

AN ABSTRACT OF THE THESIS OF

Peter A. Giordano for the degree of Master of Science in Forest Science presented on October 6, 1989.

Title: Growth and Carbon Allocation of Red Alder Seedlings Grown Over a Density Gradient

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The amount and quality of competition among individuals in developing plant communities is an important factor determining community structure, composition and development. In perennial plant communities, this competition is reflected by shifts in carbon allocation among plant parts and can result in long-term structural differences between neighboring individuals. This study was designed to provide information on the mechanics of the competitive process and the effect of competition on aboveground tree growth. Plots with a wide range of spacings of red alder seedlings were planted 4 years ago in the Cascade Head Experimental Forest on the central Oregon Coast Range of mountains.

Biweekly growth measurements of stem and branch components and predawn plant water potential were made throughout the growing season. Branch samples taken from the plot were destructively analyzed to determine biomass and leaf area. Combining these measurements with regression equations previously developed from the site, parameter values from regression models are used to compare differences in growth and carbon allocation among trees grown at different levels of intraspecific competition. Increased density produced significant reductions in leaf area, height, basal diameter and biomass of the red alder trees. Increased density also produced significant reductions in the relative biomass growth rate. A gradient of plant water potential was present on several measurement days during the growing season. Growth analysis of these dates showed that predawn plant water potential was a significant factor determining overall tree relative growth rate as well as branch and leaf area relative growth rate. A negative exponential relationship described the relationship between overall relative aboveground biomass growth rate and predawn water stress. Relative growth rate declined sharply at a water stress level between -0.3 and -0.4 MPa. Above this water stress level, yearly relative growth rates were fairly uniform at a value of 1. The relationship between water stress and branch and leaf area relative growth rate also approached

a negative exponential relationship as the intensity of the water stress gradient increased. Examination of the tallest and shortest trees at the two lowest spacings found significant differences in leaf area, percent biomass allocated to branches, and crown depth. This study showed that the effects of competition on growth and allocation of biomass, and leaf area can be significantly affected by periods of water stress lasting only a few weeks.

Growth and Carbon Allocation of Red Alder Seedlings
Grown Over a Density Gradient

by

Peter A. Giordano

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Acknowledgements

When I started writing this thesis I thought that the acknowledgements would be the easiest section to write. Having now finished writing the rest of my thesis, I find that writing this section has proved to be much harder than I originally thought. My difficulty writing this section arises not from the fact that I do not have many people to thank for their contributions to this work, quite the contrary. My difficulty arises in finding the words which will accurately express all the thanks that the many people who helped me complete this work so richly deserve. Without them this thesis would never have become a reality for me. There are several individuals I would like to thank specifically for their contributions to this thesis.

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Table of Contents

	Page
Part I. Introduction	1
Resource Use	6
Allocation of Resources	9
Competition Studies	11
Justification	12
Part II. General Methods	14
Site Description	14
Nelder Specifications	15
Experimental Design	16
Sample Measurements	18
Allometric Equation Development	21
Error Associated with Allometric Prediction	22
Relative Growth Rate	24
Other Growth Analysis Equations	26
Part III. Effects of Competition on Growth and Carbon Allocation of Red Alder Seedlings	28
Introduction	28
Methods	29
Results	31
Discussion	36

Part IV. Effects of Water Stress on Growth and Carbon Allocation of Red Alder Seedlings	43
Introduction	43
Methods	45
Results	47
Discussion	50
Part V. The Role of Canopy Dynamics in Patterns of Tree Mortality	54
Introduction	54
Methods	57
Results	58
Discussion	59
Part VI. Synopsis and Discussion	63
Synopsis	63
Discussion	65
Bibliography	118
Appendix	125

List of Figures

	Page
1. Definition of available growing area per tree	78
2. Mean initial basal diameter and mean basal diameter growth of sample trees	79
3. Mean initial height and mean height growth of sample trees	81
4. Mean ratio of height/diameter of sample trees	83
5. Mean initial aboveground biomass and aboveground biomass growth of sample trees	85
6. Mean relative growth rate of aboveground biomass of sample trees	87
7. Mean initial branch biomass and mean net branch biomass growth of sample trees	89
8. Mean net aboveground biomass growth and mean net branch growth of sample trees	91
9. Mean branch mortality and mean gross branch growth of sample trees	93
10. Mean net branch biomass growth of the lower, mid, and upper sections of sample tree crowns	95
11. Mean branch mortality and mean gross branch growth in the lower section of sample trees	97
12. Mean maximum leaf area of the lower, mid, and upper sections of sample trees	99

13.	Mean canopy depth of sample trees	101
14.	Mean maximum leaf area index of sample trees	103
15.	Mean leaf weight ratio and mean net assimilation rate of sample trees	105
16.	Plot of predawn plant water potential vs. time during the season	107
17.	Plot of water potential vs. Ln (Density) on June 29, August 9, and September 13	108
18a.	Plot of aboveground biomass relative growth rate vs. predawn water potential on June 29	109
18b.	Plot of aboveground biomass relative growth rate vs. predawn water potential on August 9	109
18c.	Plot of aboveground biomass relative growth rate vs. predawn water potential on September 13	109
19.	Plot of mean relative growth rate of aboveground biomass vs. predawn plant water potential for June 29, August 9, and September 13	113
20.	Height distribution of the 4 trees with the smallest and largest initial heights for 0.10 m ² and 0.26 m ² spacing	114

21. Aboveground biomass distribution of the 4
trees with the smallest and largest initial
heights for 0.10 m² and 0.26 m²
spacings

116

List of Tables

	Page
1. Crown spread of 4 year old red alder trees in relation to available growing area	72
2. Type of competition and topography of experimental plots	73
3. Regression coefficients for aboveground components of red alder	74
4. Relationship between mean relative growth rate, mean leaf weight ratio, specific leaf area and mean net assimilation rate	75
5. Regression equations for branch and leaf area relative growth rate vs. predawn water potential	76
6. Growth characteristics of successful and non-successful competing trees	77

List of Appendix Tables

1. Mean initial basal diameter and basal diameter growth	125
2. Mean initial height and mean height growth	125
3. Mean Height/Diameter ratio	125
4. Mean initial biomass and mean biomass growth	126
5. Mean relative growth rate	126
6. Mean initial branch biomass and mean net branch biomass growth	126
7. Mean net aboveground biomass growth and mean net branch growth	127
8. Mean branch mortality and mean gross branch growth	127
9. Mean net branch biomass growth of the lower, mid, and upper sections of sample tree crowns	127
10. Mean branch mortality and mean gross branch growth in the lower section of sample tree crowns	128
11. Mean maximum leaf area of the lower, mid, and upper section of sample tree crowns	128
12. Mean canopy depth	128
13. Mean maximum leaf area index (LAI)	129

Preface

The structure and composition of developing plant communities is dependent on, among other factors, both the quantity and quality of competition among individuals in the communities. In perennial plant communities, competition is reflected, in part, by shifts in carbon allocation among plant parts which can result in long-term structural differences between neighboring individuals. Shifts in carbon allocation among plant parts allow individuals to better acquire or utilize limiting resources. As competition for these limiting resources increases over time, the capacity of some individuals to adjust to reductions in resource availability is exceeded and they die. The ability of individuals to respond plastically to increased competition differs among species. Species, like red alder, which are sensitive to decreased light availability may reach their plastic limit much sooner than less light sensitive species.

Community response to competition stress is characterized, in part, by the sum of these individual responses, and so is dependent on the initial composition of the community. In addition, as communities develop over time, differences in the way communities approach the self-thinning threshold is an important factor determining between-community differences in composition and structure.

In order to study the competition process and its effect on tree growth, several density series of red alder (Alnus rubra Bong.) seedlings were established 4 years previous to this study as part of a long-term comprehensive program to study interaction between plants. In these density series, I measured a variety of growth parameters throughout the growing season. These measurements were used to compare differences in growth and carbon allocation among trees grown at different levels of intraspecific competition.

Water stress of trees at different spacings was monitored biweekly through the growing season. Predawn plant water potential of each sample tree was measured concurrently with growth measurements. This provided a way to link tree growth with resource availability.

This study was designed to answer several questions about the nature of competition and its effects on plant growth. These primary questions were: How does competition between individuals in a plant community affect growth and carbon allocation of these individuals? What are the implications of these effects on community composition and development? What role does resource availability play in determining the effects of competition between individuals? If self-thinning is regulated by a plant's ability to shift carbon allocation, can measurements of canopy dynamics be used as an

indication of the probability of tree survival? Answering these questions will help define the important mechanisms involved in the competitive process.

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Part I: Introduction

Competition among plants is one of the most important factors affecting survival and growth. Plants affect their neighbors by changing their environment (Harper 1977). Changes in the environment caused by competition can take the form of direct effects such as limiting resources or indirect effects such as reduction of wind velocity or temperature. Negative interference between individuals is defined as competition. Regardless of the specific influence an individual has on its surrounding environment, competition can be defined as the strain induced on one individual as a result of the use of resources by another individual (Weldon and Slauson 1986). In this definition, strain is the internal physiological changes in an organism in response to a stress. Stress is "an external condition, apart from the activities of other organisms, that induces strain in an organism" (Weldon and Slauson 1986). For example, low soil water content can be thought of as an external stress for plants while a drop in growth rate or photosynthetic rate is the strain induced by low soil water content in the plant.

Competition consists of two distinct characteristics

which determine its role in plant development. These are the intensity and importance of competition (Weldon and Slauson 1986). The intensity of competition addresses the amount of strain induced by the competing plant. The importance of competition addresses the role of competition in determining plant attributes such as growth, metabolism, and survival, relative to other factors (Weldon and Slauson 1986). In other words, the intensity of competition is concerned with the competition process alone. The importance of competition is concerned with the amount of overall strain on a plant which is attributable to competition. Other factors independent of competition which result in differences in growth between two individuals include genetics, stochastic events, and herbivory. This study utilizes measures of growth attributes in an attempt to determine the importance of competition in an experimental red alder monoculture system.

The response of a community to competition is a result of the sum of the responses of individual members of the community. Plant response to competition varies among species and among individuals of the same species. As the importance of competition increases, plants alter their morphology through changes in resource allocation (Ford 1975). Change in resource allocation by plants is known as a plastic response to competition stress. When

the ability of a plant to respond plastically to competition is exceeded, mortality occurs. Mortality of the individual plant is preceded by mortality of plant parts to which resources are not adequately allocated. As plant parts are shed, the remaining plant parts are eventually unable to support the respiratory demands of the plant, resulting in death of the plant.

Plant vigor describes this relationship between growth and respirational demand. High growth relative to respirational demand results in high vigor. Community vigor can be thought of as the sum of each individual's plant vigor. Because plant vigor is inextricably bound to the relationship between plant parts and the whole plant, knowledge of the mortality patterns of plant parts provides important information on the future vigor of the plant and subsequently the community. Community vigor is a way of assessing the overall response of a community to competition among its individuals.

The variability of plant response to competition produces a skewed distribution of individual plant weights within a population (Westoby and Howell 1986). This skewed distribution within a population is characterized by a few plants greatly above the population mean weight and many plants slightly below the mean weight (Ford 1975; Watkinson et al. 1983). As a population develops, this size hierarchy becomes more pronounced. Survival of

individual plants becomes more and more dependent on its position in this hierarchy (Watkinson et al. 1983). The effect of competition on survival and growth, therefore, occurs on two levels of organization; individuals and populations.

