 (continued)

	t_o	No.	$\overline{R^2}$	MSE
ln (DBR)				
1st H = 2nd H				
2nd H = 3.00998 − .0380194 (lnRSH)		37	.84	.0101
− 1.5195 (X3) − 1.43667 (X4)				
+ .836985 (X5) + .0262963 (X7)				
+ .21417 (X8) + .200595 (X9)				
− .134224 (X10) − .0209106 (X11)				
3rd H = 2nd H				
4th H = 1.52256 + .160135 (lnRSH)		46	.70	.0296
5th H = 1.16837 + .195671 (lnRSH)		30	.75	.0315
6th H = −2.63753 + .504161 (lnRSH)		50	.87	.2069
7th H = 1.66671 + .126311 (lnCW2L)		30	.78	.0283
ln (LA)				
1st H = −4.30948 + .683226 (lnRSH)		58	.91	.2371
2nd H = .343158 + .851424 (lnRSH)		34	.81	.3696
3rd H = −.795717 + .914086 (lnRSH)		74	.87	.4120
4th H = 1.29954 + .932841 (lnRSH)	.994	64	.89	.5385
5th H = −1.53264 + .881155 (lnRSH)		65	.94	.4455
6th H = −1.19903 + .757855 (lnRSH)	.978	50	.77	1.2165
7th H = −.606235 + .675646 (lnCW2L)		49	.92	.4278
+ 2.7891 (V4) − .219144 (V9)				
ln (NOLVS)				
1st H = −1.05225 + .712712 (lnRSH)		58	.79	.3046
− 1.86172 (X3) − 2.75249 (X4)				
2nd H = −3.5280 + .795095 (lnRSH)		34	.81	.4896
3rd H = −4.07784 + .942452 (lnRSH)		74	.87	.4669
− .978576 (X2) − .828618 (X3)				
− .748343 (X4) + .96397 (X5)				
4th H = −5.50476 + .938919 (lnRSH)	.994	64	.88	.5849
5th H = −5.30158 + .870689 (lnRSH)		66	.94	.4452
− 1.04735 (X2)				
6th H = 5.58817 + .772642 (lnRSH)	.978	48	.73	1.0825
7th H = −4.54347 + .643231 (lnCW2L)	.992	49	.88	.6654
ln (NODS)				
1st H = −6.09754 + .432092 (lnRSH)	.994	57	.60	.6909
2nd H = −8.17818 + .738713 (lnRSH)	.991	45	.68	.7694
3rd H = −8.67931 + .919386 (lnRSH)		74	.87	.4226
− .495626 (X2) − .695329 (X3)				
− .899187 (X4)				
4th H = −9.33912 + .908743 (lnRSH)	.97	45	.88	.5763
5th H = −8.06335 + .775457 (lnRSH)		65	.93	.4470
6th H = −7.4695 + .726576 (lnRSH)	.995	53	.82	.7704
7th H = 6th H				

Table 5 (continued)

	t_o	No.	$\overline{R}^2$	MSE
ln (NOBR)				
1st H = -1.79225 + .390028 (1nRSH)		66	.78	.4350
2nd H = -.418295 + .110342 (1nRSH)		53	.70	.1444
- .981231 (X4) - 1.71503 (X5)				
+ .196469 (X9) + .343063 (X10				
- .113326 (X11)				
3rd H = -2.191992 + .542295 (1nRSH)		37	.73	.3701
4th H = -2.87862 + .544242 (1nRSH)		46	.82	.3444
5th H = -1.54208 + .356910 (1nRSH)		66	.78	.4004
- 1.61665 (X4) + .18642 (X9)				
6th H = -2.63753 + .504161 (1nRSH)		53	.87	.2069
7th H = -2.01217 + .361151 (1nCW2L)		49	.80	.3829
ln (LVS)				
1st H = -4.30948 + .683226 (1nRSH)		58	.91	.2513
2nd H = -6.08988 + .852985 (1nRSH)		34	.85	.4086
3rd H = -6.50542 + .908407 (1nRSH)		74	.87	.4136
4th H = -6.64601 + .937017 (1nRSH)	.996	64	.89	.5338
5th H = -6.85828 + .882266 (1nRSH)		66	.94	.4275
6th H = -6.5576 + .7685 (1nRSH)	.975	53	.79	1.2405
7th H = -5.96976 + .685533 (1nCW2L)		49	.92	.4616
+ 2.59197 (V4) - .216241 (V9)				
ln (ACT)				
1st H = 5.80769 + .147242 (1nRSH)	.994	39	.49	.6529
- 2.30462 (X3) - 1.87754 (X4)				
+ .250596 (X10)				
4th H* = 24.4825 + .0308846 (RSH)*		45	.47	.0206
+ 22.8016 (X3)				
5th H = 1.22148 + .137551 (1nRSH)	.998	47	.49	.6946
+ .121055 (X7) + .126567 (X9)				
- .110102 (X10) - .169703 (X11)				
6th H = 1.41506 + .200333 (1nRSH)	.970	47	.35	1.4681

Notes

t_o = Finney's log bias adjustment factor (Flewelling and Pienaar 1981).

No. = Number of observations.

$\overline{R}^2$ = Multiple coefficient of determination.

MSE = Mean squared error.

All equations $\log_e$ except * for weighted regression.

RSH = root-collar diameter squared x height (mm^2 x cm)

CW2L = crown width squared x crown length (cm^2 x cm)

All other abbreviations as in Table 3.

1st H, 2nd H, 3rd H ... = harvest date (see Chapter II, General

Methods for exact dates).

The model for the above analyses was:

$$Y = b_0 + b_1 \ln X1 + b_2 X2 + b_3 X3 + b_4 X4 + b_5 X5 + b_6 X6 \quad (2)$$
$$+ b_7 X7 + b_8 X8 + b_9 X9 + b_{10} X10 + b_{11} X11$$

where X1 = RSH or CW2L (if CW2L then V(I) replaces X(I))

X2 = 1 if forest soil; 0 if else

X3 = 1 if 4 x 4 cm initial spacing; 0 if else

X4 = 1 if 8 x 8 cm initial spacing; 0 if else

X5 = 1 if 4 x 4 cm initial spacing, forest soil; 0 if else

X6 = 1 if 8 x 8 cm initial spacing, forest soil; 0 if else

X7 = ln (X1) if forest soil; 0 if else

X8 = ln (X1) if 4 x 4 cm initial spacing; 0 if else

X9 = ln (X1) if 8 x 8 cm initial spacing; 0 if else

X10 = ln (X1) if 4 x 4 cm initial spacing, forest soil; 0 if
else

X11 = ln (X1) if 8 x 8 cm initial spacing, forest soil; 0 if
else

Table 6. Analysis of indicator variables for seedling red alder estimating equations[1].

Harvest date[2]	Dependent variable[3]	Intercepts					Slopes				
		FS (X2)	4x4 cm (X3)	8x8 cm (X4)	4x4 cm on FS (X5)	8x8 cm on FS (X6)	FS (X7)	4x4 cm (X8)	8x8 cm (X9)	4x4 cm on FS (X10)	8x8 cm on FS (X11)
1	NOLVS		--	--							
	ACT		--	--						+	
2	CL			--							
	CV			--					+		
	NOBR			--	--				+	+	--
	DBR		--	--	+	+	+	+	+	+	
3	RT	+		+	--					+	
	CSA		--	--				+	+		
	NOLVS	--	--	--	+						
	NODS	--	--	--							
4	ACT		+								
5	CV		+		--				+		--
	CW			--			--	+	+		
	LBR						+				--
	NOBR			--					+		
	ACT						+		+	--	--
6	ST	--			--					+	
	CSA			+							
	CV	--		+							
7	LBR	--			+					--	
	LA			+					--		
	LVS			+					--		

[1]This analysis based on Table 5, and Equation 2.
[2]Harvest dates listed in Chapter I, General Methods.
[3]Dependent variable abbreviations listed in Table 3.

The biomass components did indeed show the greatest allometric stability. They were also, generally, the most highly correlated to the independent variables used. Other dependent variables tended to display fluctuations in intercept and slope with increasing time but biomass components usually had decreasing intercept and increasing slope with increasing time, though the 5th and 6th harvest data showed a levelling off or decrease from the 4th harvest (peak growth period) data. For instance, the intercept values for stem biomass decreased from −5.7 to −6.2 over the course of the experiment, while the slope value increased from .74 to .92.

Conclusions

It would have been desirable to examine each harvest date data set for the best regression equation. Time and monetary constraints forced me to determine the best estimating equations across time, and to apply the general equation forms to each harvest date. Similarly, it would have been more effective to measure more variables on all harvested trees, e.g., crown width, crown length. Again, this was not feasible. Generally, apart from the acetylene reduction estimating equations (see Chapter V for a more detailed discussion), all results presented in Table 5 satisfied the objectives.

CHAPTER III. EFFECTS OF SOIL TYPE, INITIAL DENSITY AND PROXIMITY

TO EDGE ON STRUCTURE AND BIOMASS OF SEEDLING RED ALDER

Introduction

The purpose of this section is to describe and analyze the effects of soil type, initial spacing and proximity to edge on the estimated biomass, growth and stand structure of the red alder seedlings throughout the course of the experiment. In addition, I present data on the underlying estimated plant weight distribution and its variation with time. In essence, this chapter synthesizes the measured and estimated data (Chapters I and II, respectively) for all harvested trees and provides a solid foundation for the ensuing analyses.

Objectives

(1) Determine the effects of soil type and initial density on estimated seedling alder biomass and tree geometry with time.

(2) Examine the effects of proximity to edge on estimated biomass and estimated crown geometry.

(3) Examine the underlying distribution of estimated individual plant biomass with time.

Methods

The equations generated in Chapter II (Table 5) were applied to all harvested trees from their respective harvest dates to estimate biomass and tree structure. The shifts in estimated individual plant weight were examined by computing the variation in Pearson's skewness and kurtosis statistics with initial spacing, soil type and time via

SPSS (Hull and Nie 1981). The only variables not estimated by equations were root-collar diameter and height for all dates and crown width plus crown length for the first and seventh harvests. These were measured directly on all trees. The analyses of acetylene reduction are presented in Chapter V.

The mean tree and per unit area biomass and stand structure estimates were examined for variation with soil type, initial density and time, using a split-plot analysis via a General Linear Model approach on SAS (Helwig and Council 1979).

In addition, the effects of proximity to edge on the allometric variability in estimated individual tree biomass and geometry were examined by the following model using SPSS (Nie et al. 1975).

$$\hat{Y} = b_0 + b_1 \cdot X + b_2 \cdot E2 + b_3 \cdot E3 + b_4 \cdot E2 \cdot X + b_3 \cdot E3 \cdot X \qquad (1)$$

where, $\hat{Y}$ = ln (estimated dependent variable per tree), e.g., stem biomass, leaf area.

X = ln (total biomass per tree).

$E2$ = 1 if edge = 2; 0 if else.

$E3$ = 1 if edge = 3; 0 if else.

b_i = parameter estimates

Trees were assigned to one of three levels in edge proximity, i.e., edge 1 = closest row to edge, edge 2 = second closest row to edge, edge 3 = remaining interior trees. In addition, the linear effects of time were examined on the above model, viz.,

$$\hat{Y} = a_0 \cdot T + a_1 \cdot T \cdot X + a_2 \cdot T \cdot E2 + a_3 \cdot T \cdot E3 + a_4 \cdot T \cdot E2 \cdot X + a_5 \cdot T \cdot E3 \cdot X \qquad (2)$$

where notation same as preceeding equation, and

     T = time (days of continuous growing since planting).

     a_i = parameter estimates.

Results and Discussion

Soil Type and Initial Density Effects on Tree Biomass and Structure

Figures 1 through 9 present some of the average tree biomass and tree structure estimates, other data are in Appendix II. Table 7 gives a breakdown of biomass, while Table 8 presents an analysis of variance for average tree biomass and per unit area yields. Table 9 shows pertinent unit area biomass and leaf area estimates.

Figure 3 shows the change in average tree biomass during the course of the experiment. The pattern revealed in this graph was consistently repeated in Figures 1 and 2 and 4 through 9. (1) Treatment differences were accentuated with time, the wider initial spacings almost always displayed greater size, although there was a significant interaction ($p < 0.01$) of spacing and date (Table 8). Within each density level, trees on forest soil consistently outproduced those on the loam soil type, though there was a significant interaction of soil type and date ($p < 0.05$). At the final harvest, trees growing on the forest soil considerably outperformed their counterparts on the loam. (3) There was a decrease in average tree size in the wider initial spacings at the 6th harvest, which was generally rectified by the final harvest.

Visual observations of the data presented in Table 7 indicated that the component biomass percentages between soil types did not vary

Figure 1. Average tree root-collar diameter of seedling red alder
growing at various density levels and on two soil types under green-
house and lath house conditions. Dashed lines are loam, solid lines
are forest soil. Points are means of 2 or 3 values. The number of
days since planting are based on actual growth days, and do not
include any dormant periods. The approximate coefficient of varia-
tion for each mean is 12% (from log transformed ANOVA, see Appendix
IV).

LEGEND (initial spacing, soil)
X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
◯ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
♦ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING

Figure 2. Average tree height of seedling red alder growing at
various density levels and on two soil types under greenhouse and
lath house conditions. Dashed lines are loam, solid lines are
forest soil. Points are means of 2 or 3 values. The number of
days since planting are based on actual growth days, and do not
include dormant periods. The approximate coefficient of variation
for each mean is 16% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)
X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
O =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
✦ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING

Figure 3. Average tree biomass of seedling red alder growing at various density levels and on two soil types under greenhouse and lath house conditions. Dashed lines are loam, solid lines are forest soil. Points are means of 2 or 3 values. The number of days since planting are based on actual growth days, and do not include any dormant periods. The approximate coefficient of variation for each mean is 44% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)

X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
○ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
⊻ =8 X 8CM,FOREST SOIL

TOTAL BIOMASS (GRAMS.)

DAYS SINCE PLANTING

Figure 4. Average tree stem biomass of seedling red alder growing
at various density levels and on two soil types under greenhouse and
lath house conditions. Dashed lines are loam, solid lines are forest
soil. Points are means of 2 or 3 values. The number of growing days
are based on actual growth days, and do not include any dormant
periods. The approximte coefficient of variation for each mean is
37% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)
X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
○ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
✦ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING

Figure 5. Average tree leaf area of seedling red alder growth at various density levels and on two soil types under greenhouse and lath house conditions. Dashed lines are loam, solid lines are forest soil. Points are means of 2 or 3 values. The number of growing days since planting are based on actual growing days, and do not include any dormant periods. The approximate coefficient of variation for each mean is 35% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)
X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
○ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
♦ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING
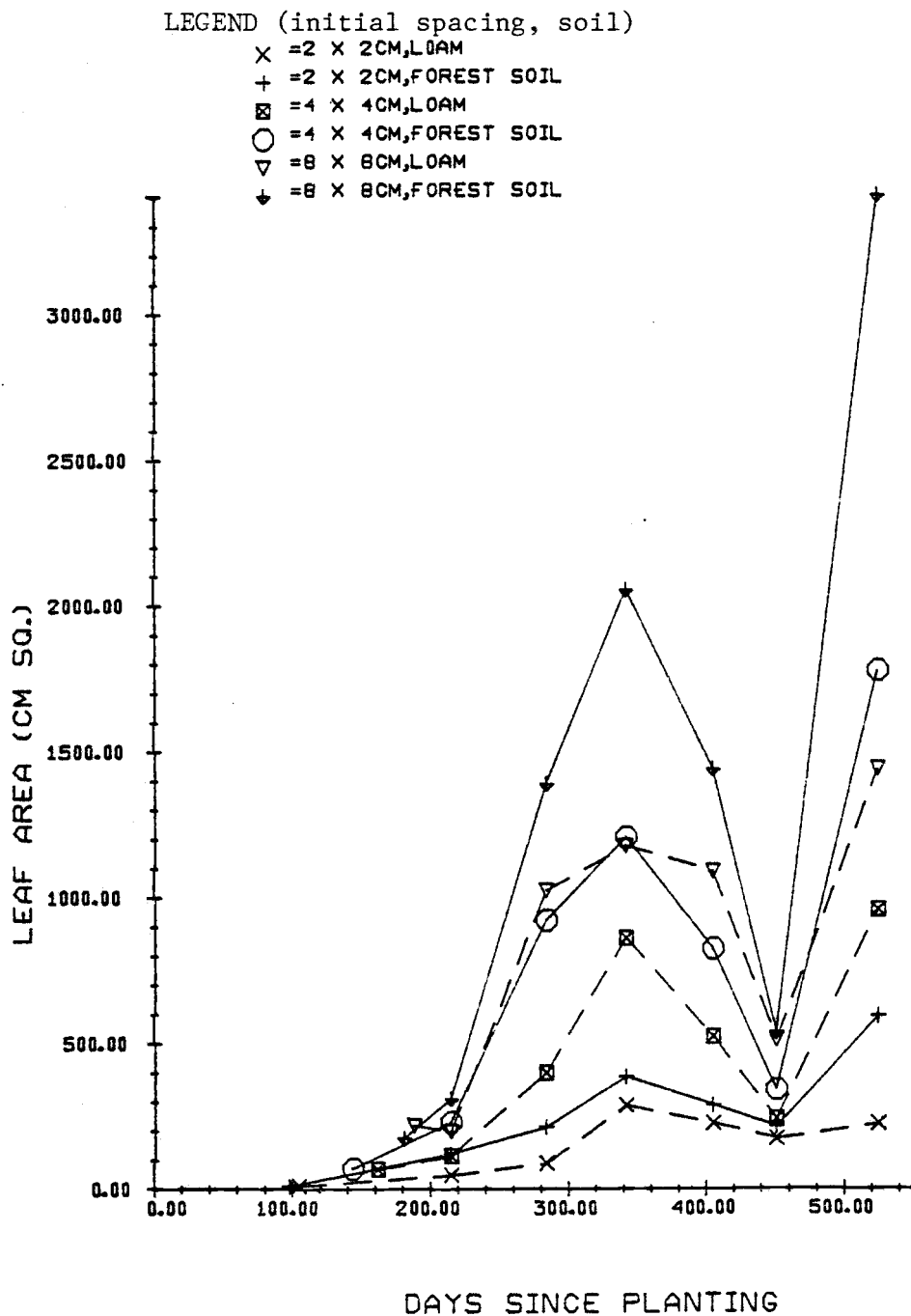
Figure 6. Average tree branch length of seedling red alder growing at various density levels and on two soil types under greenhouse and lath house conditions. Dashed lines are loam, solid lines are forest soil. Points are means of 2 or 3 values. The number of growing days since planting are based on actual growing days and do not include any dormant periods. The approximate coefficient of variation for each mean is 22% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)

X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
◯ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
✦ =8 X 8CM,FOREST SOIL

BRANCH LENGTH (CM.)

DAYS SINCE PLANTING
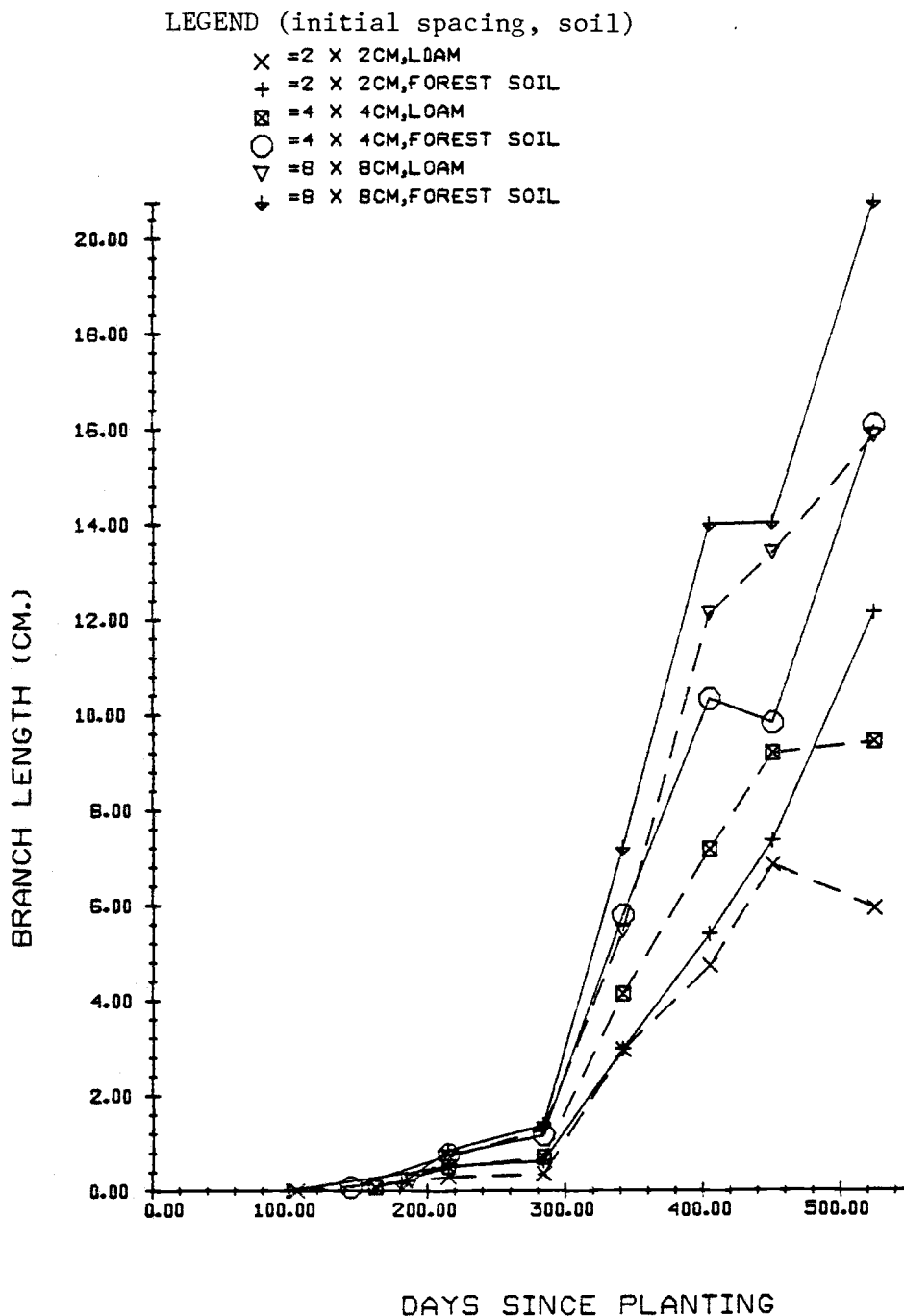
Figure 7. Average tree branch number of seedling red alder growing at various density levels and on two soil types under greenhouse and lath house conditions. Dashed lines are loam, solid lines are forest soil. Points are means of 2 or 3 values. The number of growing days since planting are based on actual growing days, and do not include any dormant periods. The approximate coefficient of variation for each mean is 32% (from log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)
× =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
○ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
✦ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING
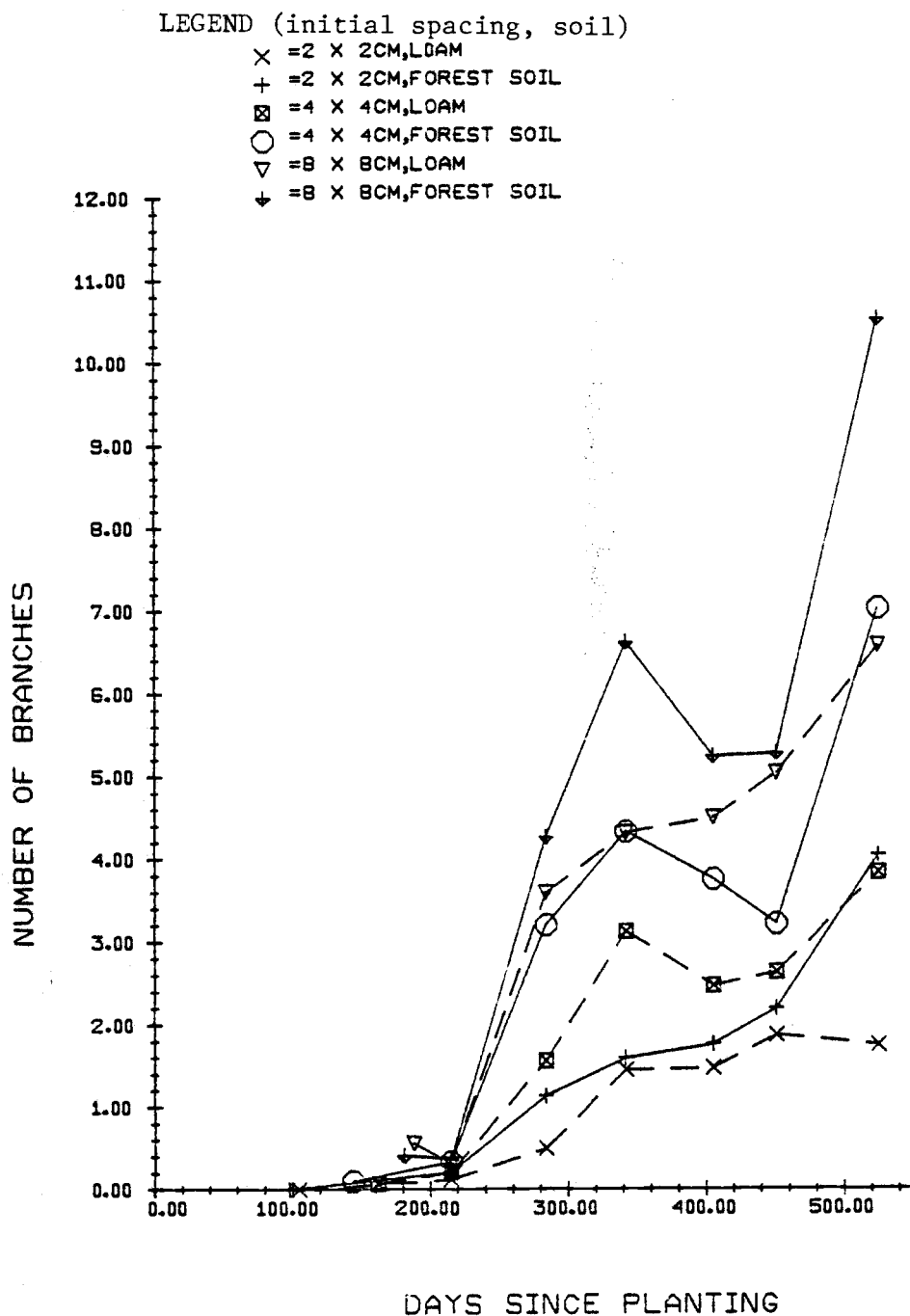
Figure 8. Average tree crown volume of seedling red alder growing
at various density levels and on two soil types under greenhouse
and lath house conditions. Dashed lines are loam, solid lines are
forest soil. Points are means of 2 or 3 values. The number of days
since planting are based on actual growing days, and do not include
any dormant periods. The approximate coefficient of variation for
each mean is 53% (from log tranformed ANOVA, see Appendix IV).
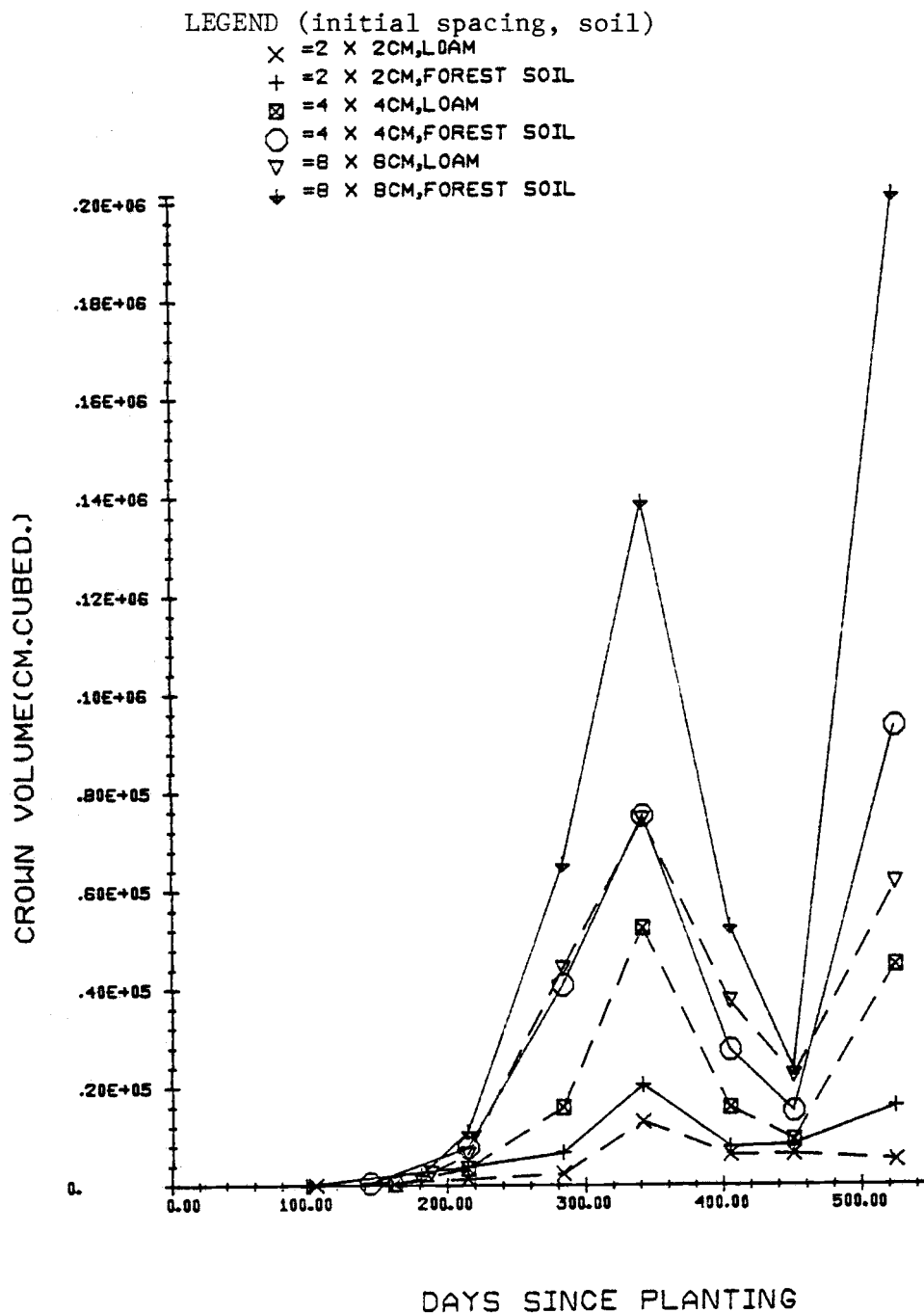
Figure 9. Average tree crown surface area of seedling red alder growing at various density levels and on two soil types under greenhouse and lath house conditions. Dashed lines are loam, solid lines are forest soil. Points are means of 2 or 3 values. The number of days since planting are based on actual growing days, and do not include any dormant periods. The approximate coefficient of variation is 31% (from log transformed ANOVA, see Appendix IV).