Modeling the self-thinning process is a useful tool for predicting changes in population structure as a community develops. Models are commonly used to help make management decisions concerning growth and yield of crops, both annual and perennial. Several models have been developed describing the dynamics of plant competition (Spitters 1983; Slatkin and Anderson 1984; Firbank and Watkinson 1985). These models have been based on the growth characteristics of annual plants because of the importance of crop yield prediction in agriculture and the difficulty of modeling perennial plants. There have, however, been some steps taken towards applying the dynamics of self-thinning populations to forest situations (Hara 1984, Hibbs 1987). These models are generally based on the "self-thinning rule" or $-3/2$ power rule.

The "self-thinning rule" is one of the most widely accepted models of the thinning process of plants. This rule relates mean plant size (biomass or volume) to stocking density by the equation:

$$\log W = K - X \log d$$

where W = mean plant size, d = stocking density, and X and K are constant (Yoda et al. 1963 and others). Based on dimensional analysis, Yoda et al. (1963) proposed 1.5 as the value of X . Since this relationship was first hypothesized by Yoda et al. (1963), it has been shown to represent the thinning process of a wide range of plant species (White and Harper 1970; White 1980; Lonsdale and Watkinson 1983). The value of X has been shown to range from -1.2 to -1.8 for a variety of annual and perennial plants (Perry 1984).

Although there appears to be general acceptance of this relationship on an empirical basis (not without some disagreement on the assumptions of the relationship, see Mohler et al. 1978; and the value of X , see Weller 1985, 1987), researchers do not adequately understand the theoretical basis of the rule. There have been several attempts to derive the thinning rule from growth models (Aikman and Watkinson 1980; Hozumi 1980) and plant allometry (Mohler et al. 1978; White 1981). Of these attempts, derivations based on plant allometry seem to provide a more sound biological basis for the rule (Weller 1987).

Models based on interactions between individuals are also useful methods of identifying important competition mechanisms and predicting performance. These models are

commonly based on information about the "neighborhood" surrounding an individual plant (Lemmon and Schumacher 1962; Opie 1968; Silander and Pacala 1985; Brand 1986; Wagner and Radosevich 1987). These models are usually developed from natural or manipulated stands. Specific systematic experiments concerning effects of interactions between individuals can provide important information for better model development.

In addition to providing predictive ability, models also provide a foundation for understanding the different mechanisms involved in the competitive process. The lack of general acceptance of a theoretical basis for the self-thinning relationship illustrates the need for an experimental approach which seeks to identify important mechanisms driving self-thinning. The information gained from this approach will help improve the predictive ability of existing models while establishing a biological basis for these models.

Resource Use

There is no question that resources play a vital role in plant growth and survival (Harper 1977). Resources are defined as any substance or factor which increases the growth rate of an organism as its availability in the environment increases (Tilman 1982). Resources may be categorized as "supply factors" or "quality factors" (Harper 1977). Supply factors are consumable, in contrast

to quality factors which may restrict growth but are not consumable. Light, water, nutrients, and space are examples of supply factors while temperature and other climatic conditions are examples of quality factors (Harper 1977). While competition only occurs for supply factors, both types of factors play a role in determining the importance of competition in plant communities. At the broadest scale, climatic conditions mediate which species are able to survive and subsequently compete with each other in a given area. Climatic conditions influence plants through factors such as the amount of annual precipitation, length of the growing season, and air temperature. These gross environmental characteristics act to regulate potential community composition.

On a smaller scale, microsite conditions of the seedbed determine which seedlings are able to establish. Seedbed characteristics such as depth and composition of the litter layer (Minore 1972; Ryker 1975), and depth to water table (Minore 1970) can be important to seedling establishment. These factors have a large role in determining initial structure and composition of the community.

Somewhere between the scales of local climate and microsite is usually where competitive interactions between plants and resources occur. Once plants establish on a particular site, they begin to compete for resources

with those individuals surrounding them. Plants which successfully compete for resources generally develop a competitive advantage over other plants through at least one of two fundamental characteristics. These are timing of resource acquisition and resource use efficiency.

Time of establishment is an important determinant of future survival and growth in many types of communities. Plants which establish before other plants are able to preempt resources (Harper 1977). Preemption of resources results in increased growth rates which allow these plants to maintain a competitive advantage over neighboring plants.

Plants which utilize resources efficiently can also gain a competitive advantage over their neighbors. For example, plants with a high water use efficiency are able to support more leaf area than similar sized competitors (Waring and Schlesinger 1985). This allows them to increase their carbon gain through photosynthesis, thus having a higher relative growth rate than plants with a low water use efficiency.

Competition for resources is not a function of resource use alone. Plant growth and resource levels are intimately connected; a change in one often results in a change in the other. Only rarely are resources so abundantly available that plant uptake has a negligible effect on future resource availability. Thus, those

plants which are consistently able to garner a larger share of what is often a diminishing supply of resources, are competitively superior to their neighbors.

Allocation of Resources

Competition for resources is also closely connected to the carbon allocation patterns of plants. The ability to modify carbon allocation patterns enables plants to effectively acquire resources under high competitive conditions. Relative abundance of particular resources prompts shifts in carbon allocation of plants in order to better capture these resources. These shifts also have a substantial impact on future resource levels as carbon allocation leads to increased depletion of a resource. A good illustration of this principle is the development of leaf area in young plant communities. Early stages of development are characterized by a high abundance of light. In order to capture this resource, individuals allocate a greater amount of carbon towards leaf production as opposed to other components. As the canopy closes, competition for light becomes increasingly severe due to the large amount of carbon allocated towards leaf production.

In addition to the ability to acquire resources, allocation of these resources, such as mineral nutrients, biomass, and energy, within a plant, is an important response to competitive stress. Resource allocation

patterns are thought to be linked to the fitness of the plant (Harper 1977; Abrahamson and Caswell 1982; Waring 1987). Implicit in this statement is the assumption that the supply of some crucial substance is limited, so that an increase in allocation to one structure or function means a decrease in allocation to another (Harper 1977). Under conditions where resources are not limited, plants usually show some "normal" pattern of growth (Waring 1987). Several studies of resource allocation have indicated that plants allocate resources according to the relative importance of a plant function (Smith 1983; Waring and Pitman 1985; Waring 1987). Stress causes departures from these normal patterns of allocation (Hickman 1975, 1977; Pitelka 1977; Waring 1987). For example, shading causes a reduction in carbon gain by the plant. This results in a shift in allocation towards shoot growth which reduces carbon stress (Chapin et al. 1987). These shifts in allocation tend to produce plants which utilize limiting resources more efficiently, thus increasing their chance of surviving stressful conditions (Chapin et al. 1987; Waring 1987). Therefore, by studying carbon allocation patterns of trees experiencing competition, we can determine which structures are most important in compensating for competitive stress. Also, by comparing the vigor of different trees grown under similar competitive conditions, we can determine the

interaction between carbon allocation and total growth. This can be used to help predict tree survival, since trees with higher growth rates compared to other trees experiencing similar growing conditions, have a greater probability of survival (Chapin et al. 1987).

Competition Studies

The study of mechanisms driving the competitive process is complex due to the several levels of organization necessary to understand the complete process. Plant response to competition is dependent on the life-history characteristics of the plant, the nature of the competition, and the environment (Harper 1977). Studying all three of these aspects simultaneously is complex and difficult to do in an experimental situation. Most often, studies of competition involve annual plants (Concannon 1987; Pacala and Silander 1987; Roush 1988). Annual systems are easier to manipulate than perennial systems and somewhat easier to control resource levels.

The majority of studies concerning competition in perennial plant systems have focused on the description of survival, growth and carbon allocation of natural plant communities. Competitive effects on biomass, leaf area, and productivity of the forest stands are most commonly studied (DeBell 1972; Zavitkovski 1972; Cole et al. 1983; Bormann and Gordon 1984; Pearson et al. 1984; Oren et al. 1987). Over the past several years, Oregon State

University has developed a long term comprehensive program to study the competitive process. This program is studying both herbaceous plant systems (Concannon 1988; Roush 1988) and perennial plant systems (Coates 1987; Chan et al. 1989; Shainsky 1988; Simard 1989). The strength of the OSU program lies in its ability to combine several levels of organization into a focused study. Hibbs and Radosevich (in progress) have established a series of replacement experiments involving red alder and Douglas-fir (Pseudotsuga menzeisii), in order to study the effects of species interactions and resource levels on tree growth. Studies by Chan et al. (1989) and Dukes (in progress) contribute information on the morphological and physiological characteristics of red alder and Douglas fir in response to resource manipulation. Shainsky (1988) studied the effects of density, species proportion, and resource availability on the growth and morphology of a young red alder/Douglas-fir system. This study was intended to contribute to the overall competition program by providing information on the morphological response of red alder to intraspecific competition and water availability.

Justification

Competition is an important process both in natural and managed plant systems. Unfortunately, there have been few studies which address the mechanisms driving the

competitive process. In order to better predict the results of management decisions on vegetation, it is necessary to understand how plants interact with their neighbors.

Red alder was chosen for several reasons. First, the role of red alder in forest management in the Pacific Northwest is in the process of being reevaluated. Its rapid juvenile growth and its ability to fix nitrogen give red alder the potential to inhibit or enhance growth of Douglas-fir seedlings. Also, the market for red alder lumber has recently been expanding, encouraging growth of pure and mixed stands of red alder for sawlog production.

Part II. General Methods

Site Description

The site for this study is located in the Oregon central Coast Range in the Cascade Head Experimental Forest. Elevation is 330 m above sea level. The site borders the Picea sitchensis and Tsuga heterophylla vegetation zones (Franklin and Dyrness 1973). Previous vegetation consisted of old-growth Picea-Tsuga/Oplopanax horridum/Athyrium filix-femina communities with abundant components of Rubus sp. and red alder (Alnus rubra Bong.). The site was clearcut 5 years previous to this study and the slash was burned. The soil parent material is basalt with local pockets of duff present extending 1 m below the soil surface. The growing season averages approximately 180 days. The study site is located within 2 km of the Pacific ocean which results in relatively mild temperatures and a high percentage of cloudy days even during the summer months. The average minimum temperature is 2.2°C and the average maximum temperature is 20.9°C. Average annual precipitation is 250 cm. The climate is characterized by high precipitation between October and May, often in the form of cloud condensation. June through September is characterized by periodic rainfall events separated by 3-4 week periods without

precipitation.

Nelder Specifications

Nelder type 1a plots were used for this study (Nelder 1962). Each complete Nelder occupied 0.34 hectares. The plots consisted of 15 concentric circles and 24 radii. Nelder plots are characterized by the angle between radii and the rectangularity (Nelder 1962). For my Nelder plots these two parameters were 15° and 0.069, respectively. The radius of each plot was 32.4 meters. The innermost and outermost circles were designated as border rows. Each Nelder consisted of densities ranging from 101,000 trees per hectare at the second most inner circle, to 238 trees per hectare at the second most outer circle.