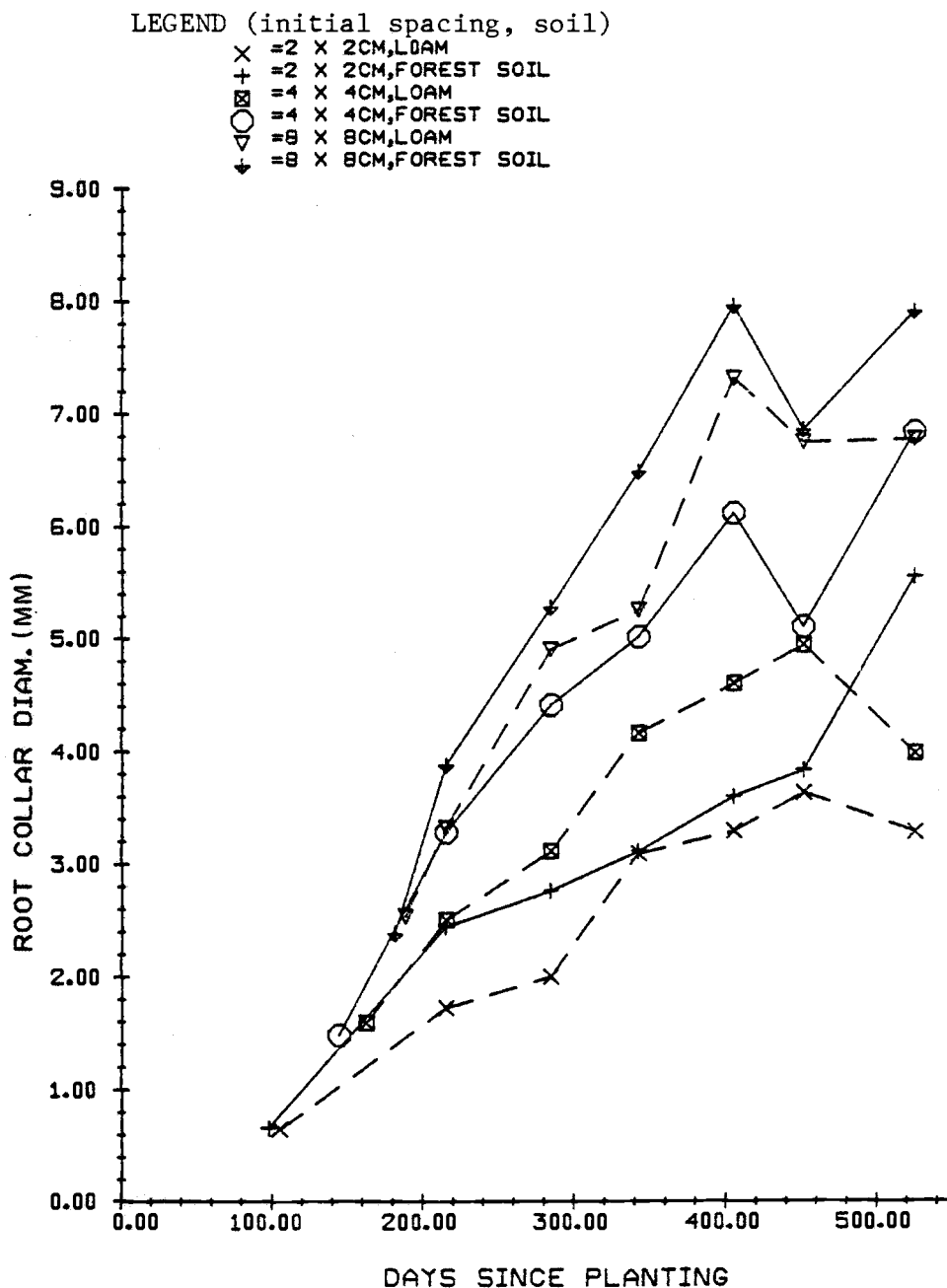LEGEND (initial spacing, soil)
X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
◯ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
✦ =8 X 8CM,FOREST SOIL

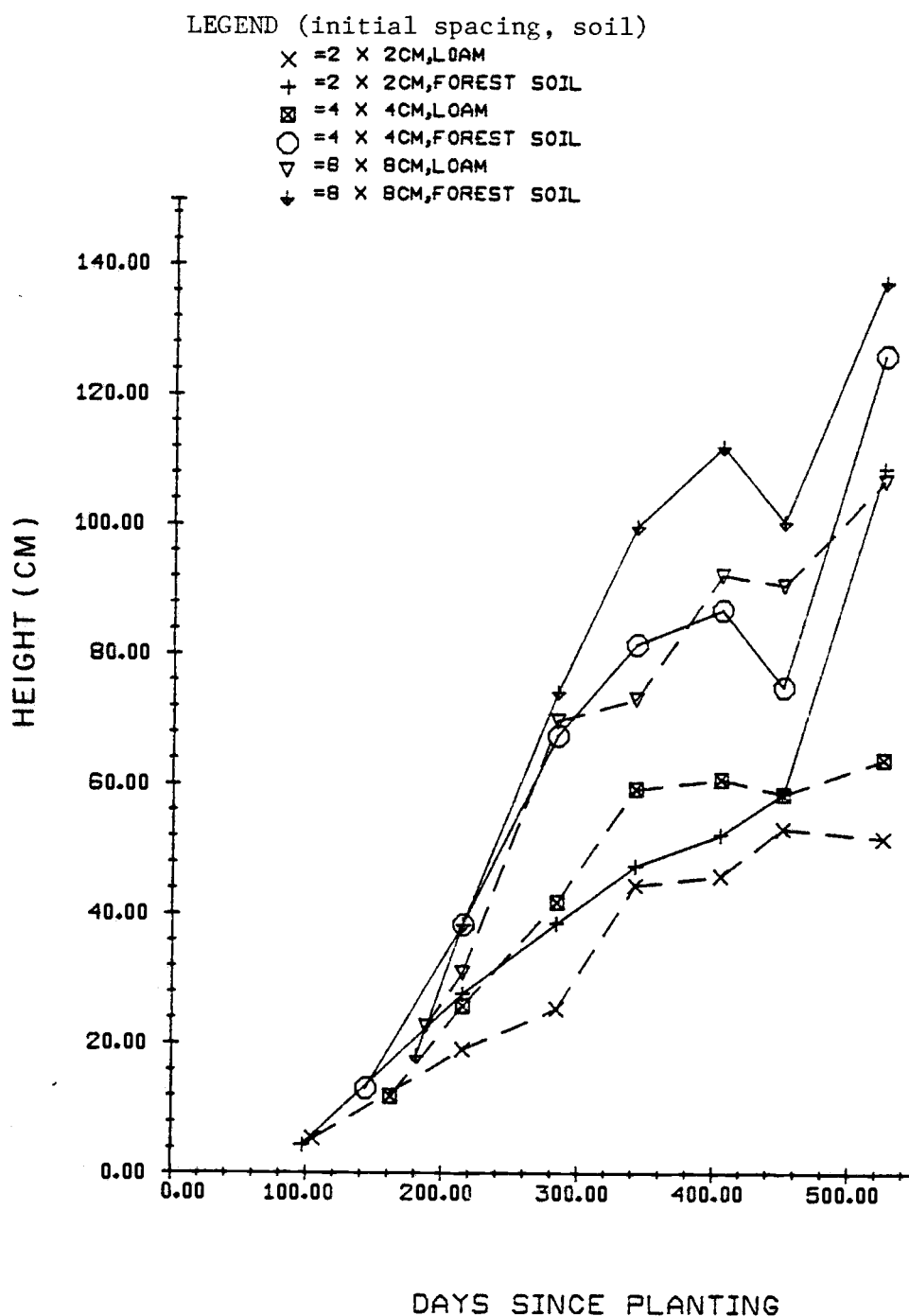CROWN SURFACE AREA(CM SQ.)

DAYS SINCE PLANTING
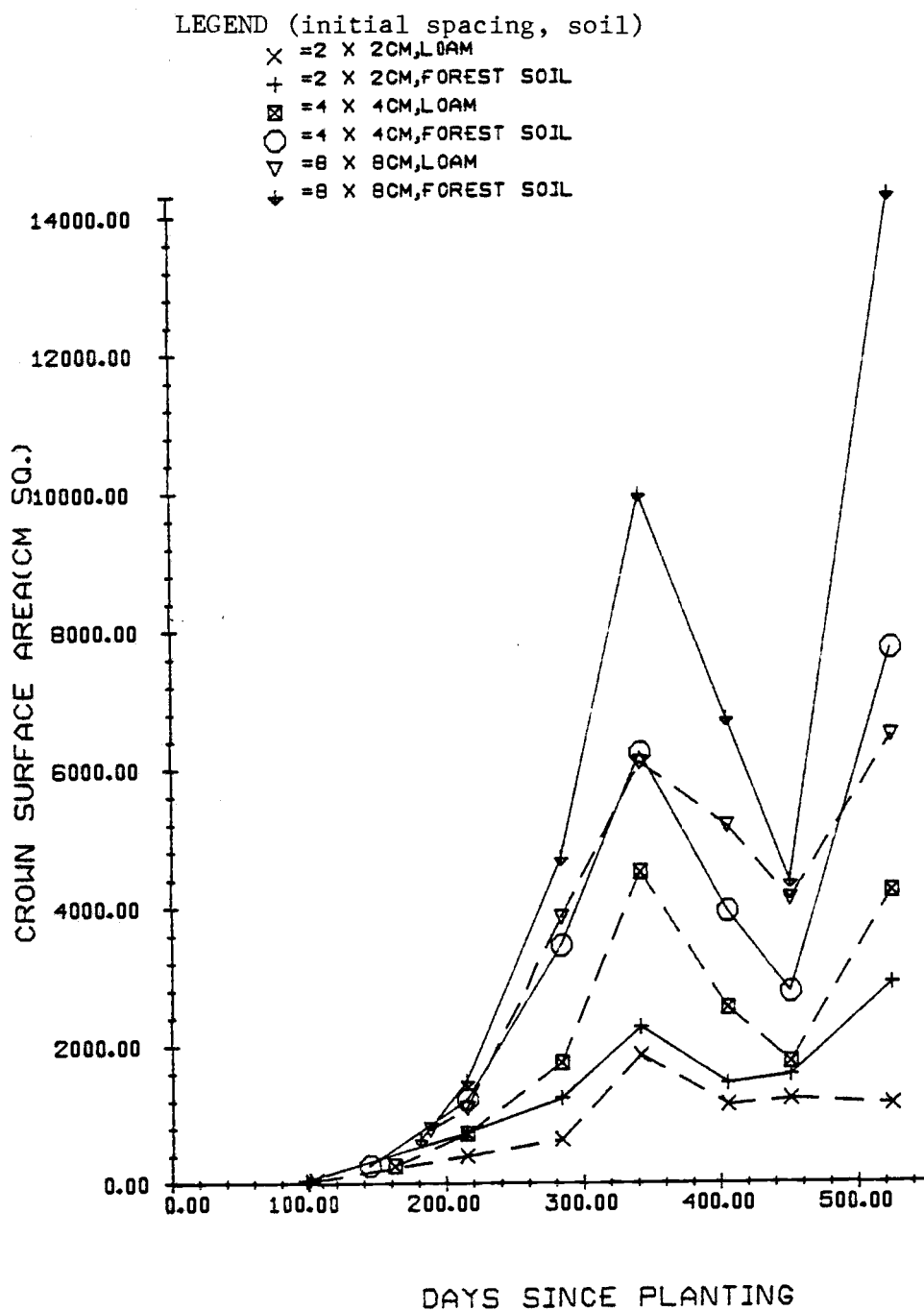
Table 7. Percentage breakdown of average tree biomass for seedling red alder grown at various density levels and on two soil types under greenhouse and lath house conditions.

Initial spacing (cm between plants)	Harvest date[1]	Total plant weight (g)		Percent stem	Percent leaves	Percent roots	Percent branches	Percent nodules
		Loam	Forest soil					
2	1	0.049	0.041	16	61	21	0	1
4	1	0.282	0.288	20	63	17	0	0
8	1	0.734	0.904	22	63	15	1	0
2	2	0.423	1.021	36	28	22	1	3
4	2	0.965	1.929	36	39	21	1	3
8	2	1.650	2.593	36	39	20	2	3
2	3	0.991	2.133	27	30	29	10	4
4	3	3.575	7.78	32	36	19	8	5
8	3	8.661	11.371	34	38	17	7	5
2	4	3.843	5.193	39	37	13	9	2
4	4	11.595	16.267	39	37	12	11	2
8	4	15.885	27.781	39	37	11	11	2
2	5	5.417	6.896	46	20	19	13	2
4	5	12.712	20.249	46	20	18	14	2
8	5	28.902	35.883	45	20	18	15	2
2	6	6.617	8.557	52	13	24	8	3
4	6	9.596	15.130	53	12	23	9	3
8	6	22.370	23.805	53	12	23	9	3
2	7	5.400	8.864	45	22	22	8	3
4	7	16.518	36.647	39	28	18	13	2
8	7	27.531	61.439	38	28	18	14	2

[1]Harvest date: for code see Chapter II, General Methods.

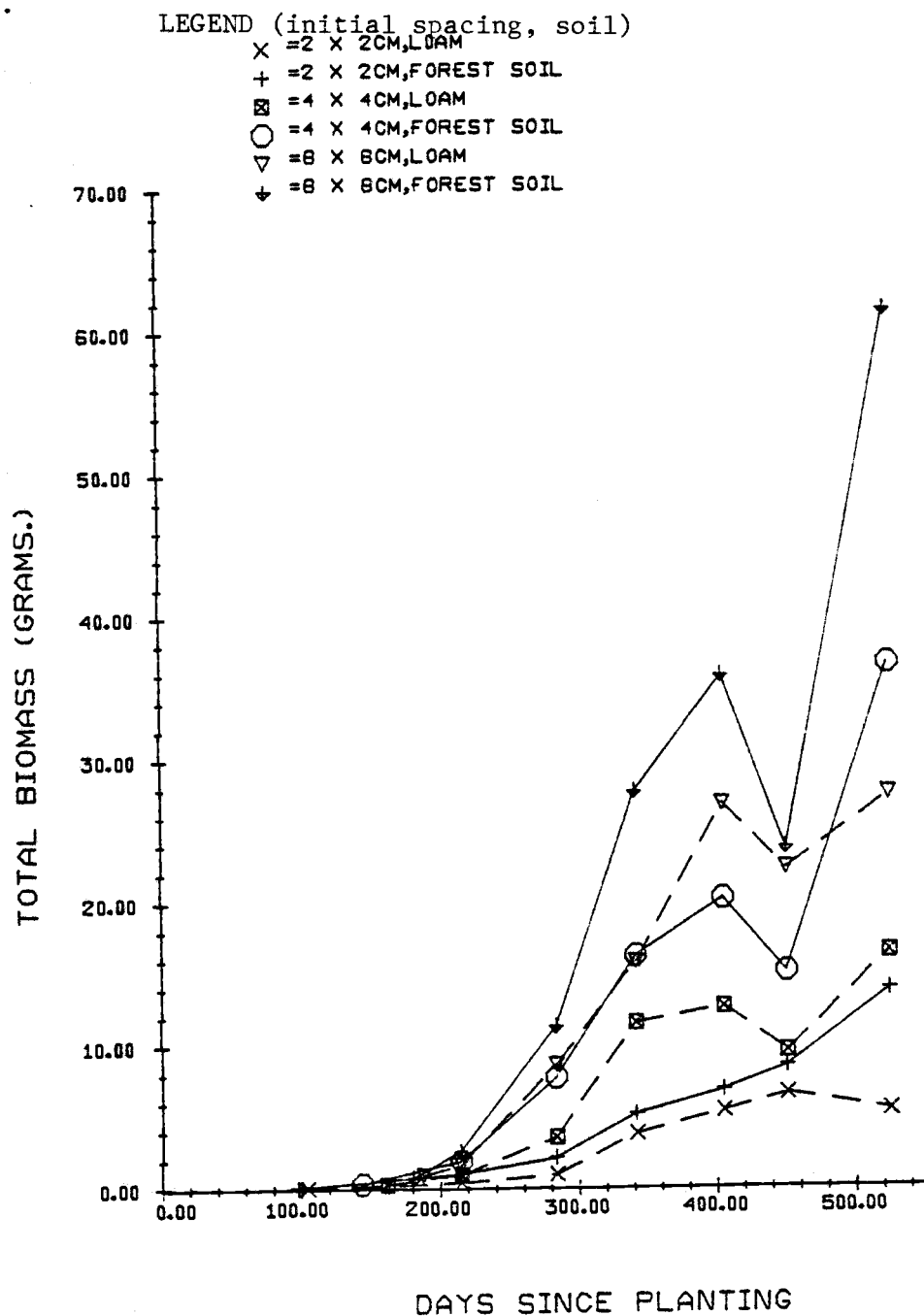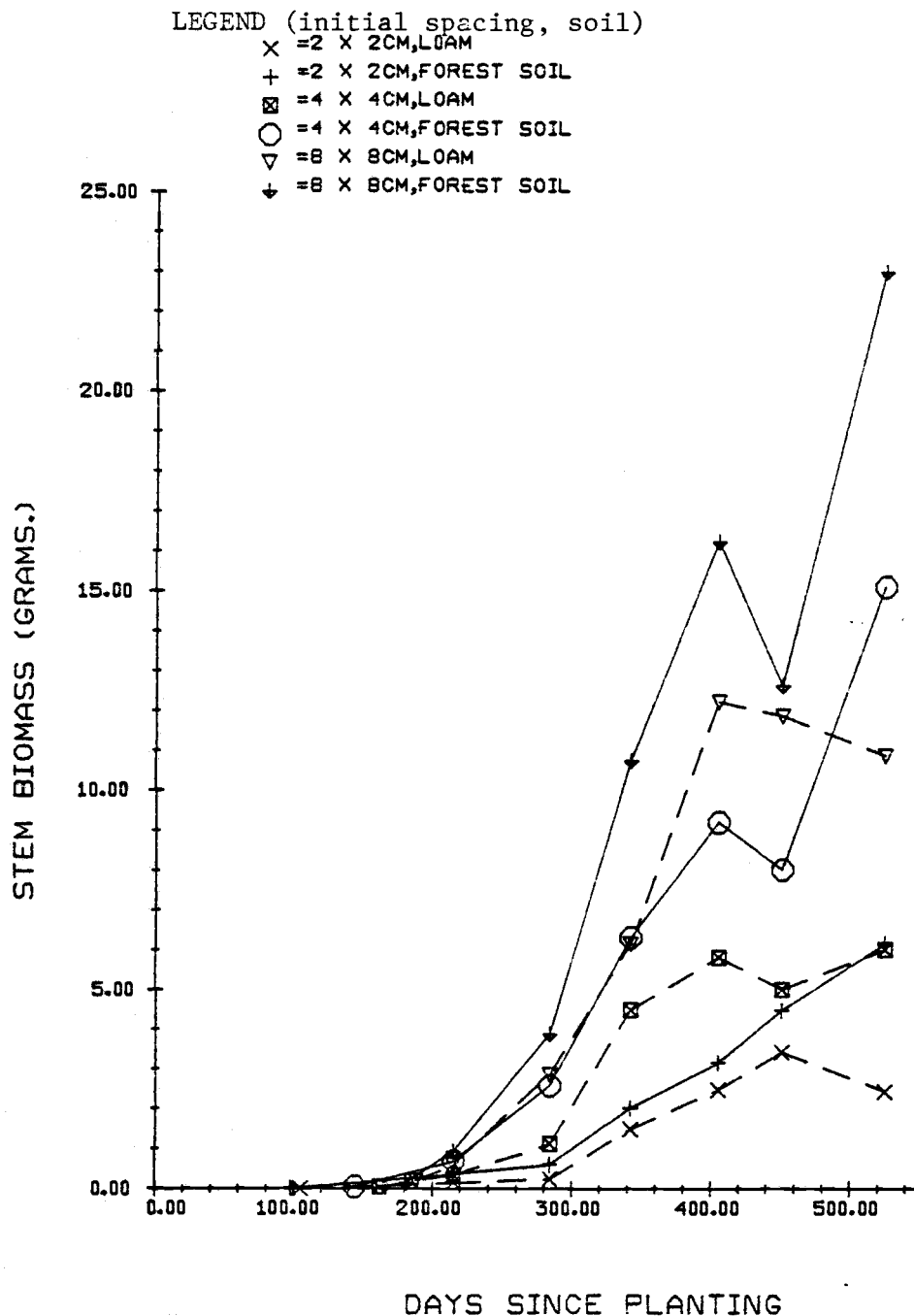Table 8. Analysis of variance for average tree and per unit area biomass and biomass production for seedling red alder grown at various density levels and on two soil types under greenhouse and lath house conditions.

Source of variation	df	[2]ln (BIO) g/tree	ln (BIO) g/tree/day	ln (BIO) g/m^2	ln (BIO) g/m^2/day	[5]ln(S:R ratio)
				[1]PR > F		
[3]Block	2	0.0068**	0.0068**	0.0179*	0.0265*	0.0005**
Date	6	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**
Block x Date (Error A)	12	0.2576	0.2582	0.1682	0.1943	0.6987
Soil	1	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**
[4]Spac	2	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**
Soil x Spac	2	0.2759	0.2522	0.5970	0.3772	0.4001
Soil x Date	6	0.0204*	0.0402*	0.2057	0.3337	0.0193*
Spac x Date	12	0.0002**	0.0101*	0.0039*	0.0106*	0.0001**
Spac x Soil x Date	12	0.9852	0.9837	0.9511	0.9595	0.8686
Error B	62					
Total	117					

[1]PR > F = probability of a greater F-value.
[2]BIO = Biomass: Dependent variable log$_e$ transformed to homogenize variauces.
[3]Block = replicate.
[4]Spac = initial spacing.
[5]S = shoot (leaves, stem, branches), R = root (root, nodules).
**Significant $p < 0.01$, * significant $p < 0.05$.

Table 9. Biomass and leaf area per unit area for red alder seedlings growing at various levels of density and on two soil types under greenhouse and lath house conditions.

[1]Spacing	[2]Soil	[3]Date	Biomass (kg/m^2)	Leaf area (one side)	[1]Spacing	[2]Soil	[3]Date	Biomass (kg/m^2)	Leaf area (one side)
2	1	1	.113	2.7	4	2	1	.180	4.4
2	1	2	.618	7.1	4	2	2	.783	9.3
2	1	3	1.321	11.8	4	2	3	1.958	22.9
2	1	4	3.356	25.0	4	2	4	5.145	38.1
2	1	5	3.367	14.0	4	2	5	5.126	20.8
2	1	6	5.205	13.5	4	2	6	4.981	11.2
2	1	7	3.903	16.1	4	2	7	6.297	30.9
2	2	1	.095	2.3	8	1	1	.141	3.4
2	2	2	.989	11.6	8	1	2	.230	2.7
2	2	3	2.314	22.9	8	1	3	1.116	13.1
2	2	4	4.279	31.7	8	1	4	1.892	14.0
2	2	5	4.407	18.3	8	1	5	2.870	11.6
2	2	6	4.912	12.3	8	1	6	2.435	5.5
2	2	7	5.659	24.1	8	1	7	2.942	15.3
4	1	1	.170	4.1	8	2	1	.115	2.7
4	1	2	.408	4.8	8	2	2	.334	4.0
4	1	3	1.272	14.2	8	2	3	1.442	17.6
4	1	4	3.788	28.0	8	2	4	3.505	25.9
4	1	5	3.509	14.4	8	2	5	4.009	16.0
4	1	6	3.000	7.5	8	2	6	2.664	6.0
4	1	7	3.802	22.6	8	2	7	4.954	27.4

[1]Spacing: 2 = 2 x 2 m, 4 = 4 x 4 cm, 8 = 8 x 8 cm initial spacing.

[2]Soil: 1 = loam, 2 = forest soil.

[3]Date = harvest date (Table 2).

greatly with harvest date, though the absolute amounts of biomass were much greater on the forest soil. This suggested greater inherent productivity on the forest soil.

To some extent, the decrease in average tree biomass at the 6th harvest (October 30, 1981) reflects the seasonal effects that could not be excluded from the experiment (Figure 3). By this time, green leaf-fall was considerable. Figure 5 shows a decline in leaf area per tree setting in after the 4th harvest (320 days since planting). Table 7 shows that, between the 4th and 6th harvest, the leaf biomass proportion decreased by c. 23%. The average number of branches per tree appears to have also declined for some treatments between the 4th and 6th harvests (Figure 7) as did crown volume and surface area (Figures 8 and 9). Branch length also showed signs of decline for some treatments by the 6th harvest (Figure 6). It seems there may have been accelerated branch death for some treatments during the later part of the year. Also movement of the experiment from greenhouse to lath house may have altered ontological development—the percent of biomass that was invested in stem and root tissue increased noticeably (Table 7). Finally, decreased growth at the 6th harvest may be partly caused by experimental inconsistencies.

Table 8 lists the results of analysis of variance on net primary production per tree. Not surprisingly these results parallel those for average biomass per tree, except that the initial spacing by date interaction is only significant at the 95% level. The results for biomass per unit area and for biomass per unit area per unit time only show one interaction effect (spacing by date, $p < 0.05$). Thus, when

considering actual stand density there were significant differences between soil type ($p < 0.01$).