The nature of the Nelder design produces a gradient of densities from the center to the outer edge of the plot. Using the number of trees per hectare as the measure of density is misleading because of the asymmetric density around individual trees. In order to avoid this problem, the competitive state of the trees in this study will be described using a measure of available area per tree rather than number of trees per given area. Derivation of this available area is shown in Fig. 1. A rectangle around the tree is defined using the distances between adjacent trees on a spoke (c) and the distance between adjacent trees on either side on the same circle (a and b). The available area is determined by

constructing a rectangle with axis equal to $1/2$ of these distances. Each Nelder plot represents a range of available area from 0.1 to 41.99 m^2 per tree. The degree of crown overlap at each sample spacing is presented in Table 1. For example, trees planted at a 3.57 m^2 show significant crown overlap, but crown closure is not complete. Spacings above 3.57 m^2 have no crown overlap and so represent open grown trees.

Experimental Design

Nelder plots were established as part of a larger project on the effects of inter- and intraspecific competition on the growth of Douglas-fir and red alder (Hibbs and Radosevich, in progress). Three complete Nelder plots were established in a 20 hectare clearcut unit at the Cascade Head Experimental Forest. Each complete Nelder plot was divided in half along the fall line of the slope. Half of the plot was randomly selected and treated with triple super phosphate fertilizer (125 Kg/ha P) immediately after seedling establishment. Each $1/2$ of the plot was divided by 4 border rows. At the time of my study, no apparent aboveground effects of the phosphorus fertilization treatment were evident (Hibbs, unpublished data). Subsequently, the 2 halves of each plot were combined and treated as whole plots.

Individual site characteristics for each Nelder were different. Table 2 illustrates some of the important

characteristics of each plot. This arrangement of plots helped to reduce the effects of site condition by averaging treatment effects over the three complete Nelders. Each Nelder was located on sites which were fairly uniform in order to reduce the effect of within-Nelder site variation.

The 3 plots experienced different amounts of weed competition (Table 2). Plot 1 had primarily herbaceous competition in the outer 1/2 of the plot, while plot 2 experienced both herbaceous and shrub competition. Plot 3 experienced primarily herbaceous competition with a large component of low grass. For this study, shrub and herb competition was manually controlled within a 2 meter radius of each sample tree in order to minimize the effect of interspecific competition on tree growth. Bare ground conditions were maintained as closely as possible throughout the majority of the growing season.

Four sample trees were chosen at 6 different spacings in each plot. Increasing the sample size would have increased the accuracy of treatment effect estimates but was not feasible due to the frequency of the measurements. Basal diameters of all trees were measured prior to the growing season. Based on these measurements, one sample tree was selected which was closest in size to the mean tree at each density. One larger and one smaller tree were randomly selected from the remaining trees at each

density. The trees were chosen at 0.1 m², 0.26 m², 0.73 m², 3.57 m², 17.13 m², and 41.99 m² spacings. Each sample tree was divided vertically into 3 sections, each section representing 1/3 of the initial height. In each section of the sample tree, one sample branch was randomly selected from the total branch population in that section of the tree. Height above the ground of each sample branch was recorded.

Sample Measurements

Growth measurements were divided into 3 different categories. These were: biweekly measurements of each sample tree, biweekly measurements of each sample branch, and biannual measurements of the total branch population.

Tree Measurements

Measurements of basal diameter (3 cm above ground), diameter at breast height (d.b.h.; 1.30 m above ground), and total height were taken at biweekly intervals for each sample tree. Diameter measurement points were marked at the beginning of the season. These points were remarked as needed throughout the season. All diameter measurements were made with a caliper to the nearest 0.10 mm. The caliper was positioned directly over the marking paint in order to assure consistent measurements. Total tree height was measured to the nearest 1 cm, using a height pole.

Branch Measurements

Basal diameter, length to first live node, and total length was measured biweekly for each sample branch. Diameter was measured so that the calipers were orientated parallel to the tree stem and facing upward. Length to first live node and total branch length were measured to the nearest 1 cm.

Branch Population Measurements

Basal diameter, length to first live node, total length, and height of all branches on each sample tree were measured using the same techniques as biweekly branch measurements. Measurements were made at the beginning and end of the growing season.

Water Availability Measurements

Water availability was assessed using predawn plant water potential measurements. Measurements were taken concurrently with growth measurements using a pressure chamber (Waring and Cleary 1967). One leaf per sample tree was measured. Sample leaves were selected from the middle of the canopy and only healthy leaves were sampled.

Destructive Branch Measurements

In order to develop regression parameters for predicting biomass and leaf area of live sample branches, branches were systematically harvested 4 times during the study, before, twice during, and

after the growing season. Three branches were collected at each sample spacing from each plot so that the total range of branch sizes on the plot was represented. Branches for destructive measurements were not collected from sample trees and were collected far enough away from sample trees so that their removal did not affect the growth of sample trees. An equal number of branches were sampled from each section of the tree crowns.

Branches were taken back to the lab in plastic bags where the branches were measured within 24 hours. Fresh weight, total length, length to first live node, and basal diameter were measured on branches collected at the beginning and end of the growing season. In addition to these measurements, fresh leaf weight, and leaf area were measured for each branch collected during the growing season. Leaf area was measured using a LI-COR Li3100 Area Meter. Following these measurements, branches were dried in an oven (21°C) for at least 48 hours at which time the dry weight of branches and leaves was measured.

Allometric Equation Development

In addition to establishing Nelder plots, Hibbs and Radosevich (in progress) planted additional red alder trees to use for growth analysis based on destructive samples. Several of these trees were harvested each year following Nelder establishment. Non-destructive parameters such as basal diameter and height were measured, and then trees were separated into stem, branch, roots, and leaf components and weighed. Fresh weight and dry weight was recorded. Using this data, I developed allometric equations for predicting total tree biomass. Because allometric relationships change as trees age, data for 3 and 4 year old trees was used to develop the allometric equations for this study. Multiple regression techniques (Statgraphics 1988) were used to determine the best predictive model for the data. Because separate models for trees grown under dense conditions (crowns touching) and open conditions (crowns not touching) were not substantially different, all data was combined and a single predictive model was developed for this data set. Allometric equations for predicting branch biomass and leaf area were developed using data from the destructive samples I collected over the course of the season. Density did not have a significant effect on the

Error Associated with Allometric Prediction

There are many problems associated with growth analysis of plants grown in the field. These include the effects of past history on current performance, measurement difficulties, and the inability to control environmental conditions. Perhaps the greatest problem associated with growth analysis occurs when studying growth characteristics over frequent intervals. Destructive harvest of plants is the most accurate method to describe plant growth over a given time interval. Unfortunately, frequent destructive harvests present a major logistical problem even when small plants are studied. When frequent harvests are necessary over an extended period of time, a substantial number of plants are required in order to provide adequate replication for making statistical inferences about populations of plants. Location of adequate facilities for performing these kinds of studies can be a serious problem.

One of the most commonly used techniques for overcoming the problems of destructive sampling is predictive allometric equations. Allometric equations relating relatively easily measured parameters such as basal diameter and height, to difficult to measure parameters such as dry weight, are developed using a small subsample of plants from the population being studied. These relationships are then used to predict the desired

parameters of the remaining plants in the population.

One of the problems associated with the use of allometric equations results from the error associated with the predictive models. The large variability of plant growth can result in models which are not accurate enough to describe the true course of growth. One cause of the development of models which do not adequately describe the true course of plant growth occurs when variability of the samples used to develop the allometric equations is not constant. Large sample plants have much larger growth variability than smaller sample plants so that the small plants have a greater effect in determining the form of the predictive equations used in the model. The large influence of small plants on the form of the equation can lead to substantial under or overestimation of large plant parameters. The problem of under or overestimation of large plant parameters is often enhanced by unequal samples of large and small plants. As plants age and become larger, they become increasingly difficult and time consuming to destructively sample. The difficulty of sampling large trees can result in allometric equations based on a large number of small trees and only a few large trees.

Another problem associated with the use of allometric equations to predict growth characteristics is the effect of environmental conditions on plant allometry.

Differences in resource availability, as well as interference from other plants, can have a significant effect on the allometric relationships of plants (Evans 1972). These differences, if not recognized, can misrepresent important growth trends. My study used allometric equations to predict fundamental data such as branch and tree biomass. These allometric relationships were not greatly influenced by density. Leaf area was predicted using separate equations for density and position because of the important influence of these factors. Once these fundamental relationships were developed, trends in different carbon allocation components were examined over the density series.

Relative Growth Rate

Mean relative growth rate (RGR) of trees and branches was calculated using classical growth analysis (Hunt 1982). Classical growth analysis is better than functional analysis for examining changes in growth rate due to short-term environmental trends (Hunt 1982). Mean relative growth rate was calculated using the general formula:

$$RGR = (1/W) (dW/dt)$$

where W = total aboveground biomass and dW/dt = change in biomass over the measurement period.

Brand et al. (1987) have argued that relative production rate (RPR) is a better indication of perennial plant performance than RGR. RPR is calculated as the relative increase in growth increment. Brand et al. (1987) argue that the large amount of accumulated biomass often associated with perennial plants results in RGRs which are more a function of initial biomass than current growth. The trees in this study were relatively small initially and experienced large amounts of current growth. Therefore, RGR should be a reliable indication of relative plant performance.

Other Growth Analysis Equations

Mean Net Assimilation Rate

Mean net assimilation rate (NAR) for each sample tree was calculated using methods similar to those used to derive relative growth rates. The general equations used to calculate net assimilation rate was:

$$\text{NAR} = (\text{dW}/\text{dt})/\text{LA}$$

where dW/dt is change in total aboveground biomass over the measurement period and LA is leaf area of the tree at the end of the measurement period.

Leaf Area Ratio

Leaf area ratio (LAR) is calculated using the general equation:

$$\text{LAR} = \text{LA}/\text{W}$$

where LA is as above and W is total aboveground biomass at the end of the measurement period.

Leaf Weight Ratio

Leaf Weight Ratio (LWR) was calculated using the general equation:

$$\text{LWR} = \text{LW}/\text{W}$$

where LW is leaf dry weight and W is total aboveground biomass at the end of the measurement period.

Specific Leaf Area

Specific Leaf Area (SPLA) was calculated using the equation:

$$\text{SPLA} = \text{LA}/\text{LW}$$

where LA and LW are as above. Samples collected across all densities and crown position of the leaves were pooled in order to develop one relationship between leaf area and leaf weight.

Part III. Effects of Competition on Growth and
Carbon Allocation of Red Alder Seedlings

Introduction

Trees react morphologically to competitive stress in two ways: differences in total growth and differences in carbon allocation. Carbon allocation patterns determine how well a particular tree is able to acquire resources. Differences in growth between trees with similar carbon allocation patterns are an indication of how efficiently an individual is able to utilize resources. In order to study differences in total growth and carbon allocation patterns between competing trees, several specific objectives were developed.

1. Describe aboveground carbon allocation patterns over the course of the growing season.
2. Analyze the effect of the past growth of trees on current growth and allocation.
3. Elucidate carbon allocation strategies employed by plants to capture and utilize resources under different levels of competitive stress.