The shoot:root (S:R) ratio showed a significant initial spacing by date interaction ($p < 0.01$) and soil by date interaction ($p < 0.05$) due to nonadditive seasonal variability. However, the allometric relationship between S (leaves, branches, stem) and R (roots and nodules) remained very stable throughout the experiment:

$$\ln (S) = 1.303 + 1.0164 \ln (R)$$

where $\overline{R^2}$ = .97

mse = .0912

n = 118

S = shoot weight (g)

R = root weight(g)

It may be argued (e.g., Ledig et al. 1970) that allometric relationships between S and R are measures which account for tree size, and thus remove size differences which may materially effect ANOVA analyses, unless tree size is included as a covariate. Alternatively to accurately measure S:R changes with respect to tree size over time we can regress S:R against average biomass per tree at each harvest date in the form of dummy variables. The following model was significant for all parameters ($p < 0.05$):

$$\ln (S:R) = 1.717 - .586 \cdot I2 - 1.008 \cdot I3 - .253 \cdot I4 - .557 \cdot I5 - .807 \cdot I6$$
$$- .830 \cdot I7 + .142 \cdot \ln B + .153 \cdot I3 \cdot \ln B - .066 \cdot I5 \cdot \ln B$$
$$- .094 \cdot I6 \cdot \ln B$$

where, $\overline{R^2}$ = .953

  MSE = .0046

  n = 118

  S = shoot weight (g)

  R = root weight (g)

  B = tree biomass (g)

  I2 = indicator variable at 2nd harvest, i.e., if tree was from

    2nd harvest then I2 = 1.0, if not I2 = 0

  I3 = 3rd harvest dummy variable etc. (see Table 2 for harvest

    dates)

A normal probability plot showed a reasonable approximation to normality. The S:R ratio was extremely variable and interpretation of the equation is complex. However, over the experimental range of tree sizes the changes in the slope parameters at the 3rd, 5th and 6th harvests have negligible effects so that discussion can be focused on the intercept parameters. All intercept parameters (the first 7 parameters in the equation) were significant ($t_{2\alpha} < 0.05$). Generally, the S:R ratio increased with tree size across all harvest dates. The S:R was highest at the 1st harvest, declined through the 3rd harvest, increased during the 4th harvest and decreased thereafter. This pattern implies that root growth was emphasized between the 2nd (February) and 3rd (May) harvests, with shoot growth emphasized up to the 4th harvest (July), and from thereon root growth was reemphasized. This fits in with classical patterns of root regeneration during the early spring and fall (e.g., Figure 1.24 in Kozlowski 1977).

Table 9 shows unit area biomass and leaf-area estimates. It is inappropriate to extrapolate estimates based on such small sample areas (.31 m^2, .08 m^2 and .02 m^2 from widest to densest initial spacings). Smith (1975) discusses this point. For instance, Smith (1978) gives the following above-ground estimates for 8- to 10-yr old natural stands of alder: a mean of 9 t/ha/yr (40 m^2 plots) but a maximum of 53 t/ha/yr (2 m^2 plots). The values from Table 9 can be converted to a comparable basis by putting the estimates onto a 6 month growing season basis. Thus, after 525 days the mean production was ~ 16 t/ha/yr with an upper estimate of 31 t/ha/yr. These data suggest that the estimates presented here lie in the upper end of the production range but are clearly not unreasonable, especially when the artificial nature of the experiment is considered. The estimates of leaf area index (one side) after 525 days were a mean of 22 m^2/m^2 and an upper value of 31 m^2/m^2 (Table 9). This compares against a mean of 8 m^2/m^2 or upper value of 10 m^2/m^2 given by Smith (1978) for 8- to 10-yr old alder. The higher values presented here may be partly attributable to favorable edge effects on all trees. The restricted growing space is also likely to have increased the leaf density per unit area. The differences could also be due to differences in inherent growth patterns between the seedlings used in this experiment and the saplings measured by Smith (1978).

Edge Effects on Tree Biomass and Structure

Table 10 shows the edge effect allometric equations (based on Equations 1 and 2). The values of b_0 and b_1 reflect intercept and slope of the regression of the dependent variable on biomass for the

Table 10. Edge effect allometric equations for seedling red alder grown at three density levels and on two soil types under greenhouse and lath house conditions.

Dependent variable	b_0	b_1	b_2	b_3	b_4	b_5	$\bar{R}^2$	MSE
Stem wt.	-1.166**	1.098**	-.031*	-.076**	.018*	.009^{NS}	.98	.119
[1]Stem wt.	-1.227**	1.121**	.0002**	.0004**	-.000089**	-.00015**	.98	.116
Leaf wt.	-1.151**	.927**	.008^{NS}	-.005^{NS}	.002*	.0004^{NS}	.96	.178
Root wt.	-1.516**	.951**	.007^{NS}	.053**	-.018**	-.001^{NS}	.98	.094
Branch wt.	-2.77**	.760**	.288**	-.084^{NS}	-.117**	-.190**	.22	7.325
Branch diameter	1.749**	.451**	.011^{NS}	.042^{NS}	.008^{NS}	.009^{NS}	.44	1.213
Crown width	2.239**	.393**	.019^{NS}	.056**	-.010^{NS}	-.009^{NS}	.817	.155
No. of branches	.112**	.468**	.049^{NS}	-.016^{NS}	-.051**	-.048**	.44	1.23
Crown volume	7.045**	1.182**	.019^{NS}	.128**	.03^{NS}	.008^{NS}	.916	.597
Crown surface area	6.05**	.784**	.054^{NS}	.202**	-.019^{NS}	-.003^{NS}	.738	.987
Nodule wt.	-3.332**	.868**	-.001^{NS}	-.068**	-.017^{NS}	-.005^{NS}	.96	.159
Leaf area	4.417**	.866**	.023^{NS}	.038^{NS}	.02^{NS}	-.003^{NS}	.91	.344

[1]Based on Equation 2, all others Equation 1.

t-value significance: **significant $p < 0.01$, *significant $p < 0.05$; NS = not significant; $p \geq 0.01$.

$\bar{R}^2$ = adjusted multiple correlation coefficient.

MSE = mean squared error.

No. of observations = 3412.

outermost row of surviving trees, while b_2 and b_4 reflect the inter-
cept and slope indicator variables for the next row in. Finally,
b_3 and b_5 account for the intercept and slope indicator variables for
the innermost surviving trees. The first two equations listed in
Table 11 compare the fit for Equations 1 and 2. It can be seen that
the explicit use of time as a quantitative variable rather than a
a qualitative one slightly improves the mean squared error and causes
every indicator variable to be significant ($p < 0.01$). The improve-
ment was not substantial enough, considering the large number of
observations, to necessitate this analysis of every dependent varible
listed in Table 10. It should be noted that with the large number of
observations even small differences are likely to be significant. The
other results are of the qualitative time effects model. In general,
significant slope dummy variables were negative while significant
intercept variables were positive. This implies that smaller trees
did relatively better with increasing edge effect while larger trees
fared worse. Of the dependent variables considered, only stem, root,
branch weight and branch number had more than one significant dummy
variable ($p < 0.05$).

While this analysis does not fully investigate the variation of
edge effects with time, results suggest that variation in edge effects
were minimal.

Analysis of Skewness and Kurtosis on Tree Biomass

Figures 10 through 12 show the trends in average skewness values
for total tree biomass. Figures 13 through 15 show the analogous

Table 11. Analysis of variance for skewness and kurtosis statistics
of seedling red alder grown at various levels of density
and on two soil type under greenhouse and lath house
conditions.

Source	DF	LN (skewness)		LN (kurtosis)	
		F-value	PR > F	F-value	PR > F
Block	2	0.03	.9668	0.37	.6967
Date	6	5.79	.0049**	3.57	.0287*
Block x date	12	1.68	.0939	1.05	.4162
(Error A)		[1](.1429)		[1](.5593)	
Space	2	0.19	.8272	1.26	.2900
Soil	1	0.05	.8252	0.02	.8963
Space x soil	2	1.83	.1696	0.48	.6219
Soil x date	6	1.76	.1233	1.38	.2363
Space x date	12	5.24	.0001**	2.56	.0083**
Space x soil x date	12	1.78	.0723	1.06	.4047
(Error B)	62	[1](.0852)		[1](.5321)	
Total	117				

[1]Mean squared error in brackets.

Block = block or replicate.
Space = initial spacing level.
Data logarithmically transformed (base e) to homogenize variance.
** = significant $p < 0.01$, * = significant $p < 0.05$.
PR > F = probability of a larger F-value.

Mean Skewness Values for Seedling Red Alder Biomass by Initial Spacing and Soil Type over Time.
The first 4 measurements were made under greenhouse conditions while the last 3 were under lath house conditions. Each point is a mean of 2 or 3 values. Solid lines are forest soil, dashes are loam. The approximate coefficient of variation for each mean is 32% (from log transformed ANOVA, see Appendix IV). Days since planting are adjusted for any dormant periods.
Note that higher skewness values indicate that the distribution is more skewed to the right. Normal distributions have a value of zero.

Figure 10.

Figure 11.
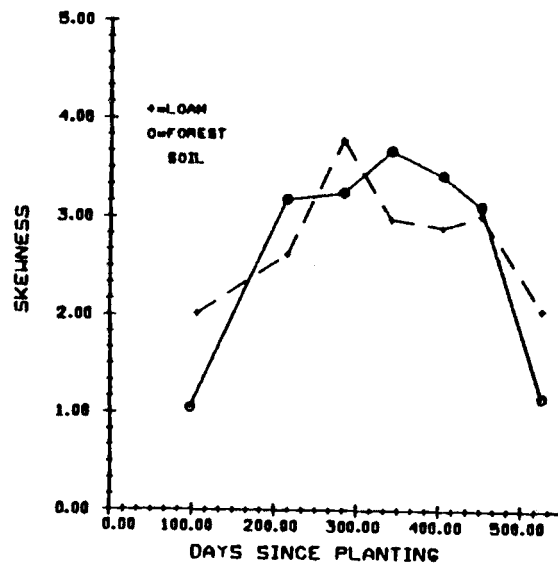
Figure 12.

2 BY 2 CM INITIAL SPACING
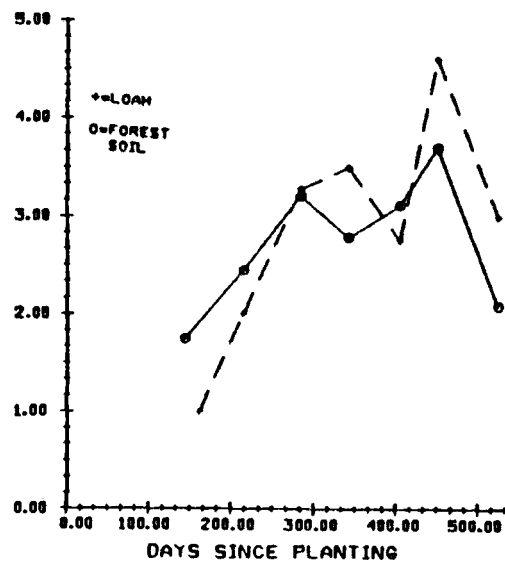
4 BY 4 CM INITIAL SPACING

8 BY 8 CM INITIAL SPACING
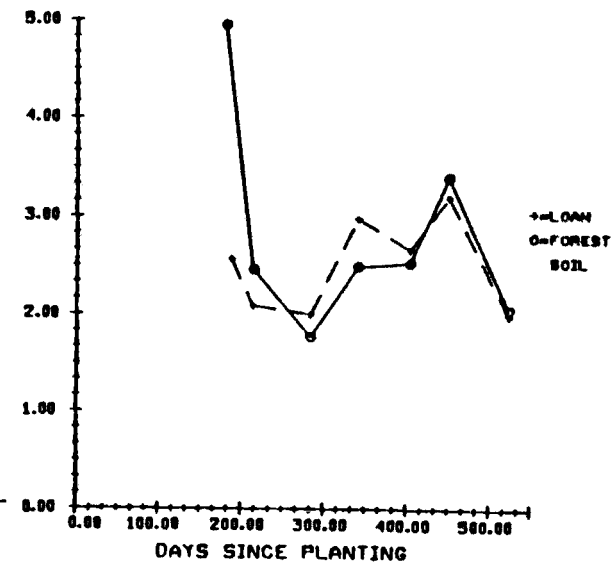
values for kurtosis. Table 11 lists analysis of variance for skewness and kurtosis statistics.

Generally, skewness and kurtosis peak at about the same time within each initial spacing regardless of soil type. The overall patterns suggest increasing skewness and kurtosis with time, followed later by a decrease.

Table 11 shows that there were no significant differences for skewness or kutsosis between soil types (p < 0.01) though there was a significant interaction between spacing and harvest date (p < 0.01). This suggests that different initial spacings behaved differently over time. Figures 10 and 13 show that, under the 2 x 2 cm initial spacing conditions, skewness and kurtosis peaked at about the third harvest. Trends in the 4 x 4 cm (Figures 11 and 14) and 8 x 8 cm (Figures 12 and 15) initial spacing levels are different. There was an initial peak at the 3rd or 4th harvest for the 4 x 4 cm spacings, followed by another peak at the 6th harvest. The 8 x 8 cm initial spacings statistics were highly skewed and peaked at the crown closure harvest, suggesting a severe initial size gradient (i.e., lots of small trees).

Mohler et al. (1978) proposed the following pattern for weight distributions in self-thinning populations: (1) initial normality: skewness = 0, kurtosis = 3, followed by (2) increasing positive skewness and kurtosis as more, smaller plants grow in size. Eventually, the suppressed, smaller plants die, leading progressively to (3) a decreasing skewness and kurtosis which is thought to be indicative of self-thinning.

The general pattern of increase and then decline in estimated skewness and kurtosis presented here follows these trends. However,

Mean Kurtosis Values for Seedling Red Alder Biomass by Initial Spacing and Soil Type over Time.
The first 4 measurements were made under greenhouse conditions while the last 3 were under lath house conditions. Each point is a mean of 2 or 3 values. Solid lines are forest soil, dashes are loam. The approximate coefficient of variation of each mean is 83% (from log transformed ANOVA, see Appendix IV). Days since planting are adjusted for any dormant periods.
Note that higher kurtosis values indicate that the distribution is more peaked. Normal distributions have a value of three.

Figure 13.

Figure 14.
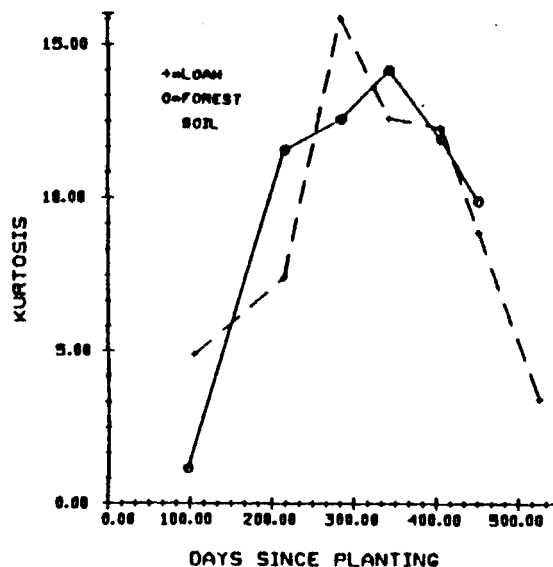
Figure 15.

2 BY 2 CM INITIAL SPACING
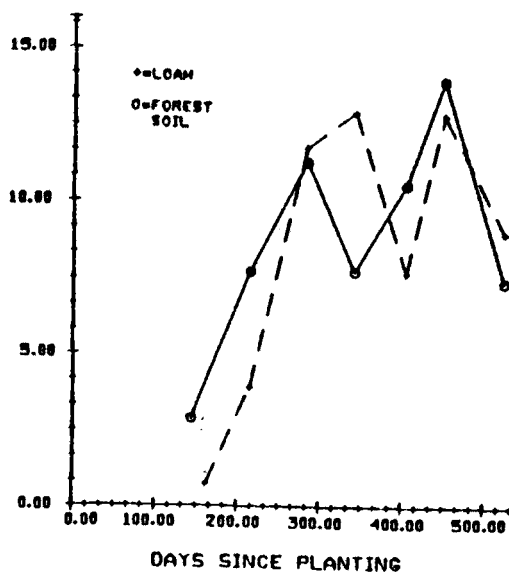
4 BY 4 CM INITIAL SPACING

8 BY 8 CM INITIAL SPACING
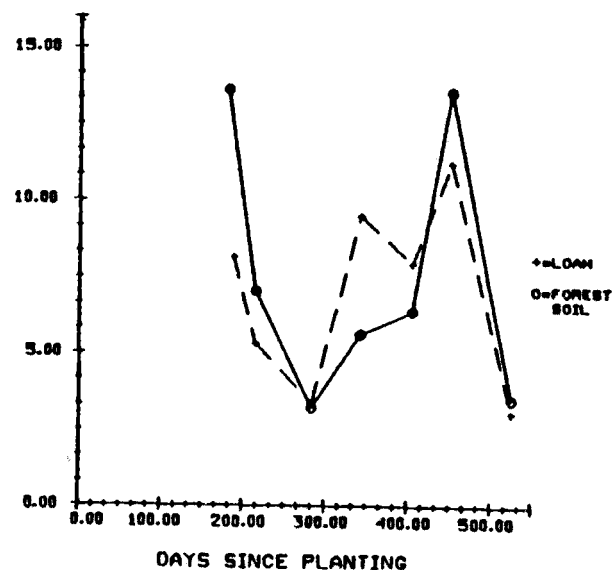
this analysis would indicate that density-dependent mortality defined by Mohler et al. (1978) did not occur in the 2 x 2 cm spacing until the 3rd harvest, or in the 4 x 4 cm spacing until somewhere between the 3rd and 6th harvest, or in the 8 x 8 cm spacing until the 6th harvest. In all cases, mortality was occurring before these dates. What actually constitutes density-independent or density-dependent mortality is not clear. Regardless, plants were able to fill up available space in a progressive, systematic fashion (Chapter IV, Figure 16).

CHAPTER IV. DEVELOPMENT OF ANALYTICAL MODELS FOR INVESTIGATION

OF SELF THINNING IN SEEDLING RED ALDER

Modelling the Relationship Between Size and Density

Introduction

The relationship between average plant size $(\overline{S})$ and stocking density $(\overline{\rho})$ in monospecific single-aged plant communities undergoing self-thinning is bounded asymptotically by the -3/2 power rule line (Yoda et al. 1963). That is,

$$\overline{S}_m = a_0 \rho^{-a_1} \tag{1}$$

or

$$\log \overline{S}_m = \log a_0 - a_1 \log \rho \tag{2}$$

where, $\overline{S}_m$ = maximum attainable average plant size (e.g., weight or volume)

ρ = actual stocking density

a_0 = intercept parameter

a_1 = slope parameter

The slope parameter, a_1 is apparently fixed at a value of ~ 1.5 for weight or volume, regardless of species, age or site conditions (Yoda et al. 1963, White and Harper 1970, Harper 1979, Gorham 1979). The intercept parameter, a_0, however, varies with species (White and Harper 1970), but only within fairly narrow logarithmic limits (Gorham 1979, White 1980, White 1981). An apparent exception to the rule occurs under decreasing light intensities. The intercept, a_0,

decreases systematically while the slope tends to stabilize at about -1.0 (Westoby and Howell 1981, Hutchings and Budd 1981). There are no other known exceptions to the rule.

Research has been hindered by lack of sound statistical analysis of the -3/2 power rule line. To date, there have been three general methods for fitting equation (2):

1. Arbitrarily hand fitting a line above an upper boundary of data points (Yoda et al. 1963, Drew and Flewelling 1977).

2. Fitting a simple linear regression through a data set subjectively chosen as undergoing density-dependent mortality (White and Harper 1970, Ford 1975).

3. Estimating the parameters via principal components analysis, again on subjectively chosen density-dependent mortality data (Mohler et al. 1978, Hutchings and Budd 1981).

All methods are statistically biased. A more direct approach would be to actually track the trajectory of average size $(\overline{S})$ as a function of density (ρ) towards an upper asymptote or self-thinning line.

The biological rationale is based on a continuum of responses in plant size between two sets of physical constraints. On the one hand, plants existing in non-self-thinning conditions are limited by plastic growth responses to finite plant space. Plant size is then a reciprocal or inverse relationship to stocking density, i.e.,

$$\log (\overline{S}) = \log b_0 - b_1 \log \rho, \quad 0 \leq b_1 \leq 1 \qquad (3)$$

This equation tells us that there is a certain maximum size a plant can attain provided initial density is maintained. The trajectory of average plant size to density (the $\overline{S}$-ρ trajectory) is then a vertical line on log-log coordinates. Equation 3 is the reciprocal yield law (Kira et al. 1953, Shinozaki and Kira 1956).

The second physical constraint is imposed by Equation 2, the -3/2 power rule. The $\overline{S}$-ρ trajectory in the interzone between Equations 2 and 3 is a continuous inelastic response in plant size to decreasing density in which the exponent of the independent variable, ρ, intergrades between -1 and -3/2. It can thus be seen why researchers have been puzzled by the apparent fluctuation of the exponent in stands which are undergoing subjectively selected density dependent mortality (e.g., -1.08 to -2.18 (White and Harper 1970) and -1.22 to -1.46 (Mohler et al. 1978)).

There is ample empirical evidence to suggest the existence of an ($\overline{S}$-ρ) trajectory such as that just outlined (Drew and Flewelling 1977, Hozumi 1977, White 1981). In the next section I suggest and test a model which actually tracks the $\overline{S}$-ρ trajectory over a series of different initial densities and site types.

A realistic interpretation of the -3/2 power rule helps make sense of empirical evidence for the existence of an inviolable -3/2 power rule. Because average plant weight ($\overline{W}$) is related to average plant volume ($\overline{V}$) as $\overline{W} \propto \overline{V}^1$ (White 1981), we may couch this discussion in terms of $\overline{V}$. This derivation involves examining how plants might fill up available space ($\overline{V}_E$). The volume the plant itself occupies is given by:

$$\overline{V} \propto \overline{d^2 h} \qquad (4)$$

where, $\overline{V}$ = average plant volume

$\overline{d}$ = diameter of average plant

$\overline{h}$ = height of average plant

For simplicity, the value of $\overline{d}$ is assumed to be approximated by average crown width $(\overline{CW})$. Thus, volume a plant may potentially occupy is given by

$$\overline{V}_E \propto \overline{d}_E^2 \overline{h}_E \tag{5}$$

where, $\overline{V}_E$ = average environmental volume

$\overline{d}_E$ = average environmental diameter

$\overline{h}_E$ = average height of environmental volume (which is

equivalent to average plant height).

Now, it can be shown that $\overline{d}_E^2 = \rho^{-1}$ or potential area per tree. The relationship between $\overline{h}_E$ and $\overline{d}_E^2$ is approximately

$$\overline{h}_E \propto (\overline{d}_E^2)^\theta, \ \theta \simeq .5 \ \text{(after Curtis 1970)} \tag{6}$$

Substituting $\rho^{-1/2}$ for $\overline{d}$ in Equations 5 and 6 and then combining these two equations:

$$\overline{V}_E \propto \rho^{-1} \rho^{-\theta} \propto \rho^{-(1+\theta)}, \ \theta \simeq .5 \tag{7}$$

The environmental volume and plant volume are related as follows:

$$\overline{V} \propto \overline{V}_E^m, \ 0 < m \leq 1 \tag{8}$$

This suggests that $\overline{V}$ incrementally fills up $\overline{V}_E$ but cannot exceed it. If crowns overlap, however, $\overline{V}_E$ may potentially be exceeded so that the upper limits of m are only tentative at present. Also, the

relationship may be more complicated than the power function suggests (Perry, unpublished). With these strictures borne in mind, if we now replace the left hand side of Equation 7 with Equation 8 we have:

$$\overline{V} \propto \rho^{-m(1+\theta)}, \; 0 < m \leq 1 \tag{9}$$

$$\theta \simeq .5$$

Because $\overline{h}_E$ must equal $\overline{h}$ (by definition), θ relates directly to the relationship between potential area per tree (ρ^{-1}) and tree height. In normal stands, $\overline{h} \propto \rho^{-1/2}$ (Curtis 1970) which conforms to the constraints in Equation 9. The relationship between $\overline{V}_E$ and $\overline{V}$ is extremely complex. White (1981) has shown that Equation 4 may be more correctly stated as:

$$\overline{V} \propto (\overline{d^2 \cdot h})^k, \; k < 1 \tag{10}$$

If we assume that crown width ($\overline{CW}$) is a reasonable measure of $\overline{d}$ in Equation 10, then:

$$\overline{V} \propto (\overline{CW^2 \cdot h})^k \tag{11}$$

Substituting Equation 9 into Equation 11:

$$\rho^{-m(1+\theta)} \propto (\overline{CW^2 \cdot h})^k \tag{12}$$

Thus, the -3/2 power rule exponent is given by:

$$m(1+\theta) \propto -\frac{k \cdot \log (\overline{CW^2 \cdot h})}{\log \rho} \tag{13}$$

Equation (13) tells us that the -3/2 power rule exponent is equal to the logarithmic response of tree volume ($\overline{CW^2 \cdot h}$) to potential tree

area. The derivation is constrained by (1) the relationship between tree height and potential tree area (θ) and (2) the relationship of actual to potential volume (m). This closely follows the interpretation given by Perry (unpublished) in which these constraining constants continually respond towards a value of c. -1.5. The validity of this derivation will be tested later in this chapter.

Objectives

(1) Develop an analytical model to characterize the average weight-stocking density relationship (the $(\overline{W}-\rho)$ trajectory) in seedling red alder growing at three initial spacing levels and on two soil types.

(2) Use this analytical model to determine carbohydrate partitioning among plant parts with changing density.

(3) Use this analytical model to determine the allometric relationship between measures of plant geometry and stocking density.

(4) Use the knowledge gained from above analyses to construct a prototype model to track the $(\overline{W}-\rho)$ trajectory over time.

Derivation of an Analytical Size-Density Model

The analytical model was designed to track the size-density trajectory [$(\overline{S}-\rho)$ trajectory] as the difference between two functions;

(1) Firstly, for a single species growing across a range of densities, the $(\overline{S}-\rho)$ trajectory should tend asymptotically towards a single self-thinning line,

$$\overline{Y}_{mji} = a_0 - a_1 X_{ji} \tag{14}$$

where, $\overline{Y}_{m_{ji}}$ = log (maximum average plant size)

X_{ji} = log (actual stocking density)

a_0 = intercept

a_1 = slope

j = number harvest dates or age of plant

i = number of initial density levels

(2) Secondly, the $(\overline{S}-\rho)$ trajectory should approach Equation 14 as a monotitically decreasing function, i.e., a negative exponential function of the change in actual density (X_{ji}) from initial density (X_{0i}):

$$\overline{Y}_{ji} = \overline{Y}m_{ji} - a_0 \cdot a_4 \cdot e^{-a_2(X_{0i}-X_{ji})^{a_3}} \qquad (15)$$

where, $\overline{Y}_{ji}$ = log (average plant size)

X_{ji} = log (actual stocking density)

X_{0i} = log initial stocking density level)

a_4 = adjustment parameter of line adjoining all initial density levels, assuming it is parallel to Equation (14)

a_2 = intercept
$\left.\right\}$ exponential function parameters
a_3 = power

The parameter a_4 in Equation (15) is the intercept adjustment to a_0 of a line joining all initial density values of $\overline{Y}_{ji}$, assuming the line is parallel to the asymptote Equation (14). If this line is not parallel, then:

$$\overline{Y}_{ji} = \overline{Y}m_{ji} - a \cdot a_4 - a_1 \cdot a_5 \cdot X_{0i} \cdot e^{-a_2(X_{0i} - X_{ji})^{a_3}} \qquad (16)$$

where, symbols as in Equation 15.

a_5 = adjustment parameter for intercept at initial density from asymptote.