Methods

Using multiple regression techniques, allometric equations were developed to predict 3 growth parameters: total tree aboveground biomass, branch leaf area, and branch biomass. Resulting equations are given in Table 3. The best model was selected by minimizing the standard error of the estimate. Log transformation of growth parameters is common in order to increase the predictive power of the equations and normalize residual error terms. Despite increasing the predictive power of the regression models for predicting tree biomass and branch leaf area, log-log transformations were avoided because the gain in predictive power was not deemed great enough to offset the log-bias associated with these transformations (Flewelling and Pienaar 1981). In the case of branch biomass prediction, Furnival's Index (1961) was used to select the most appropriate form of the predictive equation. Furnival's Index is derived by performing three steps: (1) Each equation is fitted and the mean square residual of each fitted equation is obtained. (2) The geometric means of the derivatives of each dependent variable is calculated. (3) Each root mean residual is multiplied by the inverse of the appropriate geometric mean. This index provides an indication of which model most appropriately conforms to the assumption that the

residuals are normally distributed, independent, and have a constant standard error (Furnival 1961). Two models were developed using weighted least squares with $1/(\text{dry weight})$ and $1/(\text{dry weight}^2)$ as the weights. These models were compared with a log-log transformation model. The log-log transformation model was chosen as the most appropriate.

Estimates of total branch biomass, leaf area, and leaf weight per tree at the beginning and end of the growing season were obtained by predicting the biomass, leaf area, and leaf weight of each branch and summing these results over the tree. Mean values were then calculated for each density. Branch mortality was calculated as the loss of initial branch biomass of those branches which were dead at the end of the year. Stem biomass was calculated as the difference between total aboveground tree biomass, and branch and leaf biomass.

Results

There was an increasing gradient of initial basal diameter of trees up to a spacing of 3.57 m² (Fig. 2). A slight decrease was apparent at spacings of 17.13 and 41.99 m². Initial height of trees (Fig. 3) showed a different trend than basal diameter. Initial height was not significantly different among trees at spacings of 0.1, 0.26, and 0.73 m². Height of trees at spacings of 3.57, 17.13, and 41.99 m² were not significantly different from each other, but were significantly different from trees at spacings of 0.1, 0.26, 0.73 m² (Fig. 3). These differences in initial height are partially due to browsing of the outer portions of plots by elk during the previous growing season. Approximately 7% of the trees in the Nelder plots were browsed during the 1987 growing season.

Basal diameter growth (Fig. 2) and relative basal diameter growth increased significantly up to a spacing of 17.13 m². Height growth (Fig. 3) increased significantly up to 3.57 m² where it remained constant. The trend in relative height growth was similar to that of basal diameter growth. The ratio of height/diameter at the end of the season was highest at 0.1 m² with a value of 143, and decreased with increased available area (Fig. 4).

Absolute tree biomass increased with increasing

growing area up to a spacing of 3.57 m² (Fig. 5). Trees grown at 3.57, 17.13, and 41.99 m² showed no significant difference in biomass. The relative growth rate of biomass increased significantly with increased available area (Fig. 6). Individual tree relative growth rates reached as high as 25. Trees with the highest relative growth rates were generally smaller than average at the beginning of the growing season.

Spacing also had a significant effect on absolute branch growth. Net branch growth generally increased with increased spacing, although there was a slight decrease from spacings of 0.1 to 0.26 m² and from 17.13 to 41.99 m² (Fig. 7). The increase in relative branch growth with increased available area was even more dramatic. The average percent increase of branches relative to the initial amount of branches at spacings of 0.1, 0.26, and 0.73 m² was 25% while the average percent increase at spacings of 3.57, 17.13, and 41.99 m² was 368% (Fig 7). Branch growth also accounted for an increasing proportion of total biomass growth as available area increased. Branch biomass growth increased from an average of 7.5% of total tree growth for 0.1, 0.26, and 0.73 m² spacings to 26% for 3.57, 17.13, and 41.99 m² spacings (Fig. 8). The large increase in branch growth between the narrower spacings and the wider spacings is due in part to the low mortality experienced under less dense conditions (Fig.

9). Mortality as a percent of gross growth averaged 60% for 0.1, 0.26, and 0.73 m² spacings while percent mortality averaged only 2% for 3.57, 17.13, and 41.99 m² spacings.

Decreased spacing produced a shift in relative branch carbon allocation from the upper to lower crown (Fig. 10). Although the absolute amount of branch growth in the upper third of the canopy was similar for all densities, upper canopy branch growth accounted for a decreased percent of total branch growth as available area increased. Upper canopy branch growth accounted for as much as 90% of total branch growth at low spacings while it represented only 3.6% of total branch growth at the highest spacing. There was a large amount of branch mortality in the lower 1/3 of the crown of trees at 0.1, 0.26, and 0.73 m² spacings, resulting in negative net branch growth in this portion of the crown (Fig. 10, Fig. 11). Although there was mortality present in the lower 1/3 of trees at 3.57, 17.13, and 41.99 m² spacings, mortality was offset by large amounts of growth in these trees (Fig. 11). Also, branch growth in the lower 1/3 of trees at 3.57, 17.13, and 41.99 m² spacings accounted for an average of 64% of total branch growth.

Total leaf area per tree increased significantly with increased available area although there was a slight decrease in leaf area between 17.13 and 41.99 m² spacings (Fig. 12). Maximum average leaf area per tree of 88,221

cm² was attained at a 17.13 m² spacing while minimum leaf area of 5,974 cm² was attained at a 0.1 m² spacing. Leaf area increased by a factor of 3 between 0.73 and 3.57 m² spacings reflecting the improvement in light conditions. Leaf area also increased 1.5 times between 3.57 and 17.13 m². Leaf area was not significantly different in the upper 1/3 of the canopy over all spacings. Leaf area was spread over a greater amount of stem height as growing area increased (Fig. 13). Canopy depth increased from 235 cm at a spacing of 0.1 m² to 357 cm at a spacing of 41.99 m². Leaf Area Index (LAI) was calculated using the available area per tree and the maximum leaf area achieved during the season. The maximum LAI was achieved at a 0.1 m² spacing (Fig. 14). There was a sharp reduction in leaf area index between 0.1 and 0.26 m² spacings. LAI at 0.26 and 0.73 m² was similar, but dropped substantially once the canopy began to open up at wider spacings.

Spacing had a significant effect on mean leaf weight ratio ($\alpha = 0.01$, $p < 0.0001$). Leaf weight ratio (LWR) reached a minimum value of 0.084 at 0.73 m² and stabilized at 17.13 m² (Fig. 15). Protected least significant difference analysis showed that the mean leaf weight ratios at 0.10, 0.26, 0.73, 3.57 m² were significantly different from the mean leaf weight ratios at 17.13 and 41.99 m² (Table 4). Spacing did not have a significant effect on mean net assimilation rate ($\alpha = 0.01$, $p = 0.07$). Mean net

assimilation rate (NAR) reached a maximum value of 0.88 at a 0.73 m² spacing but there was a high degree of variability at all spacings (Fig. 15).

Discussion

The results obtained from studying the effects of competition on carbon allocation patterns show some important trends. While spacing had a significant effect on both height and diameter growth, basal diameter growth was more sensitive to increased growing area than height growth. This corresponds with work by Bormann and Gordon (1984) which found that mean d.b.h. of 5-year-old alder was significantly related to initial spacing ($p < 0.01$) while mean tree height was not significantly related to initial spacing ($p = 0.41$). Smith (1983) planted red alder seedlings at 3 different initial spacings and found differences in root collar growth of the seedlings after 500 growing days. He also found that these differences were accentuated with time. Differences in height growth of the seedlings were found but these differences seemed to become less apparent with time. Cole (1984) found that diameter growth of Douglas-fir seedlings was more sensitive to initial spacing than height growth. In my study, biomass growth was more closely correlated with diameter growth than height growth. This suggests that height growth has a higher priority for photosynthate allocation than overall biomass growth even under non-competitive conditions. Increases in total biomass with increased available growing area seem to be due to an

excess of available carbon above what is needed for height growth.

Spacing also had a dramatic effect on overall tree performance as seen by the large differences in relative growth rate over the spacing gradient (Fig. 6). Increases in relative growth rate (RGR) with increased available area are closely connected with the relationship between leaf weight ratio (LWR) and initial spacing (Fig. 15, Table 4). This study supports work which has shown that there is not a clear relationship between net assimilation rate (NAR) and growth rate (Heickel and Musgrave 1969; Potter and Jones 1977). NAR was found not to differ significantly over the range of densities, despite significant differences in relative biomass growth rate. This indicates that the photosynthetic capacity of foliage is comparable at all spacings. Cole and Newton (1986) found that significant reductions in light availability not only occurred beneath dense alder stands but also occurred within the canopies of open grown trees. This would tend to reduce the differences in NAR attributable to a greater abundance of shade leaves on high density trees. Differences in RGR with increased available area could be attributable to the ability of trees grown at high initial spacings to support a greater amount of leaf area per given amount of biomass than trees grown at low initial spacings. This is due to the high amount of side

light available to leaves on low density trees, rather than just light from directly above the canopy.

The largest reduction in growth rate with decreased spacing occurred between trees at 0.73 and 3.57 m² spacings. Mean relative growth rate at these spacings reflected nearly a 3-fold reduction with decreased spacing. This reduction in relative growth rate corresponds to a substantial increase in the amount of crown overlap between trees (Table 1). The 3.57 m² spacing also appears to be a critical spacing for other growth parameters such as height, height/diameter ratio, leaf area and branch growth, mortality and allocation. This is most likely due to the unique light and water environment present at this spacing. These interactions are discussed further in Part 6.

Because mortality has not created carbon allocation patterns of trees grown at 3.57 m² which are substantially different from carbon allocation patterns of wider spaced trees, I expect trees grown at 3.57 m² to respond vigorously to release from competition. They still have the photosynthetic apparatus necessary to maintain a high relative growth rate. This is evident from the percent of total biomass allocated to branches. Trees grown at 3.57 m² allocate an average of 10.6% and 6.0% biomass to the lower and mid crown, respectively. In contrast, trees grown at 0.73 m² showed a net loss of 3.3% biomass

allocated to the lower crown and 2.9% allocated to the mid crown. Trees at spacings less than 3.57 m^2 would not be able to respond to release from competition as readily as trees grown at a 3.57 m^2 spacing, because they have lost much of the photosynthetic apparatus in the mid and lower crown. The photosynthetic rate of leaves in the upper portion of the crown is probably comparable across the spacing gradient, so increases in relative growth rate will be a result of how much more photosynthesis is possible in lower portions of the crown due to the increase in light availability at these crown positions.

In contrast to Bormann and Gordon (1984) who found that maximum leaf area index (LAI) occurred at an intermediate spacing of 2.22 m^2 , this study found that the highest LAI occurred at the highest density of 0.10 m^2 . Moreover, LAI at the highest density was significantly different from the other densities where complete crown closure had occurred, 0.26 and 0.73 m^2 ($\alpha = 0.01$). The increase in LAI found in this study at the lowest spacing could be due to the plot design. Mortality of trees in the inner border row might have allowed trees at the 0.10 m^2 spacing to exploit the open area at the center of each plot. This would result in higher values of LAI than would be expected at this spacing. This study indicates that the maximum LAI for red alder stands growing under this set of environmental conditions is approximately 3

m^2/m^2 . Although there are few studies which document the canopy dynamics of red alder, this maximum LAI is similar to the maximum found by Bormann and Gordon (1984).