Substituting Equation 14 into this equation we have:

$$\overline{Y}_{ji} = a_o - a_1 X_{ji} - a_o \cdot a_4 - a_1 \cdot a_5 \cdot X_{0i} \cdot e^{-a_2 (X_{0i} - X_{ji})^{a_3}} \qquad (17)$$

Alternatively we may commence the model at Y_{0i} and make no assumptions about the slope and intercept at initial density, viz:

$$\overline{Y}_{ji} = \overline{Y}m_{ji} - a_o - a_1 X_{0i} - Y_{0i} \cdot e^{-a_2 (X_{0i} - X_{ji})^{a_3}} \qquad (18)$$

There are two more modifications to make to Equation 17 before it is in its most generalized form:

Firstly, I expand a_2 and a_3 to accommodate possible changes in the shape of the $(\overline{S} - \rho)$ trajectory, respectively as:

$$(a_2 + a_6 X_{0i} + a_7 X_{0i}^2) \qquad (19)$$
$$(a_3 + a_8 X_{0i} + a_9 X_{0i}^2) \qquad (20)$$

Incorporating these two modifications into Equation 18 we have:

$$\overline{Y}_{ji} = a_0 + a_1 X_{ji} - (a_0 \cdot a_4 - a_1 \cdot a_5 X_{0i}) \cdot$$

$$e^{-(a_2 + a_6 X_{0i} + a_7 X_{0i}^2) \cdot (X_{0i} - X_{ji})}{}^{(a_3 + a_8 X_{0i} + a_9 X_{0i}^2)} \quad (21)$$

Finally, if we wish to test the difference between two soil types, fertilizer levels, etc. on the slope and intercept of the asymptote an indicator variable can be added to the model:

$$\overline{Y}_{ji} = (a_0 + a_{10} \cdot I) - (a_1 + a_{11} \cdot I) \cdot X_{ji} - ((a_0 + a_{10} \cdot I) \cdot a_4 - (a_1 + a_{11} \cdot I) \cdot a_5 \cdot X_{0i}) \cdot$$

$$e^{-(a_2 + a_6 X_{0i} + a_7 X_{0i}^2) \cdot (X_{0i} - X_{ji})}{}^{(a_3 + a_8 X_{0i} + a_9 X_{0i}^2)} \quad (22)$$

where, I = indicator variable; 1 if soil type 1, 0 if else

$\overline{Y}_{ji}$ = log (average plant size)

X_{ji} = log (actual stocking density)

X_{0i} = log (initial stocking density)

j = number harvest dates

i = number initial stocking density

a_0 = asymptote intercept parameter

a_1 = asymptote slope parameter

a_4 = adjustment for intercept at initial density

a_5 = adjustment for slope at initial density

a_2, a_6, a_7 = parameters for intercept for exponentiated difference function

a_3, a_8, a_9 = parameters for slope of exponential difference function

a_{10} = soil type parameter adjustment to asymptote intercept

a_{11} = soil type parameter adjustment to asymptote slope.

Model Fitting Methods

The strategy adopted was to work from simpler to more complex permutations of Equation 25. A BMDP non-linear regression procedure was used exclusively (Ralston 1981) which solves for parameters by a Gauss-Newton linearization (Draper and Smith 1966). The goal was to derive a model form with all parameters contributing significantly ($p < 0.01$) or at least in a biologically and mathematically meaningful fashion. Non-significant parameter estimates were first screened by their asymptotic standard errors. Full and reduced model residual sums of squares were then tested for significant differences ($p < 0.01$) as a basis for parameter rejection. It should be noted that, for non-linear equations, the parameter estimates are not normally distributed, nor is the mean squared error an unbiased estimate of σ^2 so that confidence intervals are only approximate or asymptotic if n is large (Draper and Smith 1966).

I commenced the model at crown closure (i.e., the 1st harvest). In its present form the model requires that $(X_{0i} > X_{1i})$ where X_{0i} = initial density, X_{1i} = density in next time period. From the data collected, this condition is only satisfied after crown closure. Thus, the values of X_{0i} in Equation 25 are replaced by X_{1i}, where X_{1i} = actual density at crown closure. The intercept and slope of the crown closure line can thus be compared to those values at the asymptote. Crown closure may conveniently be assumed to indicate the onset of considerable tree interferences. Drew and Flewelling (1979) reasoned that the volume size-density relationship for Douglas-fir at crown-closure was parallel to the asymptote and at a relative density of 0.15. This assumption is easily tested for red alder by the model presented here. Similarly, the effects of soil type (forest soil or loam) can be monitored for their effects on asymptote slope and intercept by utilizing the indicator variable in Equation 25.

To develop the model I worked exclusively with average plant biomass from all seven harvests (118 data points). To simplify matters I took the mean value for each set of treatment replicates and weighted this value by the density of each replicate. This procedure de-emphasized random, background mortality in favor of density-dependent mortality. There were a total of 42 mean data points. Finally, the non-linear regression matrix was weighted by the number of replicates that had contributed to the mean value. The convergence criterion was 1.0×10^{-5} (i.e., no change in the residual sums of squares by more than the convergence criterion for 5 consecutive iterations constitutes convergence). The self-thinning average

weight-density trajectories for components of biomass (roots, stem, branches, leaves, nodules) were then fitted by the final model form developed from average biomass. Also, other average tree measurements (i.e., height, crown volume, crown width) were modelled by the same equation form.

Model Fitting Development and Results

I was first interested in determining the correct form of the $(\overline{S}-\rho)$ trajectory. Thus, the following simplified form of Equation 22 was fit to <u>each</u> of the three initial density levels:

$$\overline{Y}_{ji} = a_0 - a_1 \cdot X_{ji} - (a_0 - a_1 X_{1i} - \overline{Y}_{1i}) \cdot e^{-a_2 \cdot (X_{1i} - X_{ji})^{a_3}} \tag{23}$$

where, $\overline{Y}_{ji}$ = ln (average tree biomass), g

X_{ji} = ln (actual stocking density), number trees/m^2

X_{1i} = ln (actual stocking density) at 1st or crown closure harvest

$\overline{Y}_{1i}$ = ln (average tree biomass) at crown closure harvest

j = no. of harvest dates

i = initial stocking density levels

a_0 = asymptote intercept

a_1 = asymptote slope

a_2 = intercept size-density trajectory

a_3 = slope size-density trajectory

The initial parameter estimates were a_0 = 10.1 (White 1980), a_1 = 1.5, a_2 = 5, a_3 = 2. The values for a_2 and a_3 were based on running

Equation 26 on all 42 data points, setting $a_0 = 10.1$, $a_1 = 1.5$, $a_2 = a_3 = 1$, i.e., I let the algorithm supply me with good estimates.

Table 12 shows that a_2 or the intercept value of the exponential term was most sensitive to initial spacings. The trend indicated steeper trajectories for the wider initial spacings (i.e., larger a_2).

To investigate these findings more scrupulously, the slope (a_1) and intercept (a_0) were fixed at the levels revealed in Table 12, then data for each initial density level were fit and the resulting responses in a_2 and a_3 examined (see Table 13).

Table 13 indicated that, while a_3 remained relatively stable, a_2 varied considerably with initial density, though the pattern was not clear. For this reason, the values of a_0, a_1 and a_3 from the highest, and presumably, most developmentally advanced density level were fixed and fitted to data for the other two initial densities. It was hoped that this procedure would indicate the form of variation in a_3.

From Table 14 I determined that a_2 was a linear function of initial density (X_{0i}), i.e.,

$$a_2 = 16.256 - 1.962 \ln X_{0i}, \quad r^2 = .981, \quad n = 3.$$

The above slope and intercept were used as initial guesses for the values of a_2 and a_6 in Equation 24. Thus, the exponent of the ($X_{1i} - X_{ji}$) term in Equation 26 was assumed to be a constant $\simeq a_3$. The following model was fitted to all data:

Table 12. Parameter sensitivity of average weight-density trajectory for three initial spacings in seedling red alder.

Parameter estimates	Initial density (plants/m^2)		
	2500	625	156
a_0	9.4550	12.8337	8.1459
a_1	1.1315	1.7907	1.0124
a_2	2.2888	51.5328	75.8184
a_3	1.3871	4.7029	2.6439
MSE	.3756	.4263	.7894

Number of observations = 14.

MSE = mean squared error.

Based on Equation 26.

Table 13. Parameter sensitivity of average weight-density trajectory
for each of three initial spacings forced towards different
asymptotes for seedling red alder.[1]

Parameter estimates	H*	M	L	H	M*	L	H	M	L*
a_0	9.45	9.45	9.45	12.83	12.83	12.83	8.14	8.14	8.14
a_1	1.13	1.13	1.13	1.791	1.791	1.791	1.012	1.012	1.012
a_2	1.38	7.41	6.56	4.24	51.53	357.83	75.82	57.24	4.75
a_3	1.39	1.46	2.54	1.18	4.7	7.34	2.64	4.6	2.11
MSE	.376	.438	.734	.583	.436	1.379	.471	.426	.656

[1]See Equation 23.

Number of observations = 14.

MSE = mean squared error.

H = 2500 plants/m^2 initial spacing.

M = 625 plants/m^2 initial spacing.

L = 156 plants/m^2 initial spacing.

* = level at which a_0 and a_1 were fixed. Data from Table 12.

$$\overline{Y}_{ji} = (a_0 + a_{10} \cdot I) - (a_1 + a_{11} \cdot I) \cdot X_{ji} - ((a_0 + a_{10} \cdot I) \cdot a_4 -$$

$$(a_1 + a_{11} \cdot I) \cdot a_5 \cdot X_{1i}) \cdot e^{-(a_2 + a_6 \cdot X_{1i}) \cdot (X_{1i} - X_{ji})^{a_3}}$$

$$(24)$$

where notation is as in Equation 22.

Initial parameter guesses for a_0, a_1 and a_2 were gleaned from reduced (4 parameter) model fits to the densest spacing (Table 14) while a_{11}, a_4 and a_5 were estimated from exploratory runs on the full (12 parameter) model, Equation 22.

Table 15 lists the sequential development of the final model form, Equation 29. The relation of the parameter estimates is given in Equation 24.

Referring to Table 15, Equation 26 shows that the slope indicator variable for soil type (a_{11}) did not significantly ($p < 0.01$) alter the slope of the self-thinning or crown closure slopes. Nor did soil type (a_{10}) significantly ($p < 0.01$) affect the intercept of these lines (Equation 27). Next, the adjustment parameter for slope differences between crown closure and the self-thinning line (a_5) was insignificant ($p < 0.01$), Equation 28. Plots of the six parameter model (Equation 28) indicated good visual fits to the data. However, the intercept and slope of the exponential term (a_2 and a_6 in Equation 24) were both insignificant ($t_{2\alpha} < 0.05$). The asymptotic standard errors indicated a wider relative confidence band around a_6. The final 5 parameter model (Equation 29 and Figure 16) indicated a_6 was insignificantly contributing to the model ($p < 0.01$). Exclusion of

Table 14. Sensitivity analysis of intercept parameter of average
weight-density trajectory for three initial spacings in
seedling red alder.[1,2]

Parameter estimates	Initial density (plants/m^2)		
	2500	625	156
a_0	9.45	9.45	9.45
a_1	1.13	1.13	1.13
a_2	1.3871	3.055	6.649
a_3	1.39	1.39	1.39
MSE	.376	.498	.781

[1]See Equation 26.

[2]a_0, a_1 and a_3 fixed from highest initial density (see Table 13).

Number of observations = 14.

MSE = mean squared error.

Table 15. Comparison of average weight-density trajectory model parameter estimates for seedling red alder (see Equation 24 for model form).

Equation no.	Parameter estimates (asymptotic standard errors in brackets)									
	a_0	a_1	a_{10}	a_{11}	a_4	a_5	a_2	a_6	a_3	MSE
25	9.8281 (2.021)	1.2163 (.331)	.1120 (.961)	.0038 (.145)	.4205 (1.425)	.2676 (1.245)	13.1649 (3.541)	1.3964 (.440)	1.4249 (.136)	.6827
26	9.6541 (1.695)	1.1921 (.285)	.1353 (.176)	--	.4179 (.156)	.0533 (.257)	13.7782 (9.8)	1.4700 (1.215)	1.4456 (.376)	.6643[NS]
27	9.9142 (1.776)	1.2169 (.302)	--	--	.4295 (.155)	.0782 (.261)	12.5025 (8.734)	1.3160 (1.086)	1.4155 (.302)	.6563[NS]
28	9.5821 (.945)	1.1614 (.166)	--	--	.3830 (.063)	--	13.3292 (8.452)	1.4248 (1.023)	1.4367 (.363)	.640[NS]
29	11.4499 (.725)	1.4601 (.110)	--	--	.3142 (.004)	--	2.9147 (.1085)	--	1.1944 (.311)	.7373[NS]

Number of observations = 42 weighted means.

MSE = mean squared error.

NS = not significantly different from preceeding model, $p < 0.01$.

Figure 16. Self-thinning trajectories for seedling red alder mean tree biomass growing at various density levels and on two soil types under greenhouse and lath house conditions. Each point is a mean of 2 or 3 values. SEE is standard error of estimate. The trajectories start at crown closure. The asymptote is drawn in with intercept and slope given by the first two terms, respectively, in the following trajectory equation.

$$Y=11.4499-1.4601(X)-(3.5982) \; EXP-(2.9147(DX)^{1.9444}), SEE=.8587$$

Y=LN(BIOMASS),X=LN(NO.TREES)
DX=CHANGE IN X FROM CROWN CLOSURE
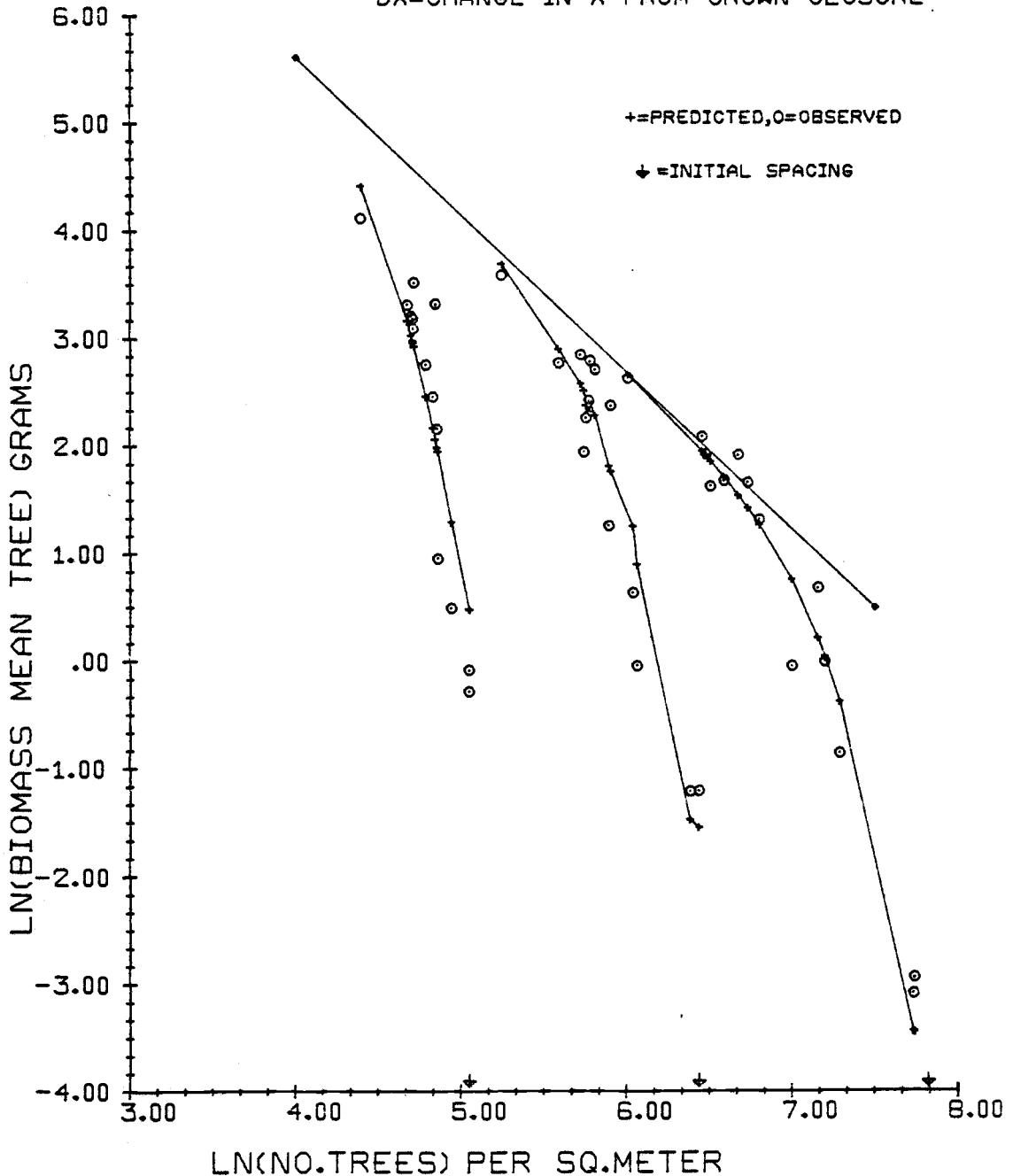
a_6 caused a steepening of slope and increase in intercept of the self-thinning asymptote and crown closure line. The <u>form</u> of the final equation is given in Equation 30.

$$\overline{Y}_{ji} = b_0 - b_1 X_{ji} - b_0 \cdot b_2 \cdot e^{-b_3(X_{1i}-X_{ji})^{b_4}} \qquad (30)$$

where, $\overline{Y}_{ji}$ = ln (average plant biomass), grams

X_{ji} = ln (stocking density) plants/m^2

X_{1i} = ln (stocking density), plants/m^2 at crown closure

j = no. of harvest dates

i = number of initial density levels

b_0 = intercept parameter for asymptote

b_1 = slope parameter for asymptote

b_2 = relative density parameter at crown closure

b_3 = intercept parameters for exponentiated function

b_4 = slope parameter for exponentiated function

Due to the costly nature of the above computer investigations, I assumed that plant parts behaved in a similar fashion to total biomass. Therefore, the same model (Equation 30) was fit to stem, leaf, branch, root and nodule biomass. Leaf area was also examined by the same model. The results are in Table 16 and Figures 17 through 22.

Table 17 documents the parameter estimates generated using Equation 30 for various other average tree relationships. The exact

Table 16. Parameter estimates for self-thinning trajectories of average tree biomass components and leaf area for seedling red alder (see Equation 30 for model form).

Components $(\overline{Y}_{ji})$	Parameter estimates (asymptotic standard errors in brackets)						
	b_0	b_1	b_2	b_3	b_4	MSE[1]	No. Obsv.
ln (avg. stem wt., g)	11.5938 (.8011)	1.5876 (.1207)	.3987 (.04771)	2.472818 (.9123)	1.0148 1.2582	.8769	42
ln (avg. branch wt., g)	15.3680 (1.7028)	2.4212 (.2546)	.5405 (.06743)	2.98754 (1.06009)	1.0397 (.2599)	3.1060	40
ln (avg. leaf wt., g)	9.0592 (.6961)	1.3424 (.1044)	.4143 (.0463)	2.9445 (1.0338)	1.1024 (.2704)	.6562	42
ln (avg. root wt., g)	8.9969 (.7356)	1.3232 (.1129)	.2813 (.0429)	3.4087 (1.8284)	1.3538 (.4861)	.7795	42
ln (avg. nodule wt., g)	6.22803 (.8254)	1.2221 (.1244)	.4613 (.0856)	2.70462 (1.4768)	1.1470 (.4374)	.9342	42
ln (avg. leaf area, cm^2)	13.3860 (.6985)	1.1825 (.1076)	.1386 (.0237)	4.09459 (2.8268)	1.4370 (.6342)	.7091	42

[1]MSE = mean squared error.

Figure 17. Self-thinning trajectories for seedling red alder mean stem biomass growing at various density levels and on two soil types under greenhouse and lath house conditions. Each point is a mean of 2 or 3 values. SEE is standard error of estimate. The trajectories start at crown closure. The asymptote is drawn in with intercept and slope given by the first two terms, respectively, in the following self-thinning trajectory equation.

$Y=11.5938-1.5876\ (X)-(4.6221)\ EXP-(2.4728\ (DX)^{1.0148}\ )$, SEE$=.9364$. N$=42$.   Y=LN(BIOMASS),X=LN(NO.TREES)

DX=CHANGE IN X FROM CROWN CLOSURE

+=PREDICTED,O=OBSERVED

↓ =INITIAL SPACING

LN(BIOMASS MEAN STEM) GRAMS

LN(NO.TREES) PER SQ.METER
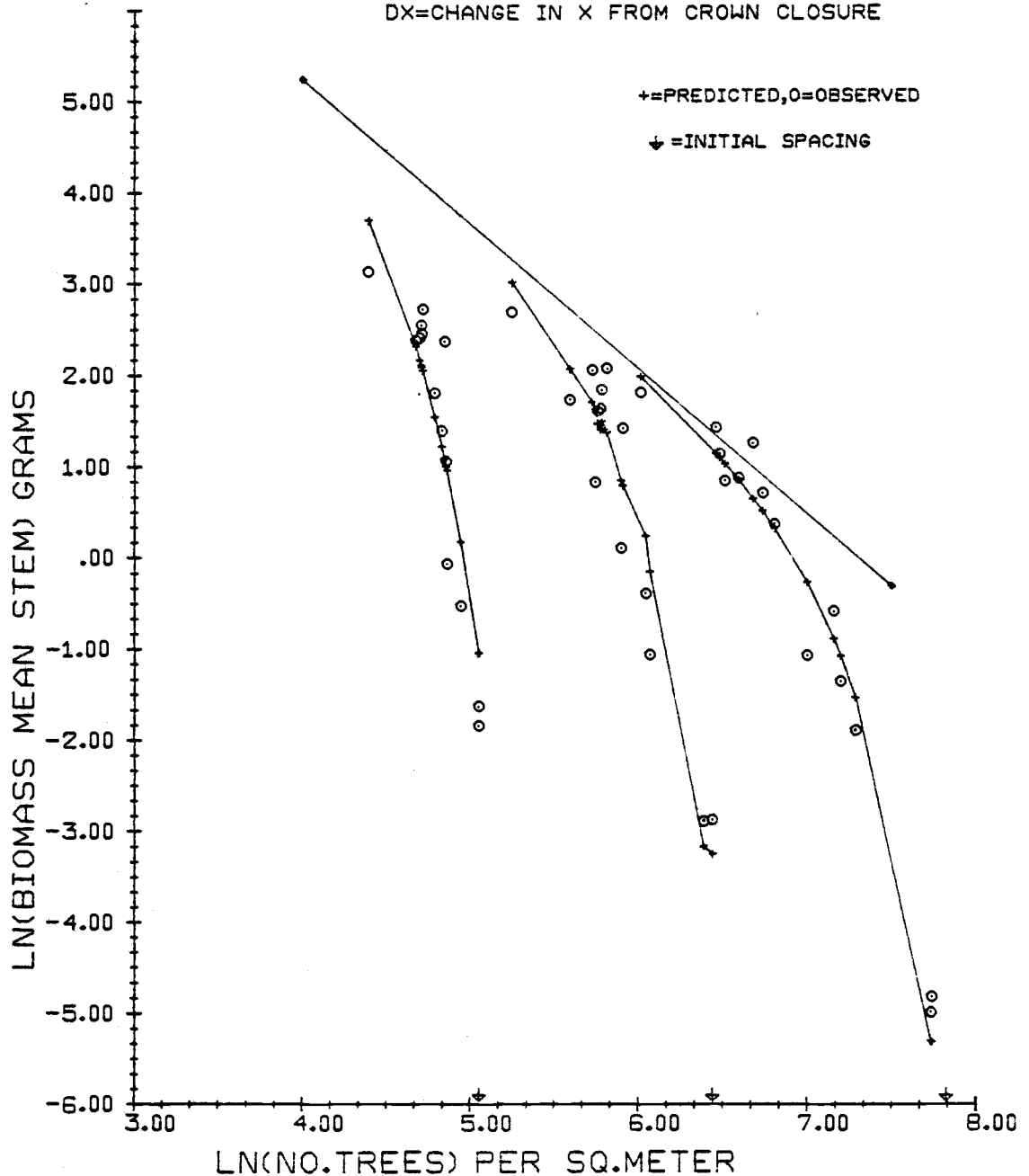
Figure 18. Self-thinning trajectories for seedling red alder mean
leaf biomass growing at various density levels and on two soil types
under greenhouse and lath house conditions. Each point is a mean of
2 or 3 values. SEE is standard error of estimate. The trajectories
start at crown closure. The asymptote is drawn in with intercept
and slope given by the first two terms, respectively, in the follow-
ing self-thinning trajectory equation.

$Y=9.05925-1.3424 (X)-(3.7529) EXP-(2.9445 (DX)^{1.1024}),SEE=.8101.$
$N=42.$ $Y=LN(BIOMASS),X=LN(NO.TREES)$

DX=CHANGE IN X FROM CROWN CLOSURE

+=PREDICTED,O=OBSERVED

↓ =INITIAL SPACING
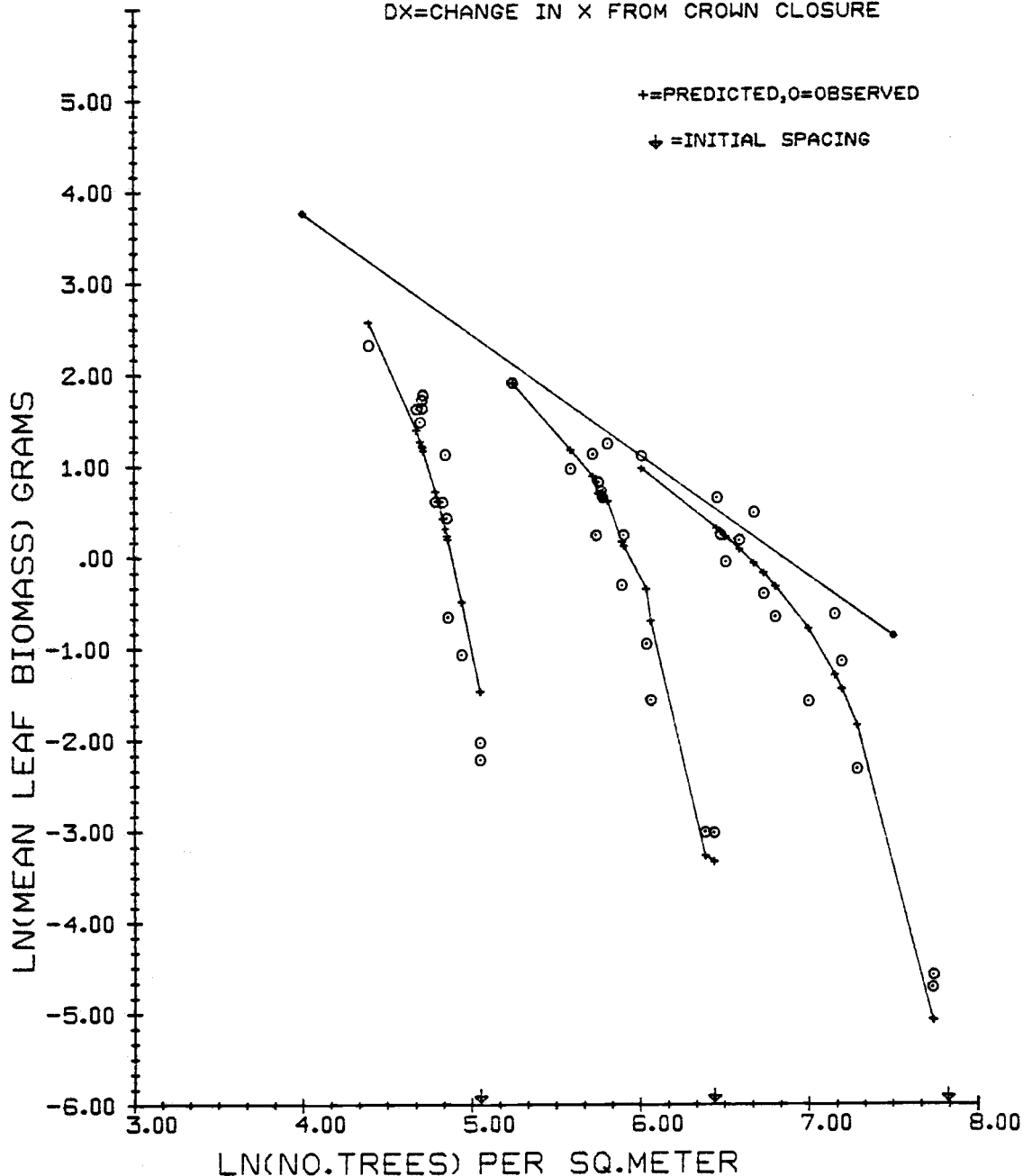
Figure 19. Self-thinning trajectories for seedling red alder mean
root biomass growing at various density levels and on two soil types
under greenhouse and lath house conditions. Each point is a mean of
2 or 3 values. SEE is standard error of estimate. The trajectories
start at crown closure. The asymptote is drawn in with intercept
and slope given by the first two terms, respectively, in the
following self-thinning trajectory equation.

$Y=8.99694-1.3232(X)-(2.5306) EXP-(3.4085(DX)^{1.3538}),SEE=.8829.$
N=42.   Y=LN(BIOMASS),X=LN(NO.TREES)

DX=CHANGE IN X FROM CROWN CLOSURE

+=PREDICTED,O=OBSERVED

↓=INITIAL SPACING

LN(NO.TREES) PER SQ.METER
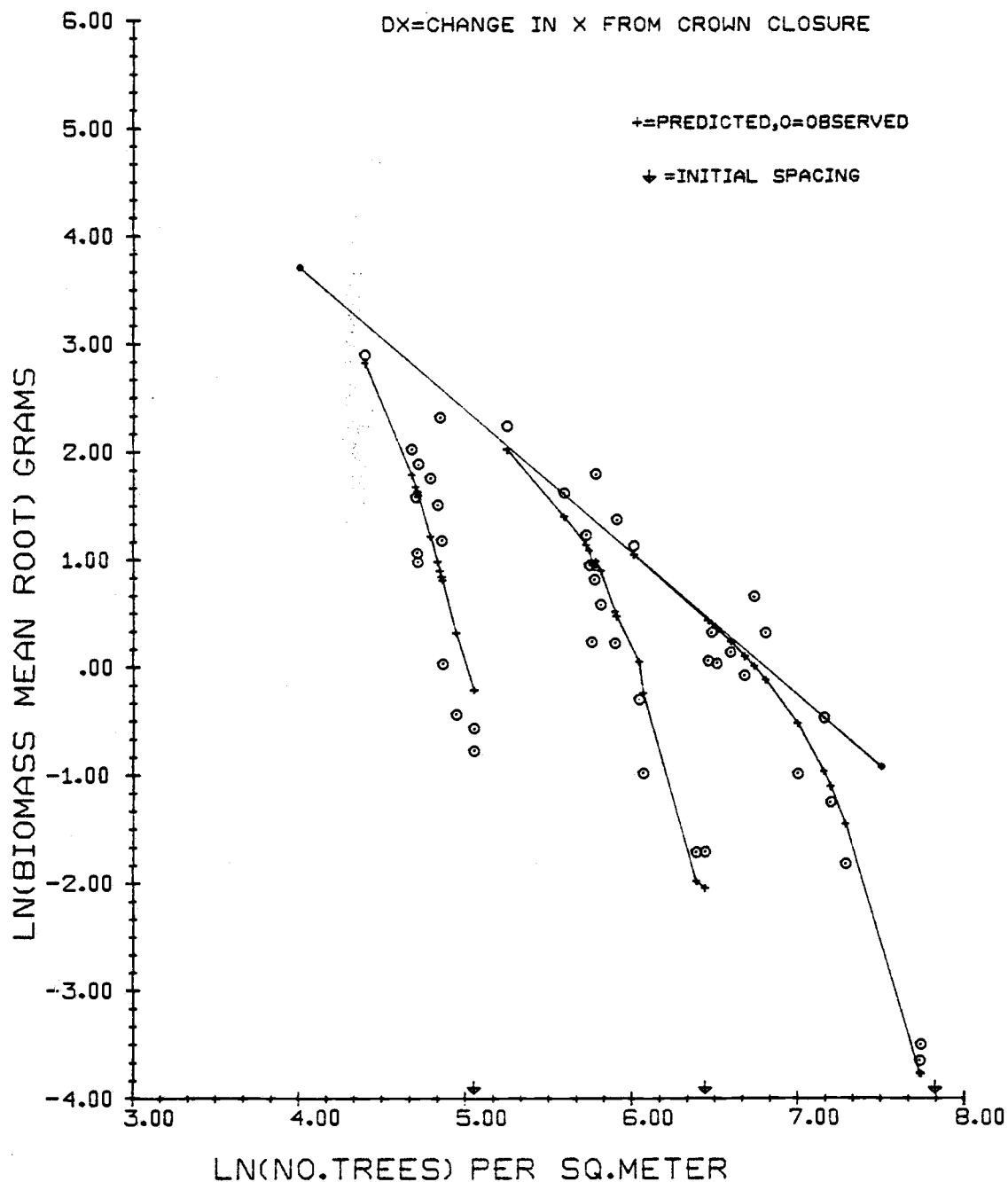
Figure 20. Self-thinning trajectories for seedling red alder mean branch biomass growing at various density levels and on two soil types under greenhouse and lath house conditions. Each point is a mean of 2 or 3 values. SEE is standard error of estimate. The trajectories start at crown closure. The asymptote is drawn in with intercept and slope given by the first two terms, respectively, in the following self-thinning trajectory equation.

$Y=15.3680-2.42117$ $(X)-(8.3071)$ $EXP-(2.9874$ $(DX)^{1.3538}$ $),SEE=1.5818$
$N=40.$ $Y=LN(BIOMASS),X=LN(NO.TREES)$
$DX=CHANGE$ IN X $FROM$ $CROWN$ $CLOSURE$

+=PREDICTED,O=OBSERVED

↓ =INITIAL SPACING
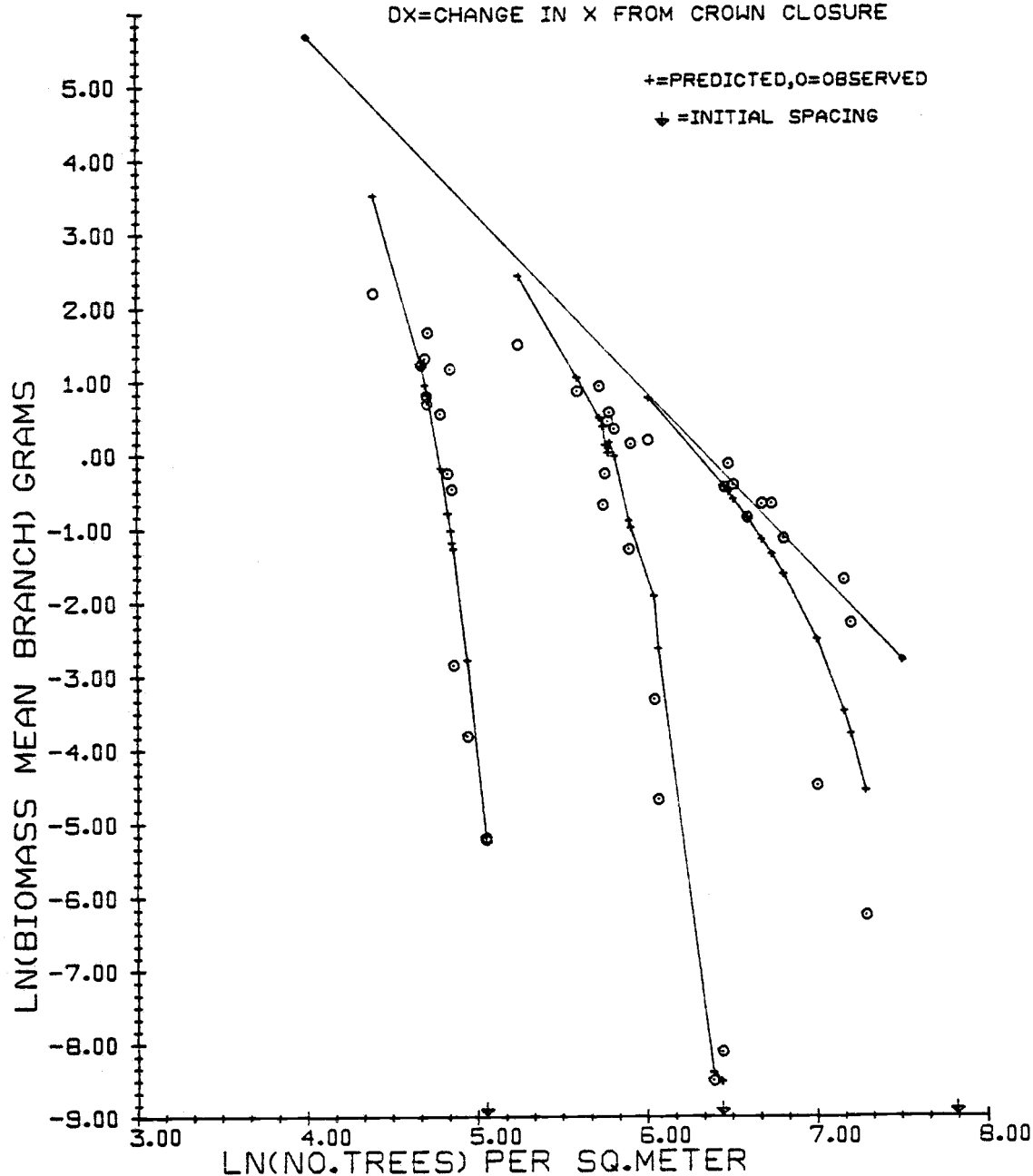
Figure 21. Self-thinning trajectories for seedling red alder mean nodule biomass growing at various density levels and on two soil types under greenhouse and lath house conditions. Each point is a mean of 2 or 3 values. SEE is standard error of estimate. The trajectories start at crown closure. The asymptote is drawn in with intercept and slope given by the first two terms, respectively, in the following self-thinning trajectory equation.

$$Y=6.22803-1.2221 (X)-(2.8731) EXP-(2.7046 (DX)^{1.1471}), SEE=.9665$$

N=42.   Y=LN(BIOMASS),X=LN(NO.TREES)

DX=CHANGE IN X FROM CROWN CLOSURE

+=PREDICTED,O=OBSERVED

↓ =INITIAL SPACING

LN(NO.TREES) PER SQ.METER
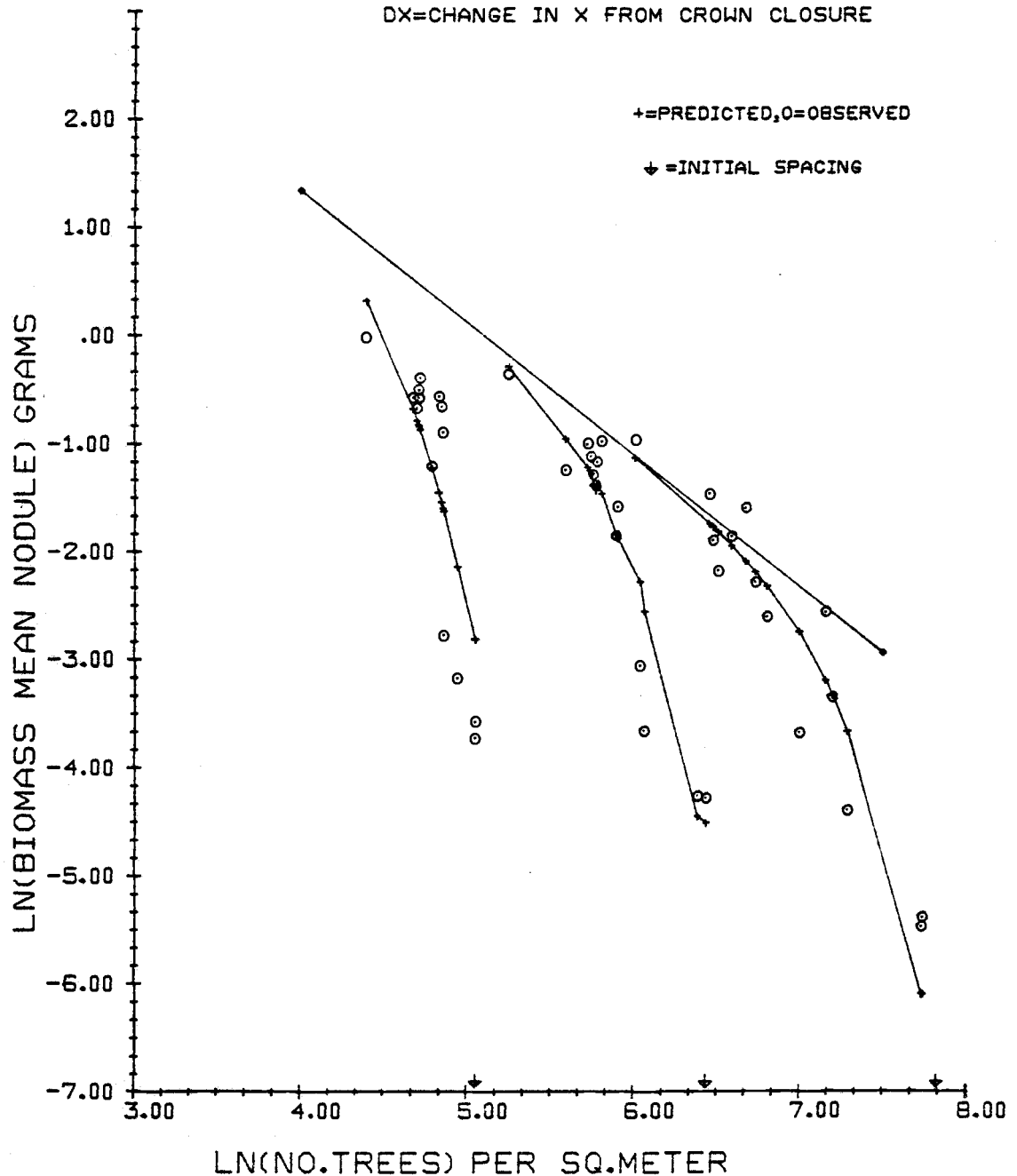
Figure 22. Self-thinning trajectories for seedling red alder mean leaf area growing at various density levels and on two soil types under greenhouse and lath house conditions. Each point is a mean of 2 or 3 values. SEE is standard error of estimate. The trajectories start at crown closure. The asymptote is drawn in with intercept and slope given by the first two terms, respectively, in the following self-thinning trajectory equation.

$$Y=13.3860-1.1825 \ (X)-(1.8560) \ EXP-(4.0946 \ (DX)^{1.4371}), SEE=.8421.$$

N=42.   Y=LN(LEAF AREA,X=LN(NO.TREES)
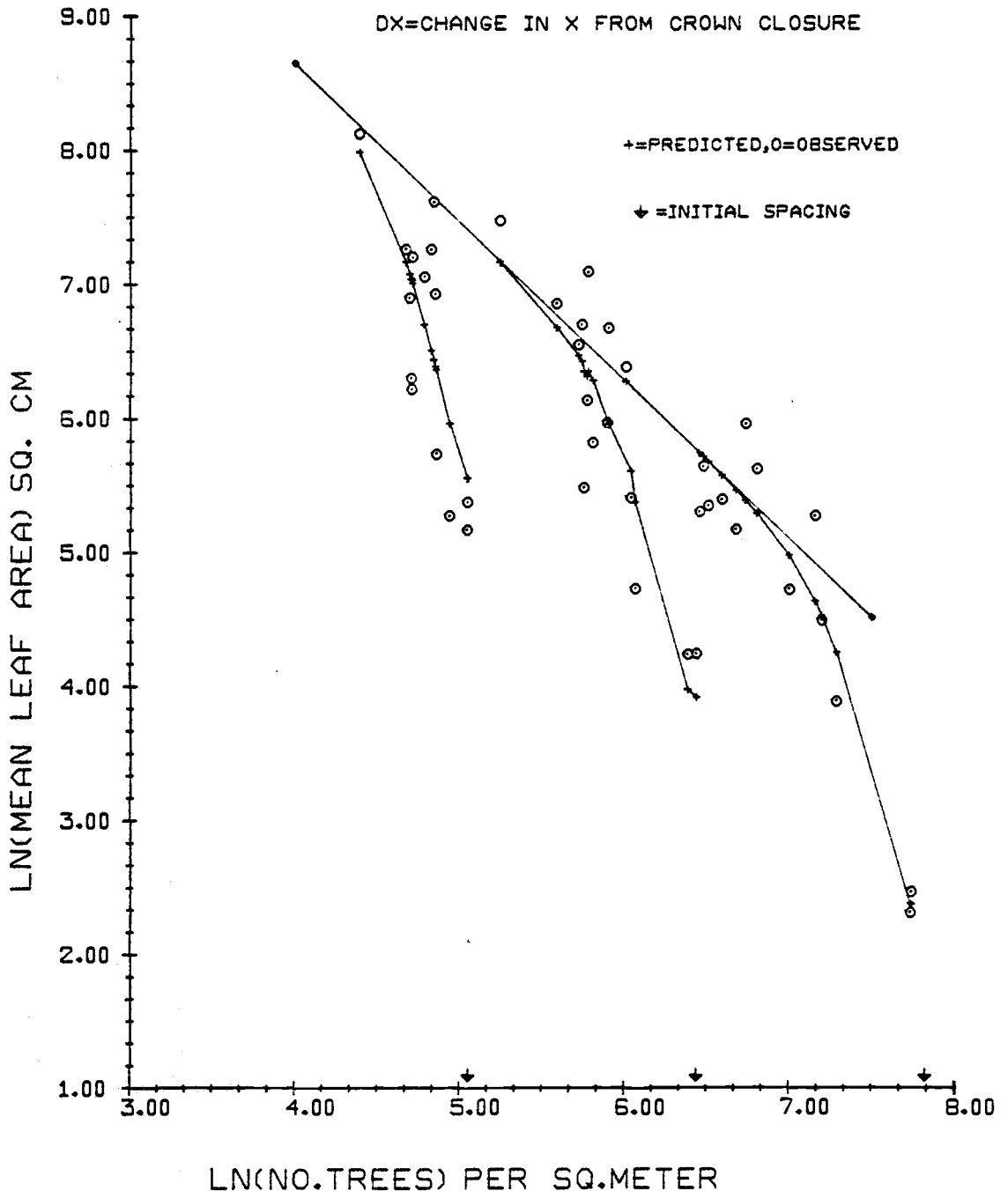
Table 17. Parameter estimates for self-thinning trajectories of various average tree measurements for seedling red alder (see Equation 30 for model form).

Measurement ($\overline{Y}_{ji}$)	Parameter estimates (asymptotic [1]S.E. in brackets)						
	b_0	b_1	b_2	b_3	b_4	MSE	[1]$Y \pm$ S.D.
ln (avg. crown surface area, cm^2)	13.3162 (1.1453)	.9545 (.1716)	.1455 (.0033)	4.2635 (3.5313)	.9718 (.8421)	1.774	7.2663 (1.2937)
ln (avg. crown volume, m^3)	18.8113 (.9887)	1.4710 (.1465)	.1985 (.0024)	3.9536 (2.2924)	.9152 (.3683)	1.298	9.2914 (1.8644)
ln (avg. height, cm)	8.25004 (.3907)	.6138 (.0449)	.2384 (.0359)	1.8553 (.8554)	.7932 (.2369)	.1216	3.8589 (.7454)
ln (avg. root collar diam. (rcd), mm)	2.3927 (.2149)	.5119 (.0291)	.4725 (.0587)	2.2900 (.9604)	.8513 (.2484)	.0511	1.0085 (.5536)
ln (avg. rcd^2 x avg. height)	18.8082 (1.0248)	1.4706 (.1459)	.1985 (.0237)	3.9526 (2.32584)	.9154 (.3726)	1.297	10.8912 (3.6487)
ln (avg. surface area of occupation, cm^2)	13.6112 (.9976)	.9794 (.1486)	.1488 (.0320)	4.1500 (4.3021)	1.0045 (.6960)	1.3321	7.3713 (1.2578)
ln (avg. potential volume of occupation, cm^3)	17.4593 (.3890)	1.6138 (.0449)	.1126 (.0181)	1.8568 (.8556)	.7930 (.2370)	.1216	7.2204 (1.5336)
[2]ln (avg. stem volume type I, cm^3)	11.0175 (.5746)	1.2667 (.0835)	.2604 (.0263)	2.9333 (1.2172)	.9123 (.2693)	.4198	2.7211 (1.4283)
[2]ln (avg. stem volume type II, cm^3)	11.7102 (.5746)	1.2667 (.0835)	.2449 (.0263)	2.9384 (1.2172)	.9133 (.2693)	.4198	3.4142 (1.4283)
ln (avg. crown volume/avg. crown surface area, cm)	5.0568 (.7558)	.5176 (.1095)	.3268 (.0712)	3.6171 (3.4100)	.8556 (.5718)	.7271	2.0256 (.8609)
ln (avg. crown volume/avg. leaf area, cm)	5.4385 (.4116)	.2923 (.0600)	.3422 (.0361)	5.2686 (4.9595)	.6022 (.4774)	.2200	3.4455 (.7242)
ln (avg. crown width, cm)	5.5436 (.3231)	.4813 (.0501)	.0954 (.0234)	6.6128 (9.5846)	1.4492 (1.1246)	.1499	2.5955 (.5116)
ln (avg. crown width squared x avg. height, cm^3)	19.0392 (.8481)	1.5746 (.1293)	.1436 (.0199)	4.1735 (2.5752)	1.1831 (.4686)	1.0040	9.0499 (1.7011)

[1]SE = standard error, SD = standard deviation.

[2]Avg. stem volume, type I = cylindrical below crown base, hyperbolic above, type II = cylindrical below crown base, parabolic above.

expected forms of these relationships are linked allometrically to plant geometry and are discussed in the next section.

Discussion

Average Weight-Density Trajectory

The average weight ($\overline{W}$) to density (ρ) equation (Equation 29) showed that the maximum self-thinning line may be properly modelled as an asymptotic boundary to the ($\overline{W}$-ρ) trajectory. The asymptote slope (-1.46) was close to the theoretically expected -1.5. It was significantly different ($t_{2\alpha} < 0.01$) from -1.0, a slope we may have expected had there been no "self-thinning" occurring. The asymptote intercept was c. 94 kg/m^2, somewhat higher than an empirically determined "barrier" of 25 kg/m^2 (White 1980)[6]. The 25 kg/m^2 figure was based on above ground biomass, whereas my data include roots. Even accounting for this (i.e., roots $\simeq$ 1/4 total biomass (Table 7)), there is still a two-fold difference. Edge effects (Chapter III) were minimal so that the supra-normal conditions of the experiment that gave leaf area indexes in excess of 30 (Table 9) appear to have raised the yield considerably over levels recorded in field situations.

Soil type did not significantly ($p < 0.01$) contribute to the equation. This represents the Suchatschew effect (Kira et al. 1953, Harper 1979) by which plants growing from the same initial density and under less fertile conditions track the same self-thinning asymptote but take longer in doing so. It will be shown that the intrinsic rate

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[6]White has since determined an upper limit of 100 kg/m^2 (D. Perry pers. comm.).

of growth was superior on the more fertile forest soil (Chapter IV, Modelling the Relationship Between Size and Density Over Time).

The same model form fit all three density levels adequately. It can be seen from Figure 16 that it would have been extremely difficult to have chosen which data points were in "self-thinning" stands. The trajectory for the widest spaced treatment, for instance, barely shows signs of mortality. However, all three $(\overline{W}-\rho)$ trajectories tend towards the self-thinning asymptote in a similar manner. I would not be justified in extending the parameter estimates to conditions outside the range of the experiment. But these findings suggest that a common $(\overline{W}-\rho)$ trajectory model form may exist over a wide range of densities.

The crown closure line was parallel to the self-thinning asymptote with intercept of .31 relative density. Mortality had occurred in about half of the crown closure observations, all in the denser stands. The stand structure of seedling alder is considerably different to Douglas-fir where imputed crown closure was at .15 maximum volume (Drew and Flewelling 1979). This model shows that there was no evidence of a zone of imminent competition mortality as suggested by Drew and Flewelling (1979). Mortality was systematic and occurred continuously after crown closure.

If the findings of these investigations are substantiated, then each species may be characterized by its $(\overline{W}-\rho)$ trajectory--the parameters derived being applicable across site-type and age. The slope and intercept of the exponentiated term (b_3 and b_4 in Equation 30) are of particular interest because they describe mathematically how plants fill the space made available by mortality. The nature of the curve

suggests that each unit of density decrease is replaced by an exponential increase in plant weight constrained by the asymptote until the self thinning line itself is tracked. This implies a physical and biological stability boundary is reached. The $(\overline{W}-\rho)$ trajectory may be as pervasive and fundamental to plant growth as the self-thinning asymptote.

Carbohydrate Allocation

The allometric derivation of the -3/2 power "law" by Yoda et al. (1963) states that plant geometry should remain constant and that, consequently, the plant components should also have a slope of -3/2. This derivation was admittedly a naive approximation (White 1981). In fact, allometric relationships between plant parts change chronologically (see Chapter II); it is only the total weight that approximates -3/2.

Table 16 shows that the slope parameter estimates for biomass components vary from 1.22 to 2.42 (see Figures 17 through 22). Confidence intervals ($t_{2\alpha} < 0.05$) on these values revealed the following subsets:

1	2	3	4	5	6	7	8	9
-1.0 45° slope)	Leaf area	Nodule biomass	Root biomass	Leaf biomass	-1.5 (56° slope)	Stem biomass	Branch biomass	-2.5 (68° slope)

Only leaf area and nodule biomass were insignificant from -1.0, indicating that production per unit area was stabilizing. (A slope of

-1.0 is a 1:1 relationship.) Roots, leaves and stem weight were not different from -1.5, implying increasing production per unit area. However, the distinction was not clear cut because leaf area and leaf biomass were not significantly different nor were nodule and root biomass. Branch biomass was significantly different from all other components and had the highest slope parameter (which was not significantly different from -2.5).

Biomass components may be ranked by their self-thinning slope exponents to suggest a relative carbohydrate allocation priority. Steeper slopes means greater per tree and per unit area allocation per decrease in density. This analysis yielded the following priorities:

branches > stem $\geq$ leaves $\geq$ roots $\geq$ nodules.

Thus, the above ground components of branch and stem receive relatively more photosynthate the further the stand moves along the self-thinning trajectory. Nodules have lowest priority while leaves and roots appeared to behave in unison.

Indeed, the asymptotes for root and leaf biomass were almost identical (see Figures 18 and 19). The similarity between these two components implies a dynamic feedback regulation.

The similar slopes for leaf area (1.18) and nodule biomass (1.22) (see Figures 21 and 22) may indicate that nodule biomass is limited by leaf area, supporting the findings of Dawson and Gordon (1979) and Bormann (1981). The close association between nodule biomass and photosynthesis (or leaf area) has been substantiated by Gordon and Wheeler (1978).

A similar ranking of biomass components was found (but not discussed) by Mohler et al. (1978), i.e.,

Stem > roots > branches > leaves for Prunus pennsylvanica

Stem > branches > leaves for Abies balsamea

The higher ranking for branches in my data may reflect the narrower range of densities I sampled. The smaller, fewer branches on the densest initial spacing may have led to an overestimate of the steepness of the slope. The model for the branch data was not begun for the densest spacings until the 2nd harvest date because there were no branches at the first harvest (see Figure 20), which would have violated the constraints of the model. Also, the standard error of estimate was substantially higher for branches than for any other component.

The asymptote intercept values quantify absolute carbohydrate allocation. They suggest the following scheme, almost identical to the relative allocation prioritization:

Branches $\geq$ stems > leaves $\geq$ roots > nodules (from Table 16).

Care should be taken when extrapolating those values to the Y axis (i.e., time $\to \infty$). It is likely that the biological carrying capacity of the site and the ontological life span of the plant will be exceeded. These values apply only to plants whose growth is limited by the $(\overline{W}-\rho)$ asymptote, so that only the ranking, not the actual values, is meaningful.

Analysis of the proportional component distribution of the net primary production (NPP) to total net production for each time

interval indicates the shifts in absolute priority per time period

(see Table 18). The values listed are percentages of $NPP/m^2/day$ but

also apply to NPP/tree/day. This analysis indicated the following

dynamic shifts in sink priority:

<pre>
0-215 days: leaves > stem > roots > nodules > branches
216-342 days: leaves > stem > root > branches > nodules
343-405 days: stem > leaves > root > branches > nodules
406-451 days: stem > root > leaves > branches > nodules
451-525 days: stem > leaves > root > branches > nodules
</pre>

We can see that much of the initial energy is being invested in leaf

production. Similarly, more photosynthate is flowing to nodules than

branches. This trend is reversed at c. 216 days when branches become

increasingly favored and undergo the largest relative sink priority

increase of c. 135 fold. Thereafter, more energy is shifted from

leaves to stems, while the position of roots remains relatively

stable. This pattern was similar across all densities.