In addition to providing information about how trees might respond to changes in the environment, carbon allocation patterns are useful in assessing some of the important mechanisms of the competitive process. Shifts in allocation provide an indication of which resources are most important to competing trees. The shift in height/diameter ratio seen in this study is a clear indication of competition for light between densely spaced trees. This shift, combined with a decrease in canopy depth and a greater proportion of total leaf area in the upper third of the crown, help trees acquire as much light as possible. Comparing trees at a particular spacing, those trees which are best able to shift allocation in ways which maximize resource acquisition show an increase growth and thus have a greater chance of surviving the self-thinning process.

Management Implications

Forest managers are commonly concerned with the amount of stemwood produced by trees under a given set of conditions. Management for solid wood use such as furniture, aims at producing a tree with as much clear bole wood as possible. This is often achieved by spacing trees so that branches self-thin as the trees age. Spacing trials are commonly utilized to determine what spacing optimizes this branch self-thinning while maintaining a high relative growth rate. A tree which allocates a high percent of total biomass to stemwood production as opposed to branch biomass would be more suited for this type of management. In this study, net stem biomass growth was greatest at a 3.57 m² spacing which is equivalent to 2804 trees per hectare. A 0.73 m² spacing resulted in a 26% reduction in net stem biomass, but percent biomass allocated to stem wood increased by 23%. Without any manipulation of spacing through thinning, the large difference in relative growth rate between trees at 0.73 and 3.57 m² will exaggerate the difference in total stemwood production with time. Thinning of the trees at 0.73 m², in order to increase the relative growth rate, could decrease some of the difference in overall production while maintaining the desirability of carbon allocation to stemwood.

Because of its extremely high juvenile growth rate

and desirable pulp qualities, red alder is an ideal tree for biomass production. The extremely high growth rates seen in this study would not necessarily occur on all sites but high rates of productivity have also been found on other sites (DeBell 1972; Zavikovski 1972). From the results of this study, the 4-year-old red alder achieved a maximum aboveground biomass production rate of 19 metric tons per hectare per year at a 0.73 m^2 spacing. Increasing spacing to 3.57 m^2 increased average biomass production per tree but reduced total biomass production by 11 metric tons per hectare per year. Further spacing studies would be necessary to determine if any increases in total biomass production would occur at intermediate spacings between 0.73 and 3.57 m^2 .

Part IV: Effects of Water Stress on Growth and
Carbon Allocation of Red Alder Seedlings

Introduction

Competition is mediated by changes in available resource levels. Competition between individuals can create a deficiency in resources where there was otherwise ample resources for growth of an individual, or competition can exaggerate an existing resource limitation (Harper 1977). Different levels of resources are closely connected with each other. Because of the interaction among resources, it is difficult to experimentally determine a cause and effect relationship between growth and resource levels. For example, if the water stress of a plant is severe enough, leaf temperature rises due to the reduced amount of heat dissipated by transpiration. This can inhibit leaf area growth and consequently total growth, by reducing photosynthesis. In order to determine the mechanisms involved in the competition process, identification of resource level-growth effect interaction is essential. Information from physiological studies involving resource manipulation under controlled conditions, can be used to make inferences about the processes taking place under more natural conditions. This study uses a combination of concurrent measures of

growth and water stress of trees in a density gradient, to examine the role of water stress as an important factor in the competitive process among individuals. The specific objectives of this portion of the study are to:

1. Relate changes in plant water potential to changes in tree growth rates and the growth rates of branches and leaves.
2. Examine the role of water stress as a competition mediator.

Methods

Predawn xylem potential measurements were taken at biweekly intervals between May and September of 1988. Single leaves were selected from each sample tree and xylem potential was measured using a standard pressure chamber (Waring and Cleary 1967). Each leaf was placed in a plastic bag between the time of removal from the tree and measurement. Individual red alder leaves are susceptible to changes in xylem potential between the time of selection and measurement if the leaves are exposed to low relative humidity air conditions. High humidity in the plastic bag was maintained by placing a wet paper towel in each bag.

Simple linear and non-linear regression techniques were used to determine the relationship between growth rate (Part III) and water potential on several days during the season. Each sample tree growth rate was regressed against the water potential for that tree. Growth rates from each biweekly sample branch were averaged over each density and each crown section to arrive at an estimate of branch growth rate for each density and crown section. Water potential of each sample tree was averaged for each density and these values were used in the regression vs. branch and leaf area growth rates.

The general non-linear model was:

$$\text{RGR} = A * (1 / (\psi)^B)$$

where A and B were the estimated parameters.

Results

June 29, August 9, and September 13 were selected as days of high water stress from graphs of water stress between May and September (Fig. 16). Because of periodic rain events which often recharged the soil so that water stress of the trees was low, water stress was not a simple function of date in the season. This resulted in periods when water stress was minimal at all spacings. No significant linear relationship was found between growth and water stress on these dates using linear regression techniques. Dates of high water stress for growth analysis were chosen because these were the dates when water stress was most likely to affect tree growth rates. All three selected dates showed approximately linear relationships between predawn water stress and the log of the spacing. The slope of the water stress gradient over the spacing gradient was lowest on June 29, and largest on September 13 with August 9 having an intermediate slope (Fig. 17).

There was a significant negative linear relationship between total tree relative growth rate and predawn water potential on each of the selected dates (Figs. 18a,b,c). Slopes of the regression lines decreased towards the end of the season from 1.87 on June 29, to 0.424 on September 13. There was a suggestion of a curvilinear response of

growth rate to water potential on August 9 and September 13. This curvilinear relationship was even more evident in a graph combining all three selected dates (Fig. 19). However, attempts to develop non-linear models were not successful.

Regression of mean branch RGR of the lower third of the canopy showed a significant linear relationship to mean water potential on June 29 and August 9 (Table 5). However, branch RGR showed a significant non-linear relationship to water potential on September 13 (Table 5). R^2 values ranged from 0.65 on June 29 to 0.92 on September 13. Mean branch relative growth rate of mid canopy branches showed a similar relationship to mean water potential as lower canopy branches (Table 5). Significant linear relationships were found for June and August while a significant non-linear trend was found for September. R^2 values were 0.88, 0.65, and 0.82 for June, August and September, respectively. As opposed to lower and mid canopy growth rates, mean upper canopy branch RGR showed a linear relationship to mean water potential on two of the three selected dates, August 9, and September 13 (Table 5). R^2 values were 0.70 and 0.88, respectively. There was no significant relationship between mean upper canopy branch RGR and mean water potential on June 29.

There was also no significant relationship between mean leaf area RGR and water potential on June 29.

However, there were significant non-linear relationships between mean leaf area RGR and water potential for the lower and mid canopy on August 9, and September 13 (Table 5). R^2 values were above 0.90 for all regressions. There was a significant linear relationship between upper canopy mean leaf area RGR and mean water potential in August and September (Table 5). R^2 values were 0.80 and 0.98 for August and September, respectively.

Discussion

Water stress is not usually considered an important factor determining tree growth at Cascade Head Experimental Forest. The highest predawn water potential found in this study was only -1.0 MPa which is well below the point at which severe inhibition of red alder photosynthesis has been found (Dukes, in progress). In spite of long periods of dry weather, periodic rain events recharge the soil so that water stress for plants is a short-term occurrence (Fig. 16). The mild temperatures which characterize the site also help to minimize the detrimental effects of water stress on plant growth. This study suggests that significant reductions in the growth rate of red alder occur at relatively low water stress levels. Similar results have been found in physiological work by Chan et al. (1989) where light and water levels were controlled and work by Shainsky (1988). These observations suggest that although competition for light may ultimately determine plant success, water stress is an important factor in determining the ability of a plant to compete for light.

A direct linear relationship existed between both branch RGR and leaf RGR in the upper canopy and water stress (Table 5). The slopes of these regression lines were generally low. This indicates that red alder is able

to maintain upper canopy growth of branches and leaves over the range of water stress levels found in this study. The relationship between lower and mid branch and leaf area growth rates was non-linear except for branch growth in June and mid-crown branch growth in August (Table 5). These relationships were characterized by a steep linear relationship at low water stress levels with a decreasing slope as water stress increased. This data suggests that lower and mid-crown growth of branches and leaves is more sensitive to changes in water stress than upper canopy growth. This implies that trees experiencing high levels of competition are able to maintain high rates of growth in the portion of the canopy in which the majority of light resources are available.

The reduction in growth rates of branches and leaves leads to decreased overall biomass relative growth rates. A clear trend of decreasing growth rate with increased water stress was evidenced (Figs. 18a,b,c). One of the interesting trends shown by this data was the shift from a linear relationship between growth rate and predawn plant water potential to a curvilinear relationship as the water stress gradient increases. This change in type of relationship was due to a wide variability in RGR at low water stress levels. As water stress becomes less of a limiting resource, differences between trees in levels of other resources produce differences in relative growth

rates among trees. These differences in relative growth rates among trees results in trees which show a response to increased water and others which are unable to respond. The upper boundary of relative growth rate at high water stress would seem to support the hypothesis that plants are limited by a single resource at any one time (Chapin et al. 1987). However, the experimental design in this study does not provide a foundation for testing that hypothesis because the majority of the trees experiencing high water stress also experience high competition for light resources. It remains to be seen whether these trees would respond to increased light in spite of water limitations.

The high degree of variability in relative growth rate within spacings creates difficulties with using a regression approach. A more informative approach is to examine the upper boundary of growth rates present over the range of predawn water potentials (Fig. 19). Using this approach, we find that a threshold potential exists between -0.3 and -0.4 MPa where maximum relative growth rate decreases sharply to a minimal level which is maintained in spite of increased water stress. This suggests that the extremely high yearly relative growth rates often characteristic of young red alder are a function of periods of low water stress. Red alder seems to be able to only maintain moderate rates of growth when

water stress levels are above the predawn threshold level of -0.3 to -0.4 MPa.

The abrupt decrease in red alder growth with increased water stress indicates some potential problems in management of this species. Although red alder is able to survive on a wide range of sites, best growth and form is likely to be achieved on more mesic sites. Establishment on harsh sites is difficult due to problems such as drought stress and frost damage (Bormann and Gordon 1984; Hibbs, personal communication). Mesic sites most likely represent excellent sites for growth of other managed species such as Douglas-fir. The suitability of both red alder and Douglas-fir management on mesic sites could lead to the reluctance of managers to grow red alder.

Part V: The Role of Canopy Dynamics
in Patterns of Tree Mortality

Introduction

The structure and composition of plant communities depends on the patterns of mortality as the community ages. The types of factors which can cause tree mortality are numerous. Abiotic factors such as fire and windthrow can kill large tracts of trees. Large scale mortality can also be caused by biotic factors such as insects (gypsy moth, mountain pine beetle) and disease (chestnut blight, Dutch elm disease). Often the cause of tree mortality is difficult to ascertain because of the complex interaction between biotic and abiotic factors. Abiotic factors often weaken individuals so that they are more susceptible to biotic factors. Waring and Pitman (1985) demonstrated a close relationship of nutrient availability and water stress with the probability of mountain pine beetle attack (Dendroctonus ponderosae Hopkins). They found that vigorous trees had a much lower rate of attack by the beetles and were also more likely to withstand attack better than less vigorous trees.

The relationship between stress and carbon allocation discussed in the previous two sections, if extended over a long period of time, will have a substantial impact on the

potential mortality of trees. In perennial plants, current carbon allocation patterns indicate adaptations by plants to both current and past stresses. These allocation patterns also provide information on how a tree should respond to stress in the future. The allocation response of trees to current stress is primarily what determines the probability that trees will survive long enough to reach maturity.