Thus, the picture of carbohydrate allocation is not fully

revealed by examination of the self-thinning asymptote alone.

Allometric Relationships

A very useful feature of the $(\overline{W}-\rho)$ model is that it may be

extended to examine the behavior of other average tree size measure-

ments $(\overline{S})$ which in turn may be linked allometrically to biomass. It

is thus possible to derive $(\overline{S}-\rho)$ trajectories to determine the beha-

vior of say, tree diameter, height or crown volume, to changes in den-

sity. Some interesting findings are presented in Table 17.

A central assumption made for all allometric derivations of the

-3/2 power rule is that average height $(\overline{h})$ is a linear logarithmic

Table 18. Percentage of components of seedling alder production per unit area by initial spacing and date.

[1]Initial spacing code	[2]Harvest date code	Stem %	Leaves %	Root %	Nodules %	Branches %	[3]NPP loam g/m²/day	[3]NPP forest soil g/m²/day
2	1	17.1	62.3	21.4	.2	.0	.979	1.072
4	1	19.6	62.7	17.5	.6	.1	1.047	1.248
8	1	21.8	62.6	14.6	.5	.4	.751	.634
2	2	35.7	38.5	22.3	2.7	.8	2.875	4.602
4	2	35.8	37.5	22.6	2.6	1.5	1.898	3.644
8	2	35.9	39.3	20.4	2.4	1.7	1.071	1.554
2	3	27.0	30.1	29.5	3.7	9.7	4.651	8.149
4	3	32.3	36.1	19.5	4.6	7.5	4.478	6.893
8	3	33.7	37.8	16.8	4.8	6.9	3.928	5.078
2	4	37.7	36.7	14.6	1.9	9.1	9.813	12.503
4	4	38.8	36.7	11.8	1.9	10.8	11.076	15.043
8	4	38.7	36.5	11.5	1.9	11.4	5.532	10.247
2	5	45.8	20.5	18.7	2.2	12.8	8.315	10.881
4	5	45.6	19.8	18.2	2.0	14.4	8.664	12.657
8	5	45.3	19.5	17.8	1.9	15.5	7.086	9.899
2	6	52.1	13.3	23.9	2.9	8.4	11.541	10.89
4	6	52.6	12.4	23.5	2.7	8.9	6.651	11.043
8	6	53.0	12.0	23.3	2.5	9.2	5.398	5.907
2	7	44.8	21.9	22.2	2.8	8.3	7.434	10.778
4	7	38.1	28.7	17.7	1.9	13.6	7.242	11.994
8	7	38.7	28.4	17.6	1.8	13.6	5.604	9.437

[1]2 = 2 x 2 cm, 4 = 4 x 4 cm, 8 = 2 x 8 cm.

[2]1 = 135 days old, 2 = 215 days old, 3 = 284 days old, 4 = 342 days old, 5 = 405 days old, 6 = 451 days old, 7 = 525 days old.

[3]NPP = net primary production = biomass/age.

function of average diameter $(\bar{d})$, where $\bar{d}$ refers to the diameter of occupancy of the average tree and may be approximated by average crown width $(\overline{CW})$ (White 1981). Because $\bar{d}^2 \propto \rho^{-1}$ (i.e., $\bar{d}^2$ is proportional to potential plant area), then $\bar{h} \propto \bar{d} \propto \rho^{-1/2}$. To rigorously test these derived relationships we need only examine the data for the asymptote slope parameter estimates (b_1) presented in Table 17. Here we find that $\bar{d} = \overline{CW} \propto \rho^{-.481}$, $\bar{h} \propto \rho^{-.614}$ and $\overline{rcd} \propto \rho^{-.512}$ (rcd = root collar diameter). Only the relationship for height is different than the expected value of $-.5$ $(t_{2\alpha} < 0.05)$. There was almost a one-to-one relationship between $\overline{CW}$ and $\overline{rcd}$, i.e., $\overline{CW} \propto \overline{rcd}^{-.939}$ (equation derived by substituting for ρ) which suggests that as plants move along the self-thinning asymptote a unit increase in $\overline{CW}$ translates into a unit increase in $\overline{rcd}$. White (1981) found considerable variation in data from published literature on this relationship (i.e., the exponent varied from .61 to 1.43). Many of these data were, however, not the stable asymptotic relationships, which may account for the apparent variability. The relationship between $\bar{h}$ and potential area of occupation, $\bar{d}_E^2$ or ρ^{-1} is given by setting the asymptotic relationship $\bar{h} \propto \rho^{-.6138}$ equal to ρ^{-1}, thus $\bar{h} \propto (\bar{d}_E^2)^\theta$ where $\theta = .6138$ (see Equation 6). Theoretically θ should be $\simeq .5$ at the asymptote. Apparently red alder height is increasing faster than potential tree area diameter. We can now test the allometric derivation presented in Chapter IV, Introduction, i.e., the self-thinning exponent is given by $m(1+\theta)$ (Equation 9). From the asymptotic relationships $\bar{V} \propto p^{-1.4601}$, and $\bar{V}_E \propto p^{-1.6138}$ where $\overline{W}$ and $\overline{V}_E$ are actual weight and potential tree volume (from Tables 16 and 17), respectively, we find that $W \propto (V_E)^{.9048}$. Thus $.9048(1 + .6138) = 1.4601$.

The allometric derivation and empirical results are in exact agreement, due, unfortunately, to mathematical circularity in the present form of the derivation, i.e., $m = \frac{1.4601}{1.6138}$, the denominator of which cancels with the value $(1 + .6138)$.

Allometrically the volume of occupancy of the average plant $(\overline{V})$ is proportional to a cylinder given by $\overline{CW^2 \cdot h}$. Thus we might expect that $\overline{V} \propto \overline{CW^2 \cdot h} \propto \rho^{-3/2}$. The asymptotic equivalency given in Table 17 was $\overline{CW^2 \cdot h} \propto \rho^{-1.575}$ or $\overline{rcd^2 \cdot h} \propto \rho^{-1.471}$. Neither exponents were significantly different $(t_{2\alpha} < 0.05)$ from the expected value of -1.5. The potential volume of occupancy $(\overline{V}_E)$, however, gave a higher slope value, i.e., $\overline{V}_E \propto \rho^{-2} \cdot \overline{h} \propto \rho^{-1.614}$. But the intercept of the asymptote for $\overline{V}_E$ (b_0 in Table 17) was lower than the actual volume $(\overline{V})$ estimates. The asymptotes for $\overline{V}$ thus lie slightly above $\overline{V}_E$. This was mainly attributable to crown overlap (crown width was measured to leaf tip).

The asymptotic relationships between average crown surface area $(\overline{CSA})$, crown volume $(\overline{CV})$ and density satisfied expected outcomes. Because $\overline{CV}$ is increasing as a cubic function of available space and $\overline{CSA}$ as a squared function of available space we have $\overline{CV/CSA} \propto \rho^{-3/2}/\rho^{-1}$. The values shown in Table 17 were $\overline{CV/CSA} \propto \rho^{-.518}$, $\overline{CSA} \propto \rho^{-.954}$ and $\overline{CV} \propto \rho^{-1.471}$. These exponents were not significantly different $(t_{2\alpha} < 0.05)$ from the expected values of $-.5$, -1.0 and -1.5, respectively. The results suggest that asymptotic crown geometry is relatively stable and that crown geometry is directly proportional to available growing space. This contrasts with the unstable allometric derivations of crown geometry as a function of $\overline{rcd^2 \cdot h}$ at each harvest date in Chapter II.

The relationship between mean leaf area ($\overline{LA}$) and density was $\overline{LA} \propto p^{-1.18}$ (Table 16), a value insignificantly higher ($t_{2\alpha} < 0.05$) than the expected outcome (an exponent of -1 (White 1980, Hutchings and Budd 1981)). Because $\overline{A} \propto \overline{V}^{2/3}$ where $\overline{A}$ = area and $\overline{V}$ = volume and $\overline{V} \propto \overline{W}^1$ (White 1981) where W = mean weight, we might expect, if leaves behaved as classical geometrical solids, that $\overline{LA} \propto \overline{LW}^{2/3}$, where $\overline{LW}$ = average leaf weight. Examining data from Table 16 and substituting for p we find $\overline{LA} \propto \overline{LW}^{.89}$ and $LA \propto W^{.81}$. The latter relationship is identical to one empirically determined by Perry (in press) for several species of plants. We might infer that under self thinning conditions $\overline{LA}$ and hence photosynthesis is increasing at a greater rate than we might expect when compared to weight or gross respiration.

In an astute paper by White (1981) it was suggested that it is the ontogenetic allometry in the development of tree shape that is the key linking the pattern of mean plant biomass and density. In other words, there is a regular manner in which plant shape changes during stand development. I have already alluded to the constant relationship between crown volume and surface area. White suggests that

$$\overline{W} \propto d_b^{2.5}$$

where, d_b = diameter at breast height

and

$$p \propto \overline{CW}^{-2} \propto d_b^{-2a} \text{ , } a \simeq .75$$

where

$$\overline{CW} \propto d_b^{a}$$

It follows that

$$\overline{W} \propto p^{-2.5/2a}$$

The last equation essentially links the relationship of tree diameter to crown width. However, it ignores a height component. White "estimates" this from diameter in his first equation. I tested White's derivation empirically for my data and found an overestimate of the -3/2 power rule, viz.

$$\overline{W} = .115 \cdot \overline{rcd}^{2.8686}, R^2 = .936, n = 118$$
$$(g) \qquad (mm)$$

$$\overline{CW} = 3.036 \cdot \overline{rcd}^{.8348}, R^2 = .777, n = 118$$
$$(cm) \qquad (mm)$$

thus,

$$\overline{W} \propto p^{-2.8686/2(.8349)} \propto p^{-1.718}$$

White's approach illustrates a major problem with determining a -3/2 power law approximation from data that includes trees which are not closely tracking the self thinning line. Recalculating the asymptotic relationship between $\overline{CW}$ and $\overline{rcd}$ we get a = .939 (from Table 17 and substituting for ρ). Similarly, because $\overline{W} \propto p^{-1.46}$ and $\overline{rcd} \propto p^{-.512}$ then $\overline{W} \propto p^{2.852}$ thus,

$$\overline{W} \propto p^{-2.852/2(.939)} \propto p^{-1.519}$$

This last equation is a much closer approximation to the -1.5 expected outcome, and empirically verifies White's derivation, provided the asymptotic relationships are considered.

Modelling the Relationship Between Size and Density Over Time

Introduction

The earliest average weight-density ($\overline{W}$-ρ) time dependent models were of the integral logistic-type (Shinozaki and Kira 1956, Bleasdale 1966). These models were based on annual plants for which self-thinning had not been substantial, although the same basic model form has been extended to plantation management in Japan (Ando 1968). The self-thinning asymptote, while not generated in the model, is estimated from fully stocked plantations of the same species. There are serious discrepancies between predicted and actual weight estimates for stands that are self-thinning (Hozumi 1977). Hozumi (1975, 1977) has attempted to combine the earlier model form with the -3/2 power rule with some success, though the model in its present form forces the (W-ρ) trajectory towards a -3/2 asymptote, i.e., it is biased.

Recently, Aikman and Watkinson (1980) and Perry (in press) have attempted to incorporate the -3/2 power rule constraints into more biologically based, but as yet, largely theoretical models. Aikman and Watkinson's model is driven by the area a plant of a given weight occupies, rather than density itself. The ($\overline{W}$-ρ) trajectory does not, however, behave in a reasonable fashion. It moves vertically towards the -3/2 asymptote rather than in the empirically observed monototically decreasing fashion (White 1981). Perry's model is based on the more general Von Bertalanffy-type equation and a Weibull type model of photosynthesis-density and produces the asymptotic approach to a maximum.

Biological modifications or explanations of the -3/2 power rule phenomenon are indeed very valuable, especially if they are verified by actual data sets, and add insights into the underlying processes. However, I do not feel that the $(\overline{W}-\rho)$ relationships have been fully documented and described. For instance, there is not one growth model that attempts to track the $(\overline{W}-\rho)$ trajectory in an unbiased fashion. In this section I will describe the development of a preliminary growth model that attempts to track the $(\overline{W}-\rho)$ trajectory over time.

Model Development - Methods and Results

Average tree weight per unit area was examined for distribution along a time axis. The data conformed to a logistic type distribution. The asymptote for the logistic model was known to be a function of density--as determined in the mean weight-density analytical model type.

To test the appropriateness of the logistic model, the data were fit to the linear form of the logistic equation. That is, if

$$\overline{W}(t) = \frac{k}{(1 + be^{-rt})} \tag{31}$$

where, $\overline{W}(t)$ = weight of mean tree at time t

    k   = asymptote

    b   = constant of integration

    r   = intrinsic growth rate

    t   = time

Then,

$$\ln[\frac{k}{\overline{W}(t)} - 1] = \ln b - rt \tag{32}$$

Equation 31 is the integral form of the logistic equation, while Equation 32 is its linear form (Causton 1977).

I set $k = a_0(\text{density})^{a_1}$ (from Equation 29) and used multiple linear regression to fit the following equation:

$$\ln[\frac{a_0 \rho^{a_1}}{\overline{W}(t)} - 1] = (\ln b_0 + \ln b_1 \text{ IS} + \ln b_2 \text{ ID4} + \ln b_3 \text{ ID8})$$
$$- (r_0 t + r_1 t \text{ IS} + r_2 t \text{ ID4} + r_3 t \text{ ID8}) \tag{33}$$

Where, IS = soil type indicator, 1 if soil type forest soil, 0 if

else

ID4 = density level indicator, 1 of 4 x 4 cm initial spacing,

0 if else

ID8 = density level indicator, 1 if 8 x 8 cm initial spacing,

0 if else

b_i (i = 0, 1, 2, 3) = constant of integration parameter

estimates

r_j (j = 0, 1, 2, 3) = intrinsic growth rate parameter estimates

To avoid correcting for non-positive logarithmic transformations on the left hand side of the above equation, I only used data where $0 < [k/\overline{W}(t) - 1]$. This eliminated 10 data points. This was considered justified because these calculations were only regarded as exploratory.

Using multiple linear regression, the best fitting model was determined by comparing mean squared errors after dropping insignificant parameter estimates ($p < 0.05$) until all parameter estimates were significant ($p < 0.05$).

The final equation was:

$$\overline{W}_i = 4.42925 - (.012267 \cdot t - .00211238 \cdot t \cdot IS + .0021549 \cdot t \cdot ID4 + .00574115 \cdot t \cdot ID8) \tag{34}$$

$$MSE = .7934, \quad n = 108, \quad \overline{R}^2 = .7395$$

Where subscripts are as in Equation 33 and $\overline{W}_i = \ln[k/\overline{W}(t) - 1]$.

This analysis indicated a reasonable snugness-of-fit to a logistic-type equation. It also suggested that in the logistic model the constant of integration was invariant of density or soil type, while the intrinsic growth rate was a function of both density and soil type.

I next fitted a full logistic type non-linear model with the asymptote as a function of density. The "traditional" form (Equation 31) was logarithmically transformed to anticipate non-homogeneity of variance and non-normality of residuals. The model below was fitted using non-linear regression (BMDP (Ralston 1981)) with a convergence criterion of 1.0×10^{-5}:

$$\ln(\overline{W}(t)) = [a_0 - a_1 \ln \rho] - \ln[1 + b_0 + b_1 \ IS + b_2 \ ID4$$
$$+ b_3 \ ID8 \cdot \rho^{-(b_4 + b_5 \ IS4 \ b_6 \ ID4 + b_7 \ ID8) \cdot t}] \tag{35}$$

where symbols are as in Equation 33.

a_0 = 11.4499

a_1 = 1.4601

$\overline{W}(t)$ = average weight at time t.

Initial parameter estimates were those gleaned from the linear transformation fits to the full model.

The full model form and its standard error (in brackets) is presented below:

$$\ln(\overline{W}(t)) = [11.4499 - 1.4601 \cdot \ln \rho] - \ln[1 + \underset{(64.853)}{141.216} - \underset{(55.743)}{4.1154 \cdot IS}$$
$$+ \underset{(122.846)}{118.278 \cdot ID4} + \underset{(122.846)}{201.856 \cdot ID8}] \cdot \tag{36}$$
$$e^{-(\underset{(.0019)}{.0161} + \underset{(.00086)}{.00163 \cdot IS} - \underset{(.0025)}{.00142 \cdot ID4} - \underset{(.0021)}{.00519 \cdot ID8}) \cdot t}]$$

MSE = .2547, n = 118, asymptotic standard errors in brackets.

Plots of residuals versus the dependent variable indicated a reasonable homogeneous variance, while a normal probability plot revealed an adequate approximation to normality.

I was thus justified in dropping all non-significant parameter estimates (p < 0.05). I fitted the reduced model which appears below; the reduced model sums of squares were not significantly different (p < 0.01) from the full model:

$$\ln(\overline{W}(t)) = [11.4499 - 1.4601 \cdot \ln \rho] - \ln[1 + \underset{(50.798)}{236.816}$$
$$\cdot e^{-(\underset{(.00129)}{.01852} + \underset{(.00497)}{.001598 \cdot IS} - \underset{(.000971)}{.004247 \cdot ID4} - \underset{(.000939)}{.00879 \cdot ID8}) \cdot t}] \tag{37}$$

MSE = .2547, n = 118, asymptotic standard errors in brackets.

The average weight was then estimated for the 42 mean observations used in Chapter IV, Methods and plotted (Figure 23) on a $(\overline{W}-\rho)$ graph as in Figure 16.

Discussion

The equations presented in the last section were a preliminary attempt to track the $(\overline{W}-\rho)$ time trajectory during self-thinning. The initial logistic equation, Equation 37, used the $(\overline{W}-\rho)$ asymptote derived in Chapter IV, Model Fitting Development and Results, and tracks the observed data very closely (see Figure 23). The use of this asymptote makes reasonable biological sense considering that potential growth is limited by available space or density. In essence though, I have empirically derived the asymptote rather than mathematically defined it via the logistic differential equation form. The next step, of course, is to model the $(\overline{W}-\rho)$ trajectory as a function of time along the curves determined in Chapter IV, Model Fitting Development and Results (see Figure 16).

Despite the preliminary nature of the $(\overline{W}-\rho)$ time trajectory model some valuable observations can be made. Firstly, the intrinsic growth rate varies with soil type and initial density ($p < 0.01$). The intrinsic growth rate is higher on the forest soil and lower the wider the initial spacings. Secondly, the asymptote is invariant of soil type ($p < 0.01$), even if measured along a time trajectory. These results confirm those presented in Chapter IV, Model Fitting

Figure 23. Mean biomass-density trajectory for seedling red alder
growing at various density levels and on two soil types under green-
house and lath house conditions, generated from a logistic-type
equation with asymptote a function of actual density. The asymptote
is the same as in Figure 16. The trajectories are generated from
Equation 37. Each point is a mean of 2 or 3 values.
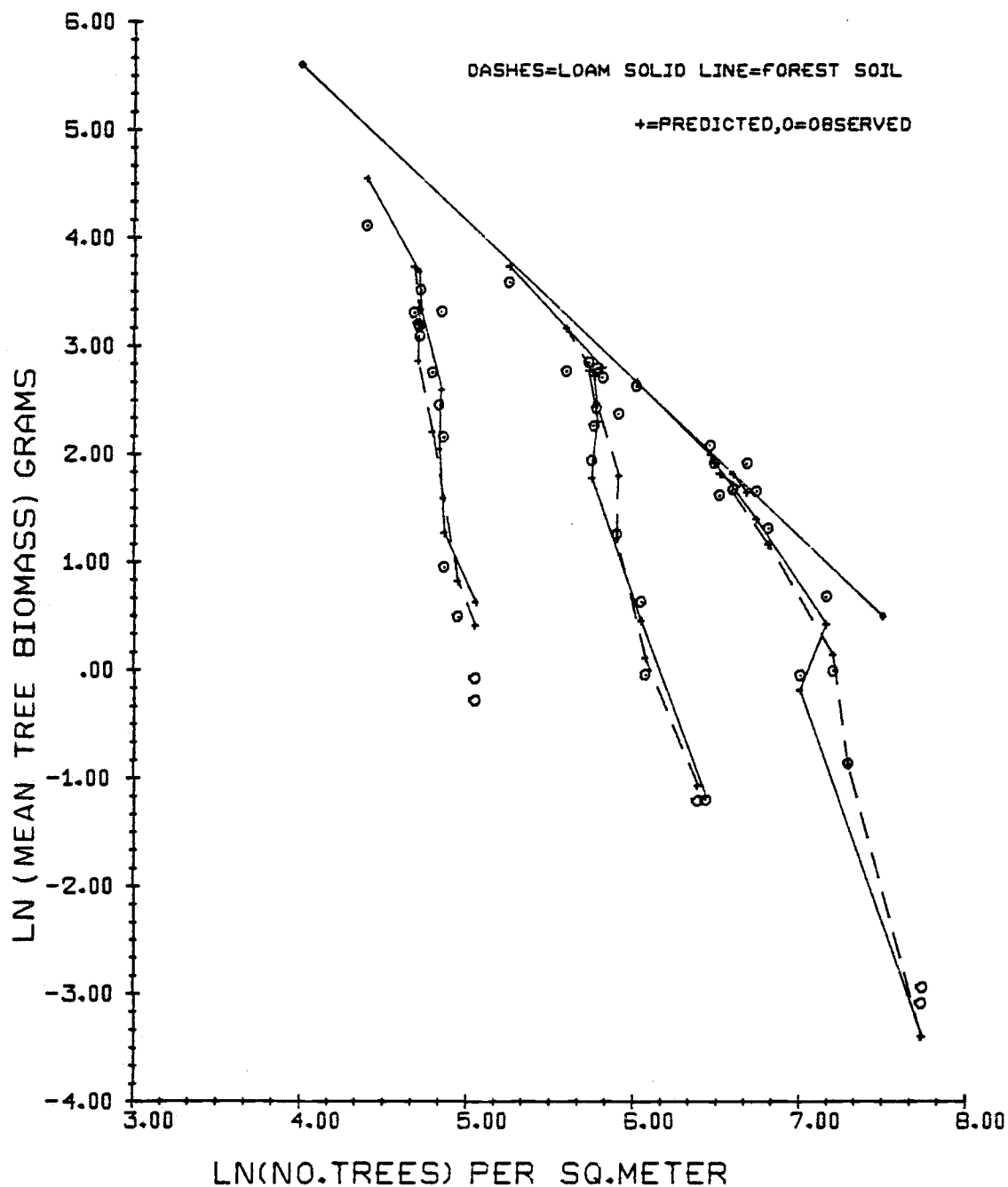
Development and Results. Figure 23 shows how closely, in fact, the two soil types track along a very similar time trajectory.

General Conclusions

The $(\overline{S}-\rho)$ model developed and tested in Chapter IV, Model Fitting Development and Results is, I feel, an important advance in the interpretation and understanding of the -3/2 power rule. It is a uniquely objective and statistically sound method for determining not only the actual asymptote but also, what happens to plants below that line. Interpretation of the -3/2 power rule has been too focused on the actual asymptote and not with the events that lead up to it (White 1981). The analysis of the $(\overline{S}-\rho)$ trajectory is a key to this understanding. This model needs to be verified and tested on other data sets, but it does open up some intriguing possibilities. What, for instance, happens to stands that are thinned? Do they merely assume the trajectory that would have been followed had the trees been planted at a wider spacing? Do stands at the extreme ranges of density conform to the observed pattern? Hozumi (1977) presents graphical evidence that at very high densities, plants may approach the asymptote from above. At very low densities it would take an infinitely long time for trees to enter a self thinning mode so that the asymptote itself may be curvilinear in its upper reaches. Various shapes of asymptote or crown closure line may be tested in the model. In a separate analysis (data not reported here), a curvilinear type asymptote was not verified for the range of data I examined.

Analysis of the $(\overline{S}-\rho)$ trajectory for the whole plant revealed a
close approximation to the -3/2 power rule slope despite the artifi-
cial nature of the experiment. It may be tentatively concluded that,
provided plants are healthy and edge effects minimized, the -3/2 power
rule may be simulated by restricting growing space. The asymptote
intercept was, however, higher than determined in other field studies
which suggests that results from these analyses should not be applied
to natural stands or plantations, though the underlying functionality
should be the same.

The asymptote is itself an inviolable physical boundary, yet the
biological interpretation remains poorly understood. The $(\overline{S}-\rho)$ tra-
jectory sheds light on the dynamic processes occurring leading up to
the asymptote itself. For instance, plant parts fill space dif-
ferently in comparison to the whole plant. While roots and leaves
appear to grow in unison, other plant components are emphasized as
stocking density decreases.

Verification of the -3/2 power rule questions some apparent
incongruities underlying current growth theory. The reciprocal yield
"law" (Shinozaki and Kira 1956) states that, with time, the rela-
tionship between stocking density and yield per unit area stabilizes,
or the "law" of constant final yield (Kira et al. 1953) is invoked.
However, the -3/2 power law tells us that there is a range of den-
sities for which yield per unit area increases with decreasing den-
sity. That is, because yield per unit area (Y) is equal to the pro-
duct of average plant weight and density $(\overline{W} \cdot \rho)$, we can transform the
-3/2 power rule equation $(\overline{W} = a\rho^{-3/2})$ by multiplying both sides by

density, thus $Y = \overline{W} \cdot \rho = a\rho^{-3/2} \cdot \rho$, or $Y = a\rho^{-1/2}$. The "law" of

constant field yield was formulated by researchers examining annual or

short lived plants over a range of densities, the least dense of which

rarely show signs of self-thinning (White 1981). The -3/2 power law,

however, states that yield per unit area would be greater in the wider

spaced stands if they were allowed to grow long enough to approach the

self-thinning asymptote (i.e., longer than one growing season).

CHAPTER V. NITROGEN FIXATION IN SEEDLING RED ALDER

Introduction

Red alder forms a symbiotic relationship with an Actinomycete
(<u>Frankia</u> sp.) which is capable of N_2 fixation. Estimates of nitrogen
accretion vary from 30 to 320 kg/ha/yr (c.f., Binkley 1981). Only one
study has examined the effects of stocking density on nitrogen fixation
(Bormann 1981). No study exists that examines the nitrogen fixation
of red alder in very dense, very young stands. The following green-
house and lath house study tests the effects of stocking density and
soil type on nitrogen fixation for alder seedling from seed to 525 days.

Objectives

(1) Examine the effects of three different stocking densities
and two different soil types on seedling red alder acetylene reduction
per tree and per unit area over time.

(2) Estimate the amount of nitrogen fixed over the course of
the experiment and how much was utilized by the plants.

Methods

Acetylene reduction was measured on four occasions; namely, the
crown closure, fourth, fifth and sixth harvests. Harvest dates were
as follows:

(1) Crown closure (initial spacing, soil type)

			Location
(a)	2 x 2 cm, forest soil	11/28/81	Greenhouse
(b)	2 x 2 cm, loam	12/7/81	Greenhouse
(c)	4 x 4 cm, forest soil	1/14/82	Greenhouse

<u>Location</u>

(d) 4 x 4 cm, loam   2/2/82   Greenhouse
(e) 8 x 8 cm, forest soil   2/20/82   Greenhouse
(f) 8 x 8 cm, loam   2/28/82   Greenhouse

(2) Fourth harvest (all treatments)   7/5/81   Greenhouse

(3) Fifth harvest (all treatments)   9/6/81   Lath house

(4) Sixth harvest (all treatments)   10/30/81 Lath house

Three trees were selected randomly from three root-collar diameter

classes per pot. Three initial spacings across two soil types repli-

cated three times summed to 18 pots per harvest.[7] Nodules were

selected from each sample tree at two locations in approximately equal

amounts: (1) just below root-collar and (2) half-way along the

lengths of the root mass. Samples were carefully removed with ~ 1 cm

root tissue left intact to ensure adequate carbohydrate supplies,

washed in distilled water, and surface dried with cloth. Nodules

from the two sample localities were bulked into a separate 70 ml.

flask for each tree (see Table 19 for sampling intensity). The proce-

dures suggested by McNabb and Geist (1979) were followed. For a more

detailed description and example of calculations see Appendix III.

Sample times were restricted to 10:00 am to 3:00 pm to avoid any

possible major diurnal fluctuations in acetylene reduction (Tripp <u>et</u>

<u>al</u>. 1979). Gas samples were stored in vacutainer tubes for anywhere

from one week to several months, within the storage boundaries

investigated by McNabb and Geist (1979).

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[7]There were only two replicates for each treatment combination in the
crown closure harvest (except 2 x 2 cm, forest soil) due to damping-
off. There were also only two replicates for the fourth harvest
4 x 4 cm, loam due to tent worm infestations.

Table 19. Sampling intensity of seedling red alder nodules per tree for acetylene reduction by initial spacing and date.

Initial spacing (cm x cm)	Date	No. of assays	Sampling intensity % total nodules (+ standard error)	Actual weight of sampled nodules (dry grams) (+ standard error)
2 x 2	1	14	97.8 (1.6)	.005 (.002)
	4	14	47.8 (10.0)	.058 (.021)
	5	16	48.0 (9.5)	.071 (.03)
	6	14	32.0 (7.8)	.083 (.02)
4 x 4	1	11	76.5 (9.3)	.013 (.004)
	4	16	24.7 (6.4)	.009 (.036)
	5	18	34.2 (7.9)	.095 (.036)
	6	18	39.7 (8.4)	.181 (.05)
8 x 8	1	15	65.1 (7.8)	.027 (.33)
	4	18	23.1 (5.7)	.206 (.036)
	5	16	18.6 (4.8)	.122 (.031)
	6	17	19.3 (4.5)	.216 (.083)

Due to large inherent variability in acetylene reduction (Tripp

et al. 1979, Bormann 1981) I elected to test two methods for esti-

mating acetylene reduction of mean tree per pot: (1) regression

equations predicting acetylene reduction per unit dry nodule weight

(specific activity) from easily measured tree parameters[8] or, (2)

assume that the mean value for the three sampled trees per pot esti-

mated the true mean value per pot. Acetylene reduction for the mean

plant per pot was then estimated from estimated specific activity

multiplied by estimated nodule biomass per tree. Nitrogen fixation

per unit area was estimated as the product of estimated acetylene

reduction per plant multiplied by conversion constants[9], and actual

density of trees per unit area. Nitrogen fixation per unit area per

day was estimated as the product of nitrogen fixation per unit area

and the number of hours of daylight per day at time of harvest. The

~ 4500 lux supplement 24 hr lighting during the greenhouse phase was

not thought to be sufficient to maintain maximal midday acetylene

reduction rates (Gordon, personal communication).

Results were analyzed by analysis of variance using a SAS General

Linear Model procedure (Helwig and Council 1979) (see Chapter II for

specific details of experimental design).

An estimate of total nitrogen fixed over the growing period was

made by multiplying the mean value of estimated N_2 fixation (per m^2

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[8]All other trees per pot not sampled for acetylene reduction were
measured for at least root-collar diameter and height.

[9]C_2H_2 reduction (μmoles/tree/hr) x 10^{-6} x 28 ÷ 3 = grams N_2/tree/hr--
this assumes a 3:1 conversion constant for C_2H_2 to N_2.

per day per spacing over the four harvests) with the number of esti-
mated growing days.

Results and Discussion

Regression equations predicting C_2H_2 reduction as a function of
rcd x height (see Chapter II for details) at each harvest date were
judged to be unbiased but of poor predictive power ($\overline{R^2} < 0.50$ and
large relative standard error), with evidences of heteroskedasticity
and non-normality. I thus adopted the alternative method and assumed
that the mean value of the stratified random sample adequately esti-
mated extant mean tree acetylene reduction.

Figure 24 presents mean specific nodule activity (μmoles
C_2H_2 reduced/dry gram/hr) by initial spacing and soil type. Table 20
gives the analysis of variance for natural logarithmic transformation
of the full data set. Logarithmic transformation adequately homoge-
nized variance and normalized residuals.

There was a significant difference ($p < 0.01$) between date means.
The crown closure harvest was substantially higher and more variable
than the other harvests. Duncan's multiple range test ($p < 0.05$),
indicated that the 1st harvest > 4th or 6th harvest > 5th harvest.
The mean value for the 1st harvest was 297.3 μmoles/g nodule/hr--this
compares to a maximum rate recorded by Tripp et al. (1979) of ~ 160
μmoles/g/nodule/hr. It is uncertain why the crown closure values are
so high compared to the other harvest values which fit snuggly into
the values previously reported in the literature (Binkley 1981). Lack
of substantial inter-tree competition and smaller nodules may be
partly to explain.

Figure 24. Mean specific activity of seedling red alder nodules
by initial spacing, soil type and harvest time. Solid lines are
forest soil, dashes are loam. Points are means of 2 or 3 values.
The first 2 harvests were from a greenhouse, the final 2 harvests
were from a lath house (late summer, early fall). The approximate
coefficient of variation of each mean is 84% (from log transformed
ANOVA, see Appendix IV).
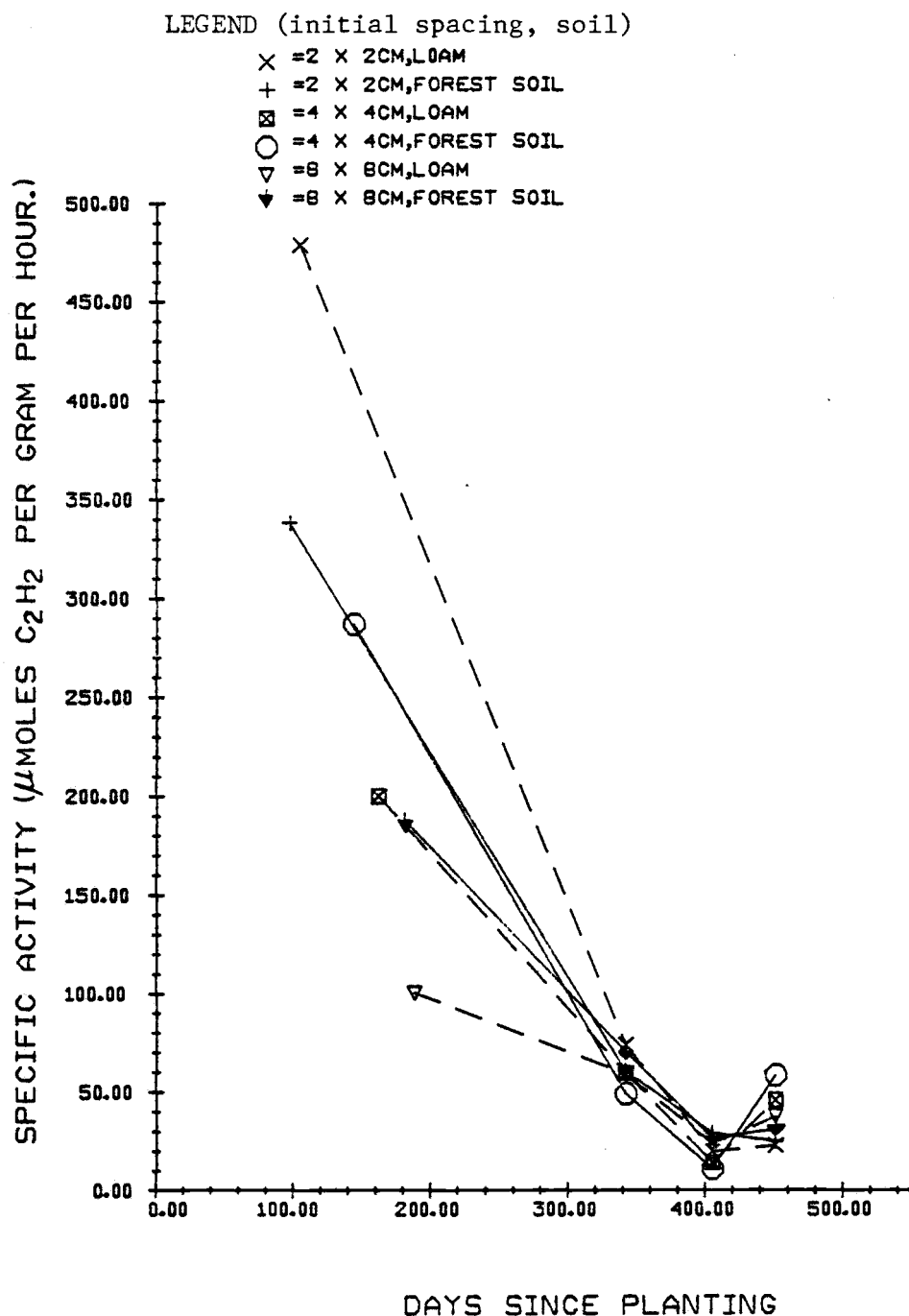
Table 20. ANOVA for ln (average specific activity), μmoles/g dry
          nodule/hr for seedling red alder.

Source of variation	DF	SS	F value	PR > F
Block	2	1.809	1.34	.3309
Date	3	38.4497	19.04	.0018**
Error A	6	4.0396	1.54	.1941
Spacing	2	0.0629	0.07	.9305
Soil	1	0.5952	1.36	.2509
Spacing x soil	2	0.5311	0.61	.5499
Soil x date	3	0.2554	0.2	.899
Spacing x date	6	6.6961	2.56	.0374*
Spacing x soil x date	6	2.6447	1.01	.4349
Error B	34	14.8324		
Total	65	82.2328		

PR > F = probability of a greater F-value.

** = significant $p < 0.01$, * = significant $p < 0.05$.

The values reported here are remarkably similar in range and pattern to those recorded by Sprent and Bradford (1977) for soybean [Glycine max (L) Merr.] who found that the densest spacings were initially higher, consistent with better early growth. However, as the season progressed, the activity of the denser spacings fell below the wider ones. The significant (p < 0.05) interaction between spacing and date (Table 20) substantiates this trend.

There was no significant soil effect on specific activity. Although growth on the loam seemed to lag behind the forest soil, it appears that the loam was sufficiently fertile and aerated to show no differences in nodulation (Elliot and Taylor 1981) or specific activity.

The increase in specific activity during the 6th harvest was unexpected and anomalous but may be speculatively linked to early fall root regeneration.

Acetylene reduction per tree and its ANOVA are presented in Figure 25 and Table 21, respectively.

Date means were significantly different (p < 0.01). Duncan's New Multiple Range Test (p < 0.05) suggested the following subsets:

Harvest	6th	4th	5th	1st
Value	22.1	11.8	10.2	0.4
(μmoles/tree/hr)				

The very small nodule biomass in the crown closure harvest reduced the per tree C_2H_2 reduction to small amounts. The 4th harvest (July) had the greatest range while the 6th harvest had the highest mean value. The mid-season peak agrees with the consensus of many researchers (Sprent and Bradford 1977, Tripp et al. 1979, Bormann 1981).

Figure 25. Mean tree acetylene reduction of seedling red alder by
initial spacing, soil type and harvest time. Solid lines are forest
soil, dashes are loam. Points are means of 2 or 3 values. The
first 2 harvests were from a greenhouse, the final 2 harvests were
from a lath house (late summer, early fall). The approximate
coefficient of variation of each mean is 82% (from log transformed
ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)
× =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
◯ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
▼ =8 X 8CM,FOREST SOIL

DAYS SINCE PLANTING

Table 21. ANOVA for ln (average acetylene reduction), μmoles/g tree nodule biomass/hr for seedling red alder.

Source of variation	DF	SS	F value	PR > F
Block	2	0.7467	0.79	.4966
Date	3	83.7826	58.97	.0001**
Error A	6	2.8416	0.77	.5975
Spacing	2	20.6341	16.81	.0001**
Soil	1	0.0617	0.1	.7530
Spacing x soil	2	0.9058	0.74	.4856
Soil x date	3	0.2117	0.11	.9507
Spacing x date	6	6.1187	1.66	.1607
Spacing x soil x date	6	2.8709	0.78	.5916
Error B	34	20.6301		
Total	65	181.6300		

PR > F = probability of a greater F-value.

** = significant p < 0.01

Again there were no significant differences between soil type (p < 0.01), however, there were significant differences (p < 0.01) between initial spacings. Each spacing mean was significantly different (Duncan's New Multiple Range Test, p < 0.05), with the wider spacings having higher values. This finding agrees with those of Bormann (1981). This reflects the importance of nodule biomass. The higher rate of C_2H_2 reduction per tree at the 6th harvest is due to the unexplained increase in specific activity.

The overall mean for these data was 11.78 µmoles/tree/hr--considerably less than the data recorded by Tripp et al. (1979) of 163.6 µmoles/tree/hr for 2 and 3 yr-old alder.

Acetylene reduction per tree was more highly correlated with tree biomass than leaf area (R^2 = .76 and .61, respectively, for logarithmic (base e) transformed data). If N_2 is indeed source limited (Havelka and Hardy 1977) then leaf area should have been more closely related. I regressed acetylene reduction per tree against biomass and various dummy variables (see Chapter II) to account for initial density and soil type. The following equation was significant for all parameters (p < 0.05):

$$\ln(Y) = -.018177 + .668277 \ln(X) + .674099 \text{ ID4} + .367012 \text{ IDX6}$$

$$\overline{R^2} = .8135, \ \overline{X} = -.554, \ \text{MSE} = .546, \ n = 66$$

Y = acetylene reduction (µmoles/tree/hr)

X = total tree biomass

ID4 = indicator variable for intercept parameter at 4th harvest

IDX6 = indicator variable for slope parameter at 6th harvest

The slope of .66828 ($\pm$ .108) suggests that C_2H_2 reduction per tree does not increase at the same rate as biomass--this would only be the case if the slope equalled 1. However, the slope for the 6th harvest approaches 1 suggesting that C_2H_2 reduction is increasing at the same rate as biomass. This indicates that the larger sixth harvest trees were fixing more per tree, whereas the higher slope value for the 4th harvest hints that the smaller trees were generally more efficient earlier in the study.

Figure 27 and Table 22 describe the estimated rate of nitrogen fixation per day and the associated ANOVA.

There was a significant difference between date means ($p < 0.01$). Again, the 4th and 6th harvests were not different ($t_{2\alpha} < 0.05$). Although the mean for the 4th harvest of .63 g N_2/m^2/day (CV% = 64) was greater than the 6th harvest of .56 g N_2/m^2/day (CV% = 85), it was much less variable.

The first two harvests were remarkably consistent in trend. The denser spacings were superior to the wider spacings (see Figure 27). The convergence of values for the 4th harvest suggests that, ceteris peribus, during periods of maximum growth nitrogen fixation per unit area tends to peak towards a common level. The exception is the 8 x 8 cm initial spacing on loam soil type. The reasons for this depression during peak growth periods are unclear, but was apparently caused by relatively low acetylene reduction per tree.

Estimates of the total amount of N_2 fixed during the experiment are presented in Table 23.

I fitted a simple linear regression to data in Table 23 and obtained highly correlated results for N_2 fixed per unit area as a

Figure 26. Mean unit area dinitrogen fixation estimates for
seedling red alder by initial spacing, soil type and harvest time.
Solid lines are forest soil, dashes are loam. Points are mean of
2 or 3 values. The first 2 harvests were from a greenhouse, the
final 2 harvests were from a lath house (late summer, early fall).
The approximate coefficient of variation of each mean is 80% (from
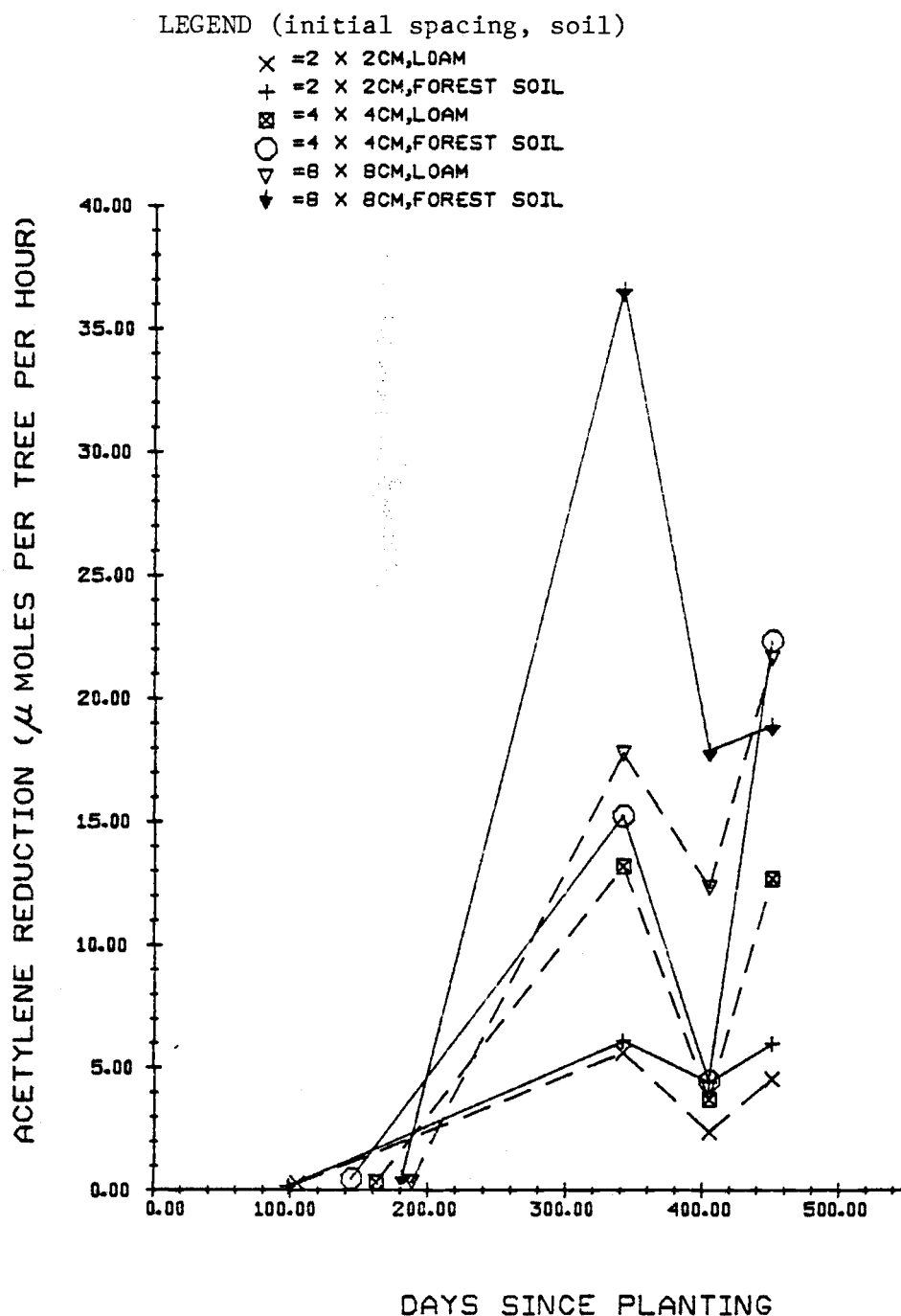log transformed ANOVA, see Appendix IV).

LEGEND (initial spacing, soil)

X =2 X 2CM,LOAM
+ =2 X 2CM,FOREST SOIL
⊠ =4 X 4CM,LOAM
○ =4 X 4CM,FOREST SOIL
▽ =8 X 8CM,LOAM
▼ =8 X 8CM,FOREST SOIL

NITROGEN FIXATION (GRAMS PER M^2 PER DAY)

DAYS SINCE PLANTING
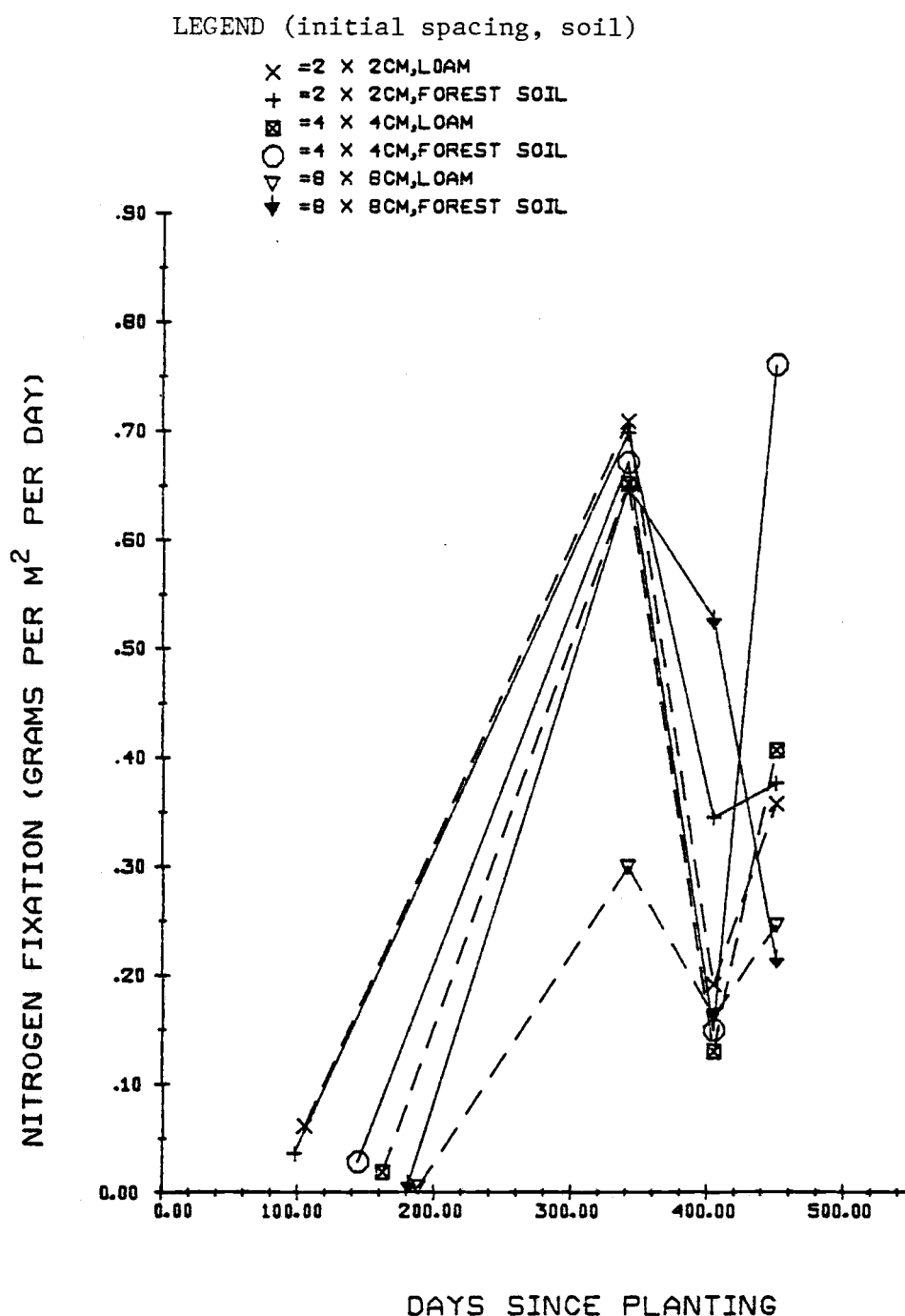
Table 22. ANOVA for ln (estimated N_2 fixation), grams/m^2/day for
seedling red alder.

Source of variation	DF	SS	F value	PR > F
Block	2	.7418	.59	.4563
Date	3	63.103	33.45	.0001**
Error A	6	2.4814	0.66	.6839
Spacing	2	4.5334	3.6	.0381*
Soil	1	0.0197	0.03	.8606
Spacing x soil	2	0.6254	0.5	.6126
Soil x date	3	0.1591	0.08	.9681
Spacing x date	6	8.9279	2.37	.0512
Spacing x soil x date	6	2.7315	0.72	.6333
Error B	34	21.3831		
Total	65	130.1097		

PR > F = probability of a greater F-value.

** = significant $p < 0.01$, * = significant $p < 0.05$.

Table 23. Approximate amounts of dinitrogen fixed per unit area, for
           seedling red alder grouped by initial spacings.

Initial spacing (no./m^2)	Per day (g N$_2$/m^2/day)	Per length of experiment (g N$_2$/m^2/525 days)	Per year (kg N$_2$/ha/6 months)
2500	.40487	212.557	680
625	.37993	199.463	638
156	.27008	141.792	454

function of the reciprocal of initial density, $R^2 = -.9999$. The equation for the per year data was:

$$kg\ N_2/ha/yr = 696.6 - 37788.1 \cdot (initial\ density\ m^2)^{-1}.$$

The equation intercept indicates that an upper level of N_2 fixation would be about 700 kg N_2/ha/yr at very high densities. Bormann (1981) found that N_2 fixation per unit area was a parabolic function of initial density for 5-yr-old red alder, i.e., N_2 fixation peaked at intermediate densities. Clearly, this pattern is part of a developmental process. The -3/2 power rule indicates that the denser stands reach the -3/2 asymptote first and more efficiently utilize growing space. If there is a point along the line at which the carrying capacity is reached, then a general decline in growth efficiency would occur, earlier in the denser stands while the wider spaced stands come into full "maturity" later. Thus, under this hypothetical interpretation, denser stands have a shorter "adolescence," an earlier but shorter "maturity" and hence, earlier decline. The denser stands had not yet reached the end of the mature phase in my experiment while "senility" may have been occurring in Bormann's analysis.

The nitrogen accretion rates are higher than any previously reported for red alder (Binkley 1981) but are comparable to the amounts recorded by Sprent and Bradford (1977) for soybean.

Analysis of estimated nitrogen production per unit leaf area sheds some light on the dynamics of the developmental process. Table 24 presents these data. It can be seen clearly that if we consider the first three harvests then, without exception, the 2 x 2 cm initial spacing N_2 fixation per unit leaf area peaks at the crown closure, the

Table 24. Estimated dinitrogen fixation per unit leaf area for seedling red alder by initial spacing, soil type and date.

[1]I.D.	N$_2$ production per unit leaf area (LA) (mg N$_2$/m^2 LA/hr) $\pm$ 95% confidence limits	Number of observations (means)
211	1.972 ($\pm$ 1.854)	2
214	1.782 ($\pm$ .296)	3
215	1.062 ($\pm$ 1.301)	3
216	2.591 ($\pm$ .796)	3
221	1.555 ($\pm$ 1.667)	3
224	1.483 ($\pm$ 2.052)	3
225	1.410 ($\pm$ 1.677)	3
226	6.709 ($\pm$ 12.314)	3
411	.915 ($\pm$ .799)	2
414	1.433 ($\pm$ 1.648)	3
415	.666 ($\pm$ .802)	3
416	6.49 ($\pm$ 3.296)	2
421	.651 ($\pm$ 1.635)	2
424	1.177 ($\pm$ .888)	3
425	.503 ($\pm$ .328)	3
426	6.091 ($\pm$ 3.296)	3
811	.152 ($\pm$ .022)	2
814	1.427 ($\pm$ 1.661)	3
815	2.649 ($\pm$ 1.966)	3
816	9.435 ($\pm$ 17.332)	3
821	.285 ($\pm$ .865)	2
824	.796 ($\pm$ .811)	3
825	1.044 ($\pm$ .697)	3
826	3.305 ($\pm$ 3.965)	3

[1]I.D.: 1st number = initial spacing - 2 = 2 x 2 cm, 4 = 4 x 4 cm, 8 = 8 x 8 cm.
2nd number = soil type - 1 = loam, 2 = forest soil.
3rd number = harvest date 1, 4, 5 or 6.

4 x 4 cm spacing at the 4th harvest and the 8 x 8 cm spacing at the 5th harvest, suggesting that most carbohydrate flow to nodules occurs earlier in the year the denser the spacings. This, of course, ignores the anomalous 6th harvest data which seem to bear little relation to leaf area because leaf area had begun to decline substantially at this time due to leaf fall. These data only suggest such a trend because, almost without exception, the 95% confidence limits overlap for all data points.

The proportion of nodule weight to tree biomass ranged from .37% to 3.08%. The lowest values were recorded in the crown closure harvest at the wider spacings. This lag effect with spacing, i.e., lower proportion of nodules the wider the spacing continued, but in diminishing amounts over the course of the experiment.

Finally, in Table 25 I present estimated nitrogen invested in biomass by the end of the experiment.