The focus of this study has been on aboveground biomass allocation, canopy dynamics in particular. The underlying assumption is that carbon allocation patterns have a long-term impact on tree growth and eventually, tree mortality. The connection between current carbon allocation patterns and long-term survival is difficult to produce quantitatively, however, because no whole tree mortality of sample trees occurred during this study. In this section I will discuss the link between growth characteristics and a tree's ability to grow to maturity.

If carbon allocation patterns are related to the ability of trees to garner resources and thus compete successfully, understanding the implications of carbon allocation patterns should provide a way of predicting success or failure of individuals in self-thinning communities. Part 3 showed how different levels of competition affect mean tree performance. However, the population dynamics of communities are driven by

individual performance relative to other individuals. By analyzing the interactions among individuals, we can gain information on how individual response to competition results in community characteristics.

In order to study interactions among individuals, it is necessary to make an initial assumption concerning the definition of successful trees. Under conditions of high competition, light will be the primary limiting resource for shade intolerant tree species. Height growth, i.e. the ability to intercept light before neighboring trees, is the most crucial growth characteristic determining which trees will survive self-thinning.

Methods

In order to assess the relationship between canopy dynamics and successful competition under conditions of high competitive stress, 4 trees were selected from the two lowest spacings, 0.10 m² and 0.26 m². Based on initial height, the two smallest and the two largest trees were selected from each spacing. These trees were selected under the assumption that height is the main indication of competitive success. A variety of crown characteristics were measured/calculated for each selected tree (Table 6).

Results

The results in Table 6 show that stratification in the canopy has begun to occur (Table 6., Fig. 20). There was a significant difference between the initial height of small trees and large trees ($\alpha = 0.01$, $p < 0.0001$). This difference in initial height paralleled a significant difference in initial biomass (Table 6, Fig. 21; $\alpha = 0.01$, $p < 0.001$). By the end of the growing season, the difference between the two groups of trees was even greater (Table 20, Figs. 20,21). Small trees also had significantly less leaf area at the end of the season than large trees (Table 6; $\alpha = 0.05$, $p = 0.018$). However, despite having a smaller amount of leaf area, small trees allocated a significantly greater amount of biomass to branches than large trees (Table 6). There was also a significant difference in crown depth between groups (Table 6; $\alpha = 0.05$, $p = 0.033$).

Discussion

Although the trees in this study were only 4 years old, significant trends in height and biomass distribution have begun to develop. The size difference between successful and unsuccessful competitors increased substantially during this study. This trend is likely to continue as larger trees capture an increasingly greater amount of resources. Successful trees have the ability to increase both height and overall biomass much faster than their competitors. The amount of height and biomass growth were good indicators of successful trees, as large trees averaged more than 3 times the height growth and close to 8 times the biomass growth of the smaller trees. Large trees also outpaced the average amount of height growth by up to 2 times, while smaller trees performed considerable worse than the average height growth. This accentuates the size hierarchy that was present at the beginning of the season.

The success or failure of individuals growing in a competitive environment is determined by the response of those individuals to competition and the effect of competition on the growth of the individuals. These two characteristics of competition are not necessarily correlated in plants (Golberg and Fleetwood 1987). The response of trees to competition from neighbors is

reflected by changes in carbon allocation patterns. The effect of competition on trees is reflected by a decrease in total growth or by a change in the position of a particular tree within the size hierarchy of the community. Carbon allocation patterns, by increasing or decreasing the ability of trees to acquire resources, influence the amount of effect competition has on the trees. Using the carbon allocation patterns of trees grown under low competition levels as a standard, the results from my study indicate that large trees did not respond to competition as much as small trees. This is shown in the differences in growth attributes presented in Fig. 6. Typical responses to competition are reduced canopy depth, reduced leaf area, and increased branch biomass relative to total aboveground biomass. The effect of competition was also less on large trees than on small trees. This is shown by the greater height and biomass growth of large trees and also by the ability of the large trees to maintain their position in the size hierarchy of the community (Fig. 6).

In order to maintain high rates of height and biomass growth, successful trees must support a larger amount of leaf area. Leaf area was found to be significantly greater in large trees ($\alpha = 0.05$, $p = 0.018$). However, the percent allocation of biomass to branches was significantly lower for successful trees ($\alpha = 0.01$, $p =$

0.006). These two characteristics play a fundamental role in the continuing development of a size hierarchy of trees within the population. The large amount of leaf area found on successful trees allows these trees to produce more carbon than unsuccessful trees while depriving unsuccessful trees of light. The ability of successful trees to produce more carbon increases any initial differences in carbon production which may have existed. In addition, the lower relative amount of biomass necessary to support leaf area of successful trees allows these trees to allocate their superior carbon resources to functions other than leaf area, e.g. height and roots. Increased allocation to components other than leaf area gives successful trees an even greater ability to garner resources and hence, increase their competitive advantage over other individuals.

The success of individuals over time is due not only to interactions with other trees, but is also due to how trees interact with biotic and abiotic factors. The ability of large trees to support large amounts of leaf area with a lower percent allocation of biomass allows these trees to allocate more resources to other uses. Waring (1987) suggests that storage and defensive allocation has a lower priority than leaves and roots. Small trees, which allocate up to 64% of their biomass to branches, will be more susceptible to attack by insects or

short term stress, such as drought, because they can only allocate a small amount of biomass to storage and defense.

Part VI: Synopsis and Discussion

In this section, I would like to first summarize the results of my study and then discuss some of the implications of these results concerning competition in general, and future research directions.

Synopsis

The results of the growth and carbon allocation measurements indicated several significant growth responses of red alder to competition. Reductions in leaf area, height, basal diameter and biomass occurred with increased amounts of competition. Although leaf area per tree was smallest at low spacings, leaf area index reached its maximum at the lowest spacing. However, LAI achieved a relatively stable value close to 2.5 at the two next higher spacings. Despite a low degree of difference in initial height and biomass over the density series, differences in height, basal diameter, and biomass growth produced significant differences over the density gradient by the end of the season. Significant differences in relative growth rate were also present over the density series. Relative growth rates were highest among the open grown trees and dropped dramatically once crowns began to overlap. These differences in relative growth rate over

the density series were most likely driven by differences in LWR between trees growing at different spacings. LWR generally increased with increased available area, while there was no clear relationship between NAR and initial spacing.

Competition among trees for water produced a plant water potential gradient over the density series. Predawn plant water potential was a significant factor determining overall tree relative growth rate as well as branch and leaf area relative growth rate. Although a significant linear model describing the effect of water stress on overall tree relative growth rate could be developed, relative growth rate seems to respond in a curvilinear fashion. Using a boundary curve approach, a threshold water stress level was apparent between -0.3 and -0.4 MPa, above which trees were able to maintain moderate amounts of growth despite increases in water stress. The relationship between water stress and branch and leaf area relative growth rate also approached a curvilinear relationship as the intensity of the water stress gradient increased.

Examination of successful and unsuccessful competitors at the two lowest spacings resulted in a size hierarchy of height and biomass. Significant differences in leaf area, percent biomass allocated to branches, and crown depth were also found.

Discussion

As this study has shown, competition among red alder trees has a significant effect on carbon allocation patterns and growth. The response of these red alder to competition and the effects of competition on their growth, are primarily a result of light and water levels which vary in availability and relative importance as competition increases. The unique light and water environment of trees grown at a transition spacing such as 3.57 m^2 produce growth characteristics which are particularly informative on the response of trees to competition and the interaction of water and light resources.

One of the growth characteristics in a state of transition at a 3.57 m^2 spacing is lower canopy branch biomass growth and leaf area. The large difference in branch biomass growth and leaf area in the lower third of the crown suggests that there is a significant change in the light environment of the lower canopy between 0.73 m^2 and 3.57 m^2 . Trees only maintain leaves which produce more photosynthate than is needed to maintain the leaves. This means that as light decreases in the lower canopy, more and more leaves drop below this compensation point, which results in reduced branch growth and leaf area in this portion of the crown. The much greater lower canopy

branch biomass growth and leaf area of trees at 3.57 m^2 as opposed to trees at 0.73 m^2 indicates that the light environment at the wider spacing enables a larger amount of leaves to remain above the compensation point.

In spite of being able to maintain a larger amount of leaf area in the lower canopy compared to trees at lower spacings, trees at a 3.57 m^2 spacing had considerably less lower canopy branch biomass growth and leaf area than open grown trees. The comparable amount of branch mortality between these densities indicates that the light environment has not reached the threshold level, but has been reduced to the point where growth is inhibited and photosynthesis is reduced. The reduction in photosynthetic production in the lower canopy could be an important factor in the substantial reduction in overall biomass relative growth rate of trees grown at 3.57 m^2 compared to open grown trees.

In addition to changes in lower canopy branch biomass growth and leaf area found at a 3.57 m^2 spacing, predawn plant water potential was generally lower for trees planted at lower spacings. The decrease in water potential between trees at 3.57 m^2 and low spacings, although only sustained for a few weeks at a time, was significantly related to reductions in growth rate of individuals. Chan (1989) found that red alder biomass production was more sensitive to low light conditions than

low water conditions, but that combinations of low light and low water produced the greatest reductions in biomass production. My results indicate that significant reductions in lower canopy branch biomass and leaf area growth were correlated with increased water stress. This should accentuate any reductions in overall biomass relative growth rate enough to account for the large difference in aboveground biomass relative growth rate between trees at 0.73 and 3.57 m² spacings.

Competition between trees is an important process in community development. As I have shown in this study, competition among red alder trees has a significant effect on growth rate. This affects how red alder grows relative to other members of the community, both woody and herbaceous. High density plantings of red alder are commonly characterized by little-to-no ground cover due to rapid red alder canopy development and crown closure. In contrast, there is typically an abundance of shrubs and herbs present at low densities. The differences in understory composition between these two types of communities produce habitat suitable for different species of animals. Understory growth also can have a significant effect on the long-term species composition on the site. For example, although red alder's high juvenile growth rate allows it to overtop shrub and herb competition, slower growing species such as conifers, may be unable to

compete with the shrubs and herbs. This can lead to the development of a shrub and herb dominated site once red alder reaches senescence (Carlton 1988; Hibbs 1987). An intermediate spacing, such as between 0.73 and 3.57 m in this study, might reduce shrub and herb presence enough to allow other tree species to become established. Species which can not tolerate the severe reduction in light shrub and herb cover might be able to tolerate the less severe light reductions found under red alder canopies.

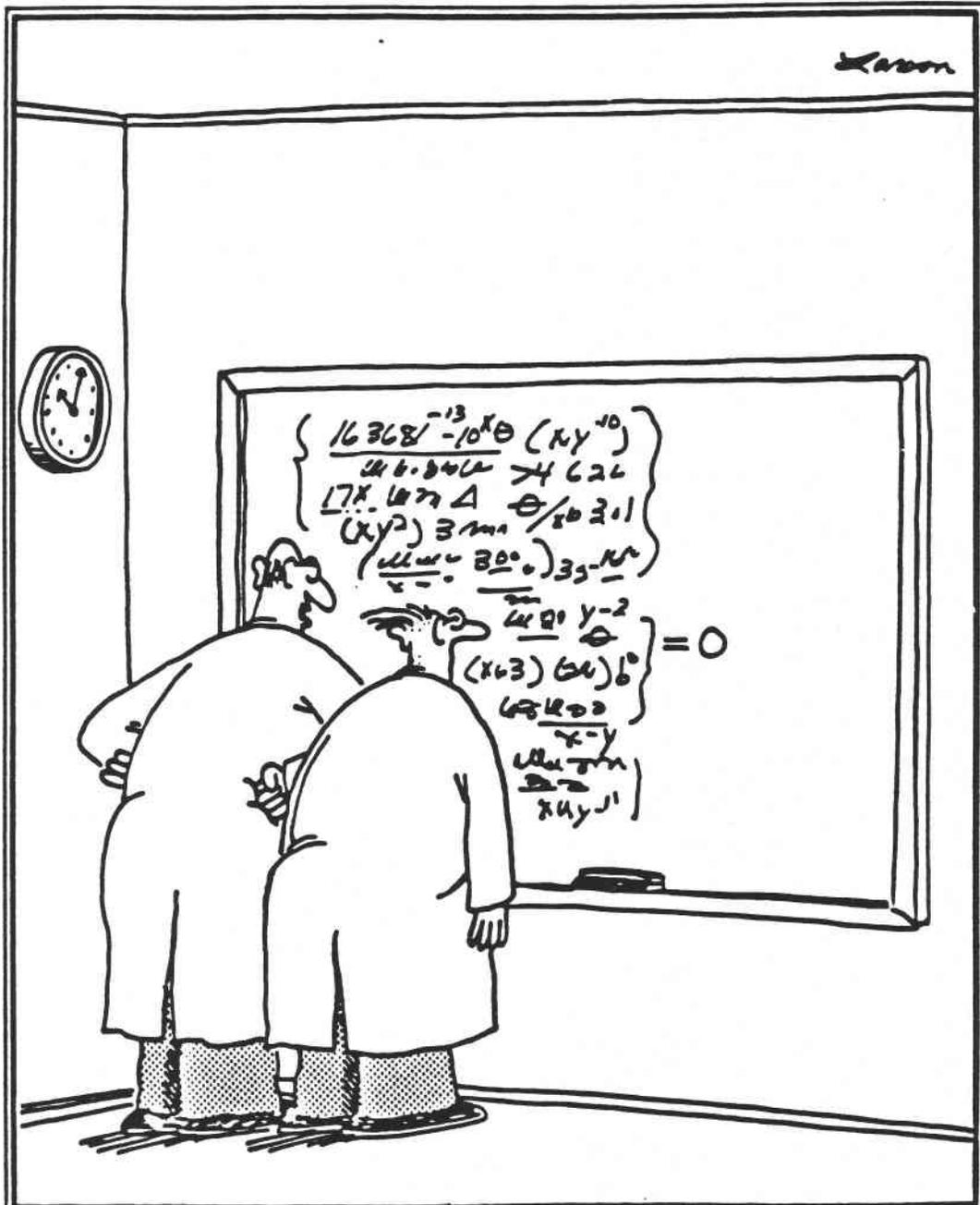
The time at which intraspecific competition occurs is also an important characteristic of the competition process. Open-grown alders seem to be much more susceptible to damage from factors other than competition, such as herbivore, frost and wind. Although not quantified in my study, elk and wind damage in the Nelder plots was largely confined to wider spacings. By severely affecting some individuals while not affecting others, these factors can produce a more severe hierarchy of tree size than would develop under low spacing conditions. The development of this size hierarchy, as seen in part 5, helps enhance the self-thinning process. Trees which avoid damage by other agents will be taller and have larger crowns than neighboring trees, making them much better competitors.

The importance of resource-level interactions among trees was apparent in this study. Even moderately low

water stress levels were seen to have significant effects on overall growth rates and growth rates of branches and leaves. The water stress levels found in this study were considerably below levels where inhibition of photosynthesis would occur. Water stress is most likely contributing to reductions in light availability with decreased spacing. The interaction of water and light availability affects the ability of these factors to modify growth. This is shown by upper canopy branch and leaf growth rates. Growth rates of upper crown components were significantly related to water stress levels, but reductions in relative growth with decreased spacing were fairly small due to the similarity in upper canopy light environment over the spacing gradient.

This study represents an intermediate step between highly controlled field experiments (Shainsky 1988) and experiments under natural conditions. Mechanistic studies are difficult to perform under field conditions due to the difficulty in controlling experimental factors and separating the effects of these factors from other uncontrollable factors. The significant results of this study indicate the potential of successfully studying the complex resource-level interactions which drive the competitive process under relatively natural growing conditions. These types of experiments provide a way of testing the relative importance of mechanisms in relation

to the myriad of other factors which influence plant growth. Continued monitoring of these experimental plots should provide important information on the role of competition in the growth and structure of perennial plant communities.



"No doubt about it, Ellington—we've mathematically expressed the purpose of the universe. Gad, how I love the thrill of scientific discovery!"

Table 1. Crown spread of 4 year old red alder trees in relation to available growing area. Crown spread is defined as the overall length of branches at the end of the study. Lateral distance is defined as the distance between trees on the same circle. Distance to the inner and outer neighbor tree is presented. Average branch length and percent of branches exceeding half the lateral distance between trees is shown for each spacing.

<u>Initial Growing Area</u>	<u>Dist. from others(m)</u>			<u>Crown Spread</u>	
	<u>Lateral</u>	<u>Radial</u>		<u>Aver.</u>	<u>% above 1/2 Lat.</u>
		<u>In</u>	<u>Out</u>	<u>(m)</u>	
0.10 m ²	0.29	0.34	0.33	0.60	96.4%
0.26 m ²	0.50	0.46	0.58	0.76	95.2%
0.73 m ²	0.84	0.73	0.97	1.07	93.9%
3.57 m ²	1.84	1.64	2.20	1.25	70.7%
17.13 m ²	4.03	3.59	4.70	1.23	0.0%
41.99 m ²	6.82	6.09	6.10	1.11	0.0%

Table 2. Type of competition and topography of experimental plots.

<u>Plot Number</u>	<u>Type of Competition</u>	<u>Topography</u>
1A	Herbaceous	Flat
1B	Herbaceous	Flat
2A	Herbaceous & Shrub	NE facing, midslope
2B	Herbaceous & Shrub	NE facing, midslope
3A	Herbaceous & Grass	Flat
3B	Herbaceous & Grass	Flat

Table 3. Regression coefficients for aboveground components of red alder. General form of the equation for tree variable and leaf area is: $Y = a + b(X*Z^2)$. Equation form for branch variable is: $\ln Y = a + b \ln X + c \ln Z^2$. TL is Total Branch Length, BD is Branch Basal Diameter, TBD is Tree Basal Diameter and TH is Total Tree Height.

Y	a	b	c	X	Z	R ²	MSE	N
Branch Biomass	-3.948	0.641	0.861	TL	BD	0.87	0.168	80
Branch Leaf Area	*	0.101	----	TL	BD	0.85	47344	44
Abovegrd Biomass	-64.679	0.001	----	TH	TBD	0.96	39680	25

* Coefficients for Branch Leaf Area are:

	.1 m ²	.26 m ²	.73 m ²	3.57 m ²	17.13 m ²	41.99 m ²
¹ Low	53.84	-29.23	142.24	303.79	300.97	-93.95
Mid	138.51	55.44	173.07	388.46	385.64	-9.28
High	156.14	73.06	190.70	406.09	403.27	-93.95

¹branch position in canopy

Table 4. Relationship between mean relative growth rate, mean leaf weight ratio, specific leaf area and mean net assimilation rate. Yearly relative growth rate using beginning and end of season measurements of tree size is presented. Leaf weight ratio was calculated using end of season biomass and leaf weight estimates. A specific leaf area of 115 cm² was calculated using samples collected throughout the growing season. Net assimilation rate was calculated using yearly biomass growth and end of season leaf area. Standard error is given in parenthesis.

<u>Growing Area(m²)</u>	<u>RGR</u>	<u>LWR</u>	<u>NAR</u>
0.10	0.732(0.104) ^a	0.127(0.011) ^a	0.031(0.005) ^a
0.26	1.255(0.103) ^a	0.110(0.025) ^a	0.066(0.015) ^{ab}
0.73	2.277(0.335) ^a	0.084(0.013) ^a	0.088(0.018) ^b
3.57	6.939(1.575) ^b	0.150(0.021) ^a	0.062(0.014) ^{ab}
17.13	10.048(1.286) ^b	0.253(0.040) ^b	0.043(0.009) ^{ab}
41.99	11.275(3.244) ^b	0.270(0.034) ^b	0.031(0.033) ^a

*RGR is Relative Growth Rate (/year), LWR is Leaf Weight Ratio (gm/gm), and NAR is Net Assimilation Rate (gm/cm²). Values with different letters are significantly different at $\alpha = 0.01$ using the protected least significant difference range test.

Table 5. Regression equations for branch and leaf area relative growth rate vs. predawn water potential. General form of the linear equation is: $Y = a - b(X)$. General form of the non-linear equation is: $Y = a*(X)^{-b}$.

<u>June 29</u>		Y	a	b	X	R ²	MSE	N
<u>Canopy Position</u>								
Lower	¹ BRGR	4.9	1.8			0.65	0.447	6
	² LfRGR	---	---			----	N.S.	-
Mid	BRGR	10.5	3.6			0.88	0.417	6
	LfRGR	---	---			----	N.S.	-
Upper	BRGR	---	---			----	N.S.	-
	LfRGR	---	---			----	N.S.	-
<u>August 9</u>								
<u>Canopy Position</u>								
*Lower	BRGR	1.7	1.1			0.75	0.294	6
	LfRGR	2.1	1.9			0.90	0.431	6
*Mid	BRGR	3.5	0.9			0.65	0.597	6
	LfRGR	2.0	1.8			0.91	0.194	6
Upper	BRGR	3.9	0.9			0.70	0.444	6
	LfRGR	4.0	1.1			0.80	0.360	6
<u>September 13</u>								
<u>Canopy Position</u>								
*Lower	BRGR	3.3	1.7			0.92	0.160	6
	LfRGR	4.6	2.1			0.96	0.138	6
*Mid	BRGR	2.2	1.2			0.82	0.181	6
	LfRGR	---	----			----	N.S.	-
Upper	BRGR	1.9	0.3			0.88	0.048	6
	LfRGR	2.0	0.3			0.98	0.011	6

* Non-linear equations

¹BRGR is Branch Relative Growth Rate

²LfRGR is Leaf Relative Growth Rate

Table 6. Growth characteristics of successful and non-successful competing trees. The 2 trees with the smallest and largest initial height at .1 m² and .26 m² spacings are shown.

	0.26 m ²		<u>Smallest</u> 0.10 m ²		0.26 m ²		<u>Largest</u> 0.10 m ²	
Initial Height(cm)	256	256	270	274	360	363	376	405
End Height(cm)	285	321	276	305	482	489	470	519
Height Difference(cm)	29	65	6	31	122	126	94	114
Ht Growth/ Ave. Ht Growth	0.29	0.64	0.12	0.61	1.21	1.25	1.83	2.22
Initial Biomass(gm)	92	116	63	111	439	380	334	520
End Biomass(gm)	140	251	104	154	1007	868	861	952
Biomass Difference(gm)	48	135	41	43	569	488	527	432
Leaf Area (m ²)	0.39	0.37	0.36	0.15	0.82	0.57	0.40	0.96
Branch/Total Biomass(%)	64	45	35	31	16	14	15	22
Branch Mortality/Branch Growth (%)	37	19	37	0	71	77	26	67
Crown Depth(cm)	185	193	125	221	303	279	190	239

Figure 1. Definition of available growing area per tree.
Growing area per tree is defined as the area bounded by lines a, b, and c. Trees are denoted by X.