Analysis of soil nitrogen at the beginning and end of the experiment (Table 1) indicates there was little change in total nitrogen. Nitrate nitrogen (not measured in the total nitrogen estimates), however, decreased, especially in the loam, possibly due to leaching from frequent watering. We may assume then, that most of the fixed nitrogen is either taken up by the plant or assimilated by microbes and lost as nitrate to leaching. Table 25 gives estimates of nitrogen incorporated in biomass by the 7th harvest and lost to leaf-fall at the end of the 6th harvest. Total estimated N_2 uptake underestimates the dinitrogen fixation estimates presented in Table 22 by a factor of about 2. This contradicts the results of Tripp et al. (1979) and Zavitkovski and Newton (1968) who found that alder fixes 70-75 percent

Table 25. Estimated nitrogen content for red alder seedlings grown at various levels of stocking density and soil types after 525 days of continuous growth under greenhouse and lath house conditions.

Spacing[1]	Soil[2]	Biomass (kg/m^2)	N$_2$[3] (kg/ha)	N$_2$[4] litterfall (kg/ha)	Total N$_2$ uptake (kg/ha)
2	1	3.903	624.5	364.7	989.2
2	2	5.659	905.4	464.9	1370.3
4	1	3.802	608.3	411.9	1020.2
4	2	6.297	1007.5	559.7	1566.7
8	1	2.942	470.7	206.8	677.5
8	2	4.954	792.6	380.7	851.4

[1]Spacing: 2 = 2 x 2 cm, 4 = 4 x 4 cm, 8 = 8 x 8 cm initial spacing.

[2]Soil: 1 = loam, 2 = forest soil.

[3]Based on 1.6% nitrogen content of biomass (computed as the mean of values given in: Monaco et al. 1982 and Bormann 1981).

[4]Based on maximum leaf biomass prior to leaf fall winter 80/81 and 2.96% nitrogen content of leaves (Bormann 1981).

of their total N. When comparing estimated uptake with per year fixa-
tion (Table 23), however, there is closer agreement. It is possible,
that with diurnal and seasonal variability in acetylene reduction
(Tripp et al. 1979) I may have overestimated the acetylene reduction
figures. Nonetheless, it does appear that the red alder seedlings are
producing via symbiosis all their nitrogen needs. No fertilization
was necessary during the duration of the experiment. Much of the
excess N_2 fixed may have been leached from the soil. The fraction
lost to herbivores (e.g., the indigenous mite population) is unknown
but may have been significant.

Conclusions

Care should be taken in interpreting these results because of (1)
the extended season of growth (July 1980 to October 1982 for the ace-
tylene reduction analysis), (2) the movement of plants from the
greenhouse to the lath house in June, 1982 and (3) the "unnatural"
restrictions in root and shoot space. With these strictures borne in
mind some interesting conclusions can be made.

Firstly, there were no apparent differences in ex situ soil type
acetylene reduction responses. It appears that there were no serious
limits of any macro or micronutrients in the loam and also that,
despite apparent compaction, aeration of root nodules was not
restricted. In most cases, the performance of nodules in the loam
soil was slightly but not significantly inferior to the forest soil.

Specific activity changed over the course of the experiment from
being higher in denser spacings to higher in the wider spacings. This
is consistent with seasonal changes in leaf area. Spacings differed

significantly for acetylene reduction per tree. Bormann (1981) also found a similar trend. Denser spacings tended to be more efficient at fixing nitrogen per unit area. Significant harvest date and spacing interactions, however, confused the issue. The increase in specific activity during the 6th (late fall) harvest also complicated the story and demands further testing to determine its validity. There was an undoubted period of root elongation during this harvest. Could it be possible that photosynthates being mobilized in the roots were snatched up by the nodules? Would this have any adaptive significance for the nodules themselves?

Specific activity and N_2 fixation per unit area were higher than those previously reported for red alder, and were surprisingly comparable to results obtained for soybean (Sprent and Bradford 1977), although the alder were grown at considerably closer spacings. This indicates that red alder is comparable in short term efficiency to a super agronomic crop but also has the advantage of perenniality.

CHAPTER VI. SUMMARY AND GENERAL CONCLUSIONS

Summary

(1) Red alder seedlings were grown at three initial densities
(2500 trees/m^2, 625 trees/m^2, and 165 trees/m^2) and on two soil types
(a forest soil and river loam) under restricted growing space in
greenhouse and lath house conditions for 525 days. The statistical
design was a split-plot arrangement by harvest date of a completely
randomized block design. There were three blocks or replicates for
each treatment combination. There were 7 destructive harvests, the
first at crown closure and then again every 2-3 months.

(2) From a 6% stratified random sample by seedling root collar
diameter, multiple linear regressions accounting for soil type and
initial spacing effects were generated for estimates of biomass and
tree structure at each harvest date. Logarithmic transformations
(base e) were most appropriate when root-collar diameter squared times
height was used as the independent variable.

(3) After 525 days of growth average tree biomass was largest in
the widest initial spacings and was always greater on the forest soil
than river loam. The mean tree biomass values (grams/tree) from
widest to densest spacings at 525 days were: 61.4, 36.6, and 8.9 for
forest soil and 27.5, 16.5 and 5.4 for river loam. The corresponding
values for mean biomass per unit area (kg/m^2) were 4.9, 6.3, 5.7 and
2.9, 3.8 and 3.9.

(4) Allometric analyses suggested that although there were some
effects of proximity to edge on tree biomass and structure these were
minimal.

(5) Skewness and kurtosis statistics both peaked by the 3rd harvest (284 days) for the densest initial spacing, between the 3rd and 6th harvest (451 days) at intermediate spacing, and by the 6th harvest for the widest spacing.

(6) The relationship between average plant size and actual stocking density was adequately modelled by the following equation:

$$\overline{Y}_{ji} = b_0 - b_1 X_{ji} - b_o \cdot b_2 \cdot e^{-b_3 (X_{1j} - X_{ji})^{b_4}}$$

where, $\overline{Y}_{ji}$ = log (average plant size) (e.g., biomass, height)

X_{ji} = log (actual stocking density)

X_{1i} = log (actual stocking density at crown closure)

j = number of harvests

i = number of initial spacing levels

b_0 = asymptote intercept

b_1 = asymptote slope

b_2 = relative density at X_{1i}

b_3 = intercept exponential term

b_4 = slope exponential term

(7) Analysis of average tree biomass using this equation ($\log_e$) gave an asymptote intercept of 11.45, a slope of 1.46 and a relative density at crown closure of .31. The crown closure line was parallel to the mortality line. Both soil types followed the same average weight ($\overline{W}$) - density (ρ) trajectory and were constrained by the same mortality line.

(8) Components of biomass behaved differently from total tree biomass (p < 0.01). Components were ranked by highest asymptote slope to give a relative carbohydrate allocation priority with decreasing density, i.e., branches > stem $\geq$ leaves $\geq$ roots $\geq$ nodules. Leaf area had an asymptote slope of -1.18 which was not significantly different from -1 (p < 0.01).

(9) Contrary to the findings of White (1981) there was a general agreement between (1) predicted allometric relationships between average tree size (e.g., diameter, crown width, crown volume) and stocking density and (2) computed asymptote values for these variables. The importance of examining asymptotic allometric relationships close to the mortality line to avoid environmental vagaries is stressed.

(10) A logarithmically transformed integral logistic equation with the asymptote a function of maximum average tree size predicted by the equation in (6) was used to track the ($\overline{W}$-ρ) trajectory over time. The intrinsic rate of growth was higher in denser spacings and on forest soils.

(11) Acetylene reduction for the mean tree per pot was estimated as the mean of a stratified random sample by root-collar diameter size classes. Acetylene reduction (μmoles/g nodule/hr) varied from 297.3 at crown closure to 46.8 at the 6th (fall) harvest. There was a significant interaction between initial spacing and harvest date (p < 0.05)., but no significant differences occurred between soil types (p < 0.01). There was a significant difference (p < 0.05) between initial spacings for acetylene reduction per tree. Wider spacings had higher values. It was estimated that, ranking densest spacings first,

the N_2 fixation rates (kg N/ha/6 months) were: 680, 638 and 454.

Nitrogen fixation supplied about twice as much nitrogen as was needed

by the plants over the course of the experiment.

General Conclusions

The two basic underlying ideas tested in this research have been

substantiated. Firstly, that analysis of self-thinning is incomplete

if it merely considers the -3/2 power rule or mortality line in isola-

tion from the average size $(\overline{S})$ - density (ρ) trajectory. Secondly,

that tests of allometric derivations of the -3/2 power rule must be

based on data derived from the asymptote itself. If this stricture is

satisfied we find a reasonable verification of allometric derivations

formulated from purely physical considerations, i.e., there is a

finite number of trees of a given size that we can pack into a unit

volume.

Although this experiment was conducted under artificial con-

ditions, the primary processes are thought to hold for natural stands.

Of fundamental importance is the finding that the $(\overline{S}-\rho)$ trajectory is

described by the same equation irrespective of initial stocking den-

sity or soil type. This idea may be extended to improve upon density-

management diagrams (e.g., Drew and Flewelling 1979). Future research

efforts should concentrate on verifying these findings and on

describing time dynamics along the $(\overline{S}-\rho)$ trajectory.

A further use for this research is in quantifying carbohydrate

allocation with changing density. The total average biomass of a

tree may conform to the -3/2 power rule but the relationship among

plant parts is continually adjusting as more (or less) space becomes

available to potentially fill. It is undoubtedly the mix of these adjustments that determines the efficiency of space capture and occupancy. Further studies should compare such characteristics for different species.

These analyses only deal with average plant size. This is an abstraction—there may be no plant in the population which fits this description. Analyses of frequency distributions of plant size during periods of density-stress-induced mortality will help explain the functional processes more clearly. What characteristics of the trends in these distributions best describe the self-thinning process?

The effects of seasonality on nitrogen fixation somewhat complicated the responses to density, but wider spaced trees had higher nitrogen fixation rates per tree, although the denser spacings fixed more nitrogen per unit area. It is conceivable that if nitrogen fixation were measured over a range of densities at peak activity for several years, we could fit the data to a $(\overline{S}-\rho)$ trajectory type model as presented above.

CHAPTER VII. LITERATURE CITED

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APPENDICES

Simple Correlation Coefficients

Simple correlation coefficients for alder sample trees (see Table 3 for abbreviations, BBA = total branch basal area; no. of observations in brackets).

1st Harvest

	ST (58)	BR (6)	RT (58)	CSA (46)	CV (46)	CW (58)	CL (57)	DBR (6)	LBR (6)	LVS (58)	LA (58)	NOLVS (58)	NOD (57)	BBA (6)	NOBR (21)	ACT (39)
RCD	.8817	.9393	.8595	.9332	.8750	.9101	.9697	.4569	.9637	.9066	.9154	.8032	.7851	.8793	.8182	-.3164
HT	.9042	.9499	.8616	.9523	.8915	.9174	.9948	.7028	.8129	.9225	.935	.8555	.7771	.9699	.9238	-.2215
RSH	.9882	.9897	.8334	.9456	.9735	.7828	.8354	.5592	.9415	.9733	.9624	.8350	.7126	.8820	.8017	-.1883
RCDS	.9714	.9695	.8933	.9728	.9627	.8632	.9210	.5096	.9575	.9806	.9188	.8540	.7859	.8641	.7920	-.2408

3rd Harvest

	ST (74)	BR (37)	RT (74)	CSA (58)	CV (58)	CW (58)	CL (58)	DBR (37)	LBR (37)	LVS (74)	LA (74)	NOLVS (74)	NOD (63)	BBA (37)	NOBR (74)
RCD	.8428	.8142	.8141	.9222	.8668	.9394	.9313	.8663	.5273	.8858	.8833	.7386	.8435	.90	.9018
HT	.7343	.6574	.6767	.8815	.7903	.9113	.9857	.8160	.5310	.8458	.8415	.8690	.7668		.8690
RSH	.9814	.9676	.9595	.9380	.9379	.8949	.8151	.8305	.4776	.9001	.8985	.7097	.9151		.8746
RCDS	.9598	.9519	.9420	.9437	.9291	.9193	.8556	.8407	.4861	.9125	.9095	.7273	.9110		.8996

5th Harvest

	ST (66)	BR (66)	RT (66)	CSA (49)	CV (49)	CW (49)	CL (65)	DBR (31)	LBR (31)	LVS (66)	LA (66)	NOLVS (66)	NOD (62)	BBA (30)	NOBR (66)	ACT (47)
RCD	.9266	.8508	.9070	.8632	.7765	.8885	.9523	.8216	.7709	.9227	.9100	.8555	.9215	.9017	.9027	.4471
HT	.8846	.7684	.8448	.8368	.7295	.8575	.9637	.7705	.736	.8881	.8761	.7881	.8618	.8407	.8604	.4921
RSH	.9910	.8861	.9540	.8926	.8447	.8657	.8791	.7060	.6778	.9495	.9394	.8193	.9425	.8754	.8589	.4134
RCDS	.9816	.8949	.9601	.8896	.8303	.8887	.9142	.7631	.7279	.9548	.9432	.8689	.9581	.9013	.8896	.4164
CW	.8743	.8917	.8395	.9605	.9212	1.0000	.8849	.7998	.7861	.8585	.8673	.8712	.8948	.8431	.8972	.6177
CL	.8870	.7793	.8204	.8999	.8003	.8849	1.0000	.8051	.8317	.9149	.9092	.8278	.8619	.8375	.9121	.5812
CW2	.8348	.8914	.7951	.9666	.9688	.9645	.7980	.7125	.7243	.7928	.8076	.8232	.8540	.8250	.8131	.6158
CW2L	.7984	.8464	.7257	.9601	.9746	.9107	.7692	.6582	.6872	.7635	.7879	.7636	.7942	.7526	.7377	.6360

APPENDIX II.

Mean Alder Seedling Structure Estimates:

Crown Width and Length, Branch Diameter and Number of Leaves

Estimates of crown width, crown length, branch diameter and number of leaves for seedling red alder by initial spacing, soil type and harvest date.

ID	CW	CS	BD	NLVS	ID	CW	CL	BD	NLVS
211	3.67	3.15	0.0	0.7	811	12.76	22.22	0.01	14.8
212	7.16	15.60	1.51	1.6	812	12.02	28.03	3.38	15.8
213	7.72	20.82	5.10	4.2	813	23.43	60.89	9.62	51.3
214	11.19	36.38	7.64	4.6	814	21.56	65.71	12.56	19.1
215	9.92	21.8	9.24	4.7	815	23.87	62.75	16.06	22.4
216	7.21	31.36	2.44	1.7	816	16.38	62.83	5.92	5.2
217	10.19	20.29	8.89	4.1	817	27.56	57.52	18.88	17.5
221	3.52	2.9	0.0	0.6	821	11.40	18.86	0.005	11.9
222	9.77	22.17	2.25	3.6	823	25.66	66.37	18.66	70.5
223	11.77	31.33	6.52	10.2	823	25.66	66.37	18.66	70.5
224	11.70	37.65	7.88	6.2	824	29.11	86.51	15.94	33.4
225	11.24	25.67	9.66	5.9	825	27.42	74.37	17.42	29.5
226	8.18	34.55	2.78	2.1	826	17.14	65.63	6.20	5.4
228	16.56	55.44	16.88	10.4	827	39.25	84.92	20.89	35.2
441	8.01	10.52	0.0	4.3					
412	9.59	21.74	2.49	3.4					
413	13.51	35.66	7.21	19.8					
414	16.75	51.69	9.74	13.9					
415	14.58	35.95	11.17	10.8					
416	9.59	40.73	3.35	2.4					
417	16.41	38.98	11.73	9.5					
421	7.82	10.36	0.0	4.4					
422	12.76	29.97	3.33	6.7					
423	21.42	55.78	9.27	46.3					
424	21.76	66.27	13.71	19.6					
425	20.37	51.90	14.77	16.9					
426	11.43	46.07	3.97	3.4					
427	26.78	69.79	18.34	23.8					

I.D. 1st digit: Initial spacing (2 = 2 x 2 cm, 4 = 4 x 4 cm, 8 = 8 x 8 cm).
      2nd digit: Soil type (1 = loam, 2 = forest soil).
      3rd digit: Harvest date (1 through 7).

CW = crown width (cm), CL = crown length (cm), BD = branch diameter (mm x 10^{-1}), NLVS = number of leaves per tree.

APPENDIX III.

Specific Activity Calculations

The computational formula used was:

no. moles C_2H_2 reduced per gram nodule per hour =

no. moles $^1C_2H_2$ x (% $^2C_2H_2$ ÷ 100) x $^31.1$ ÷ time (hrs) ÷ nodule

weight (grams)^4 injected.

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[1] $\dfrac{1 \text{ x } (.007 \text{ ml})}{.082054 \text{ x } (°K)}$ where 7 ml acetylene injected (i.e., 10% volume of flask).

$(1 \cdot atm \cdot gmole \cdot °K)$ 1 = pressure assumed to equal 1 atm.

°K = temperature of bladder containing acetylene.

[2] Value obtained from gas chromatograph analysis of acetylene/ethylene peaks.

[3] Correction factor for the particular machine used to correct for actual ratio of acetylene/ethylene.

[4] Nodules dried at 70°C for 48 hrs.

APPENDIX IV.

This Appendix contains an enumeration of all ANOVA used in the text, except for those listed fully in Chapter V.

The calculation of the approximate coefficient of correlation in Figures 1 through 15 and Figures 25 through 27 are based on an analysis presented in and modified from Snedecor and Cochran (1967). The computations are:

$$E(CV\%) = (e^{((MSE_A + MSE_B)/n)^{0.5}} - 1.0) \times 100$$

where

$E(CV\%)$ = estimated coefficient of variation of untransformed means.

MSE_A and MSE_B = mean squared errors from log transformed ANOVA and A = main-plot, B = sub-plot.

n = average number of replicates contributing to each mean.

SOURCE	DF	Ln(CSA)cm MS	F	P F	Ln(CV)cm MS	F	P F	Ln(crown width)cm MS	F	P F	Ln(crown length)cm MS	F	P F
Block	2	.9266	9.83	.0002	2.0185	6.16	.0144	.2707	10.2	.0026	.1813	5.25	.0230
Date	6	12.8936	136.86	.0001	29.8987	91.32	.0001	1.6461	62.02	.0001	4.2263	122.4	.0001
ERROR A	12	.1213	1.29	.2488	.3274	1.49	.1505	.0265	.92	.5375	.0345	.94	.5121
Soil	1	4.17	42.27	.0001	8.688	39.66	.0001	1.3009	44.86	.0001	1.7001	46.39	.0001
Spacing	2	22.735	241.31	.0001	49.8157	227.42	.0001	6.53	225.16	.0001	7.8986	215.52	.0001
SpacingxSoil	2	.0993	1.05	.3548	.1711	.78	.4623	.0596	2.06	.1364	.0946	2.58	.0837
SoilxDate	6	.2281	2.42	.0363	.4647	2.12	.0633	.0781	2.69	.0218	.1691	4.61	.0006
SpacingxDate	12	.4842	5.14	.0001	1.5775	7.2	.0001	.0855	2.95	.0027	.2471	6.74	.0001
SpacingxSoilxDate	12	.0441	.47	.9257	.1397	.64	.8017	.011	.38	.9656	.0219	.6	.8358
ERROR B	62	.0942			.2190			.0290			.0366		
Total	117	1.5875			3.7359			.2931			.5590		

SOURCE	DF	Ln(no. leaves) MS	F	P F	Ln(density) trees/m^2 MS	F	P F	Ln(no. branches) MS	F	P F	Ln(branch diam.)mm MS	F	P F
Block	2	1.0049	6.44	.0126	.0382	.90	.4339	.0661	5.75	.0177	.2315	1.16	.3454
Date	6	9.2536	56.79	.0001	1.3033	30.55	.0001	20.776	180.75	.0001	22.7394	114.24	.0001
ERROR A	12	.1629	1.4	.1905	.0427	.95	.5004	.1149	.98	.4805	.199	1.17	.3225
Soil	1	5.9264	50.91	.0001	.3662	8.2	.0057	3.7957	32.25	.0001	2.4398	14.37	.0003
Spacing	2	27.4411	235.72	.0001	37.0316	828.86	.0001	7.9794	67.81	.0001	.7677	4.52	.0147
SpacingxSoil	2	.1934	1.66	.1981	1.7209	1.19	.3108	.3752	3.19	.0481	.0866	.51	.6028
SoilxDate	6	.3574	3.07	.0107	.0584	1.31	.2669	.1287	1.09	.3763	.1371	.81	.5678
SpacingxDate	12	.664	5.7	.0001	.1486	3.33	.0009	1.8352	15.6	.0001	2.9995	17.67	.0001
SpacingxSoilxDate	12	.0311	.27	.9923	.0134	.3	.9872	.0837	.71	.7349	.3815	2.25	.0197
ERROR B	62	.1164			.0447			.1177			.1698		
Total	117	.4795			.8796			1.719			1.9443		

SOURCE	DF	Ln(branch length)mm MS	F	P F	Ln(skewness) MS	F	P F	Ln(kurtosis) MS	F	P F	Ln(shoot:root) MS	F	P F
Block	2	.2893	5.74	.0178	.0048	.03	.9668	.2085	.37	.6967	.0368	5.32	.0222
Date	6	31.162	618.29	.0001	.8271	5.79	.0049	2.0001	3.57	.0287	1.2732	183.87	.0001
ERROR A	12	.0504	.71	.7369	.1429	.06	.0939	.5597	1.05	.4162	.0069	1.34	.2209
Soil	1	1.9008	26.74	.0001	.0042	1.68	.8252	.0091	.02	.8963	.0726	14.04	.0004
Spacing	2	18.5863	261.43	.0001	.0162	9.71	.8272	.6728	1.26	.2900	.6565	126.83	.0001
SpacingxSoil	2	.2018	2.84	.0661	.1556	.19	.1696	.2547	.48	.6219	.0075	1.45	.2421
SoilxDate	6	.1098	1.54	.1787	.1495	.05	.1233	.7363	1.38	.2363	.0129	2.38	.0392
SpacingxDate	12	2.5333	35.63	.0001	.4462	1.83	.0001	1.3605	2.56	.0086	.0647	12.32	.0001
SpacingxSoilxDate	12	.0326	.46	.9314	.1513	1.76	.0723	.5666	1.06	.4047	.0097	1.87	.0562
ERROR B	62	.0711			.0852			.5321			.0052		
Total	117	2.4345			.17			.7579			.0912		

Ln(biomass)g/tree, Ln(branch)g/tree, Ln(root)g/tree, Ln(leaves)g/tree

SOURCE	DF	Ln(biomass)g/tree MS	F	P F	Ln(branch)g/tree MS	F	P F	Ln(root)g/tree MS	F	P F	Ln(leaves)g/tree MS	F	P F
Block	2	1.1879	7.75	.0069	2.5422	15.16	.0005	.8582	6.75	.0109	1.2943	10.54	.0047
Date	6	30.8466	201.23	.0001	72.1391	430.26	.0001	30.5357	239.99	.0001	18.7480	151.54	.0001
ERROR A	12	.2795	1.27	.2579	.1677	.75	.6987	.1272	1.25	.2687	.1497	1.21	.2977
Soil	1	5.9485	49.38	.0001	10.6843	47.72	.0001	4.9111	48.4	.0001	5.8004	46.84	.0001
Spacing	2	27.2521	226.22	.0001	10.5622	47.18	.0001	20.8959	205.94	.0001	29.0326	234.44	.0001
SpacingxSoil	2	.1534	1.31	.2759	.2082	.93	.4001	.1683	1.66	.1986	.12	.97	.3838
SoilxDate	6	.5025	2.73	.0204	.6173	2.76	.0193	.2966	2.92	.0141	.3378	2.73	.0204
SpacingxDate	12	.4787	3.97	.0002	11.8805	53.06	.0001	.3317	3.27	.0011	.5668	4.58	.0001
SpacingxSoilxDate	12	.0374	.31	.9852	.1244	.56	.8686	.0247	.24	.9949	.0553	.45	.9370
ERROR B	62	.1205			.2239			.1015			.1238		
Total	117	2.8974			10.6662			2.7137			2.1313		

Ln(nodules)g/tree, Ln(stem)g/tree, Ln(biomass)g/tree/day, Ln(biomass)kg/ m² /day

SOURCE	DF	Ln(nodules)g/tree MS	F	P F	Ln(stem)g/tree MS	F	P F	Ln(biomass)g/tree/day MS	F	P F	Ln(biomass)kg/m²/day MS	F	P F
Block	2	.9956	7.95	.0063	1.1173	9.03	.0004	1.1885	7.76	.0069	.9478	5.74	.0179
Date	6	44.0796	352.08	.0001	42.3451	342.34	.0001	16.1043	105.15	.0001	8.8573	53.63	.0001
ERROR A	12	.1252	1.29	.2469	.1675	1.35	.2123	.1532	1.27	.2528	.1654	1.45	.1678
Soil	1	5.2368	53.99	.0001	6.2822	50.79	.0001	6.2382	51.78	.0001	3.5833	31.43	.0001
Spacing	2	19.5464	201.52	.0001	28.9724	233.99	.0001	24.6393	204.53	.0001	1.9917	17.47	.0001
SpacingxSoil	2	.178	1.84	.1681	.2054	1.66	.1983	.1697	1.43	.2522	.0682	.60	.553
SoilxDate	6	.3061	3.16	.0091	.3561	2.88	.0154	.285	2.37	.0402	.133	1.17	.3357
SpacingxDate	12	.3413	3.52	.0005	.6388	5.16	.0001	.299	2.48	.0101	.2346	2.06	.0334
SpacingxSoilxDate	12	.0277	.29	.9897	.0363	.29	.9883	.0382	.32	.9837	.0491	.43	.9449
ERROR B	67	.0970			.1237			.1205			.1140		
Total	117	3.6889			3.7568			1.8324			.7991		

Ln(biomass)kg/m², Ln(leaf area)cm²/tree, Ln(rcd)mm, Ln(height)cm

SOURCE	DF	Ln(biomass)kg/m² MS	F	P F	Ln(leaf area)cm²/tree MS	F	P F	Ln(rcd)mm MS	F	P F	Ln(height)cm MS	F	P F
Block	2	.9481	5.73	.0179	1.2864	8.67	.0047	.0529	4.19	.0417	.2166	6.27	.0137
Date	6	20.0649	121.36	.0001	12.1111	81.58	.0001	2.6993	136.41	.0001	5.8489	169.24	.0001
ERROR A	12	.1653	1.45	.1682	.1484	1.21	.2969	.0198	98	.4813	.0346	1.08	.3931
Soil	1	3.3618	29.49	.0001	28.7857	234.58	.0001	.8497	41.9	.0001	1.7501	54.64	.0001
Spacing	2	1.5465	13.56	.0001	5.764	46.97	.0001	4.9588	244.55	.0001	4.8721	152.10	.0001
SpacingxSoil	2	.0593	.52	.597	.1207	.98	.3797	.055	2.71	.0742	2.8238	4.84	.0112
SoilxDate	6	.1668	1.46	.2057	.3365	2.74	.0199	.0736	3.63	.0038	.1293	4.04	.0018
SpacingxDate	12	.3211	2.82	.0039	.5624	4.58	.0001	.0765	3.77	.0030	.1617	5.05	.0001
SpacingxSoilxDate	12	.0476	.42	.9511	.0538	.44	.9414	.0141	.7	.7487	.0214	.67	.7754
ERROR B	62	.1140			.1227			.0203			.0320		
Total	117	1.5408			1.6741			.3297			.5897		

ABBREVIATIONS USED IN ANOVA

DF = degrees of freedom

MS = mean squares (sums of squares divided by DF)

SOURCE = source of variation

ERROR A = main-plot mean squared error (block x date)

ERROR B = split-plot mean squared error (residual error)

PF = probability of a greater F-value

APPENDIX V.

Schematic experimental design in the greenhouse for seedling alder.

BLOCK 3

2x2-L	HD1	HD7	HD2	HD4	HD3	HD6	HD5
4x4-S							
2x2-S							
8x8-L							
4x4-L							
8x8-S							

BLOCK 2

HD3	HD2	HD5	HD1	HD7	HD4	HD6

BLOCK 1

HD7	HD6	HD3	HD5	HD1	HD2	HD4

Notation: 2x2-L = 2 by 2 cm initial spacing on river loam
4x4-S = 4 by 4 cm initial spacing on forest soil
etc.
HD1 = Harvest date 1 (see Table 2)
etc.

Each of the blocks(or replicates) is made up of 7 grouped-treatment units(GTU).Each GTU is composed of 6 randomly located treatment combinations.