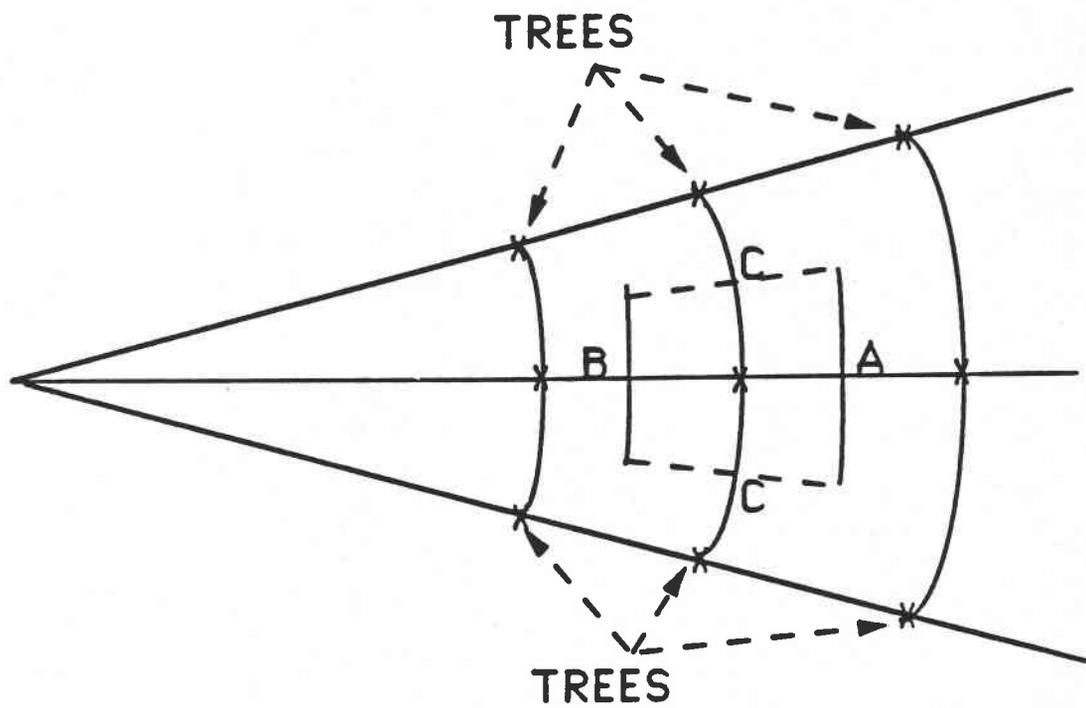
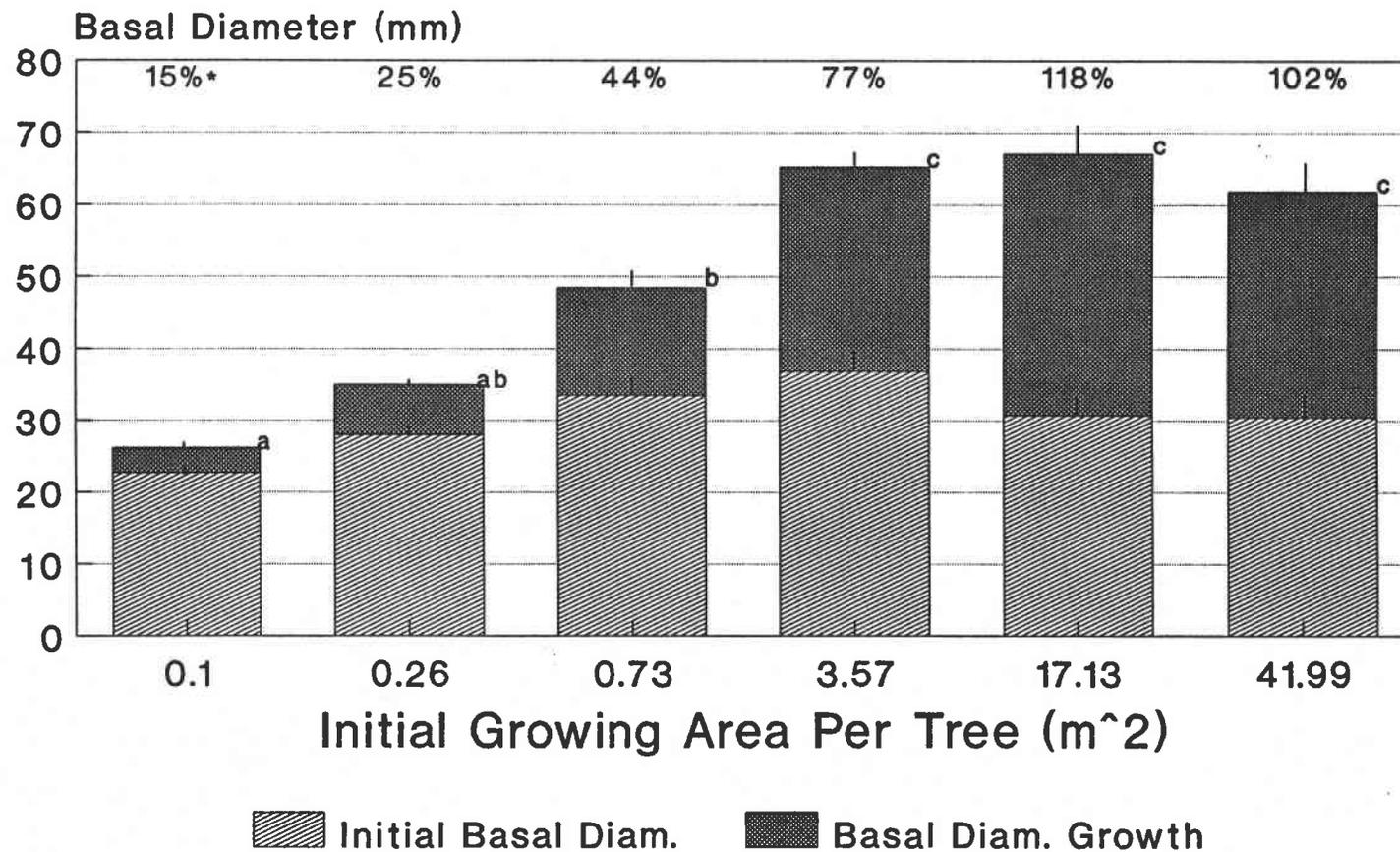


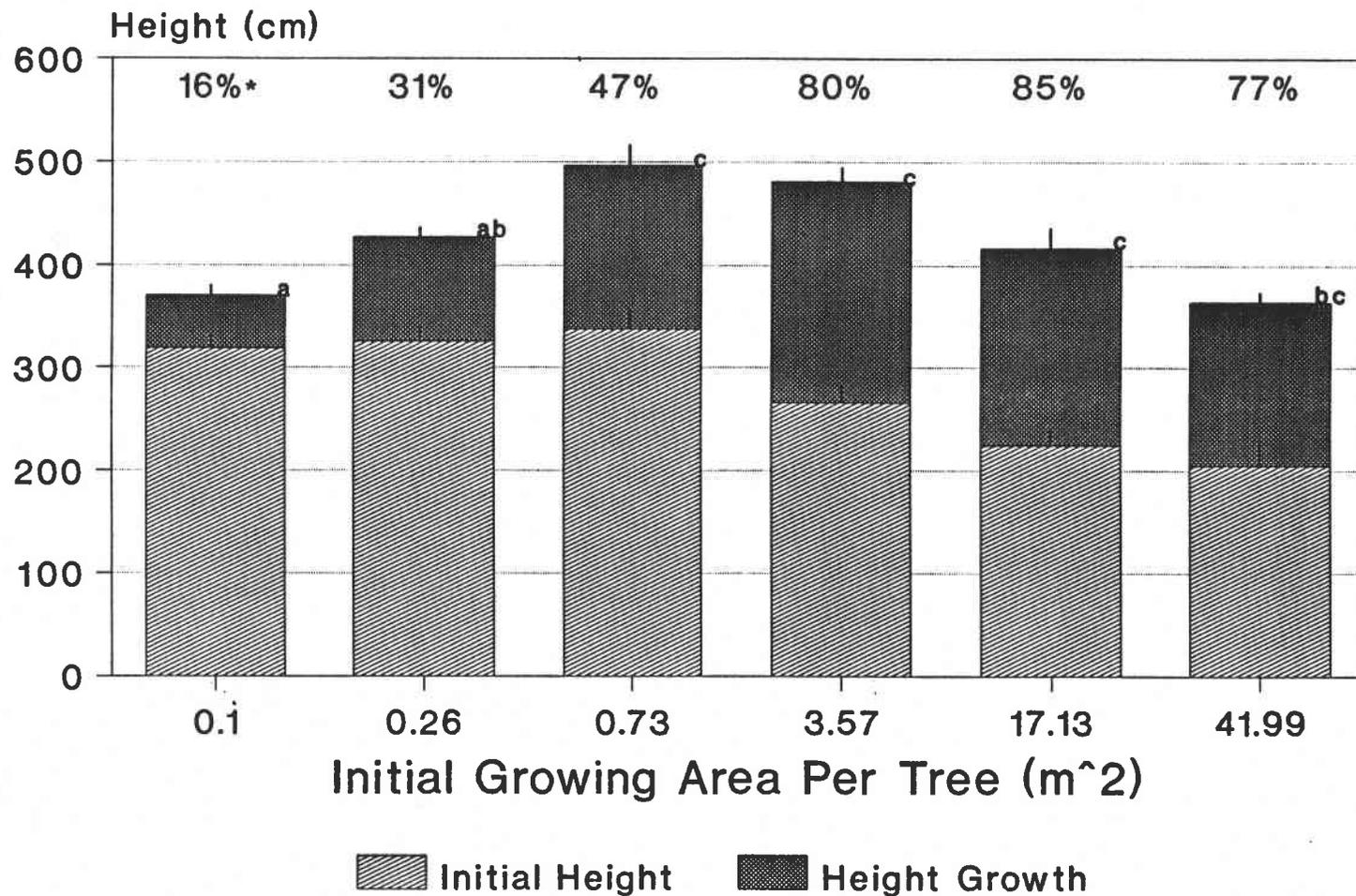
Figure 2. Mean initial basal diameter and mean basal diameter growth of sample trees. Initial basal diameter was measured prior to leaf flush and end basal diameter was measured after leaf fall. The protected least significant difference range test was used in bar graphs representing mean values. Bars with different letters are significantly different at $\alpha = .05$. Similarly, standard error of the sample bars are presented in graphs representing mean values.



* % Increase in Diameter

Figure 2.

Figure 3. Mean initial height and mean height growth of sample trees. Initial height was measured at beginning of the season before leaf flush and end height was measured after leaf fall.



* % Increase in Height

Figure 3.

Figure 4. Mean ratio of height/diameter of sample trees. Ratio is calculated using measurements of height and diameter measured after leaf fall.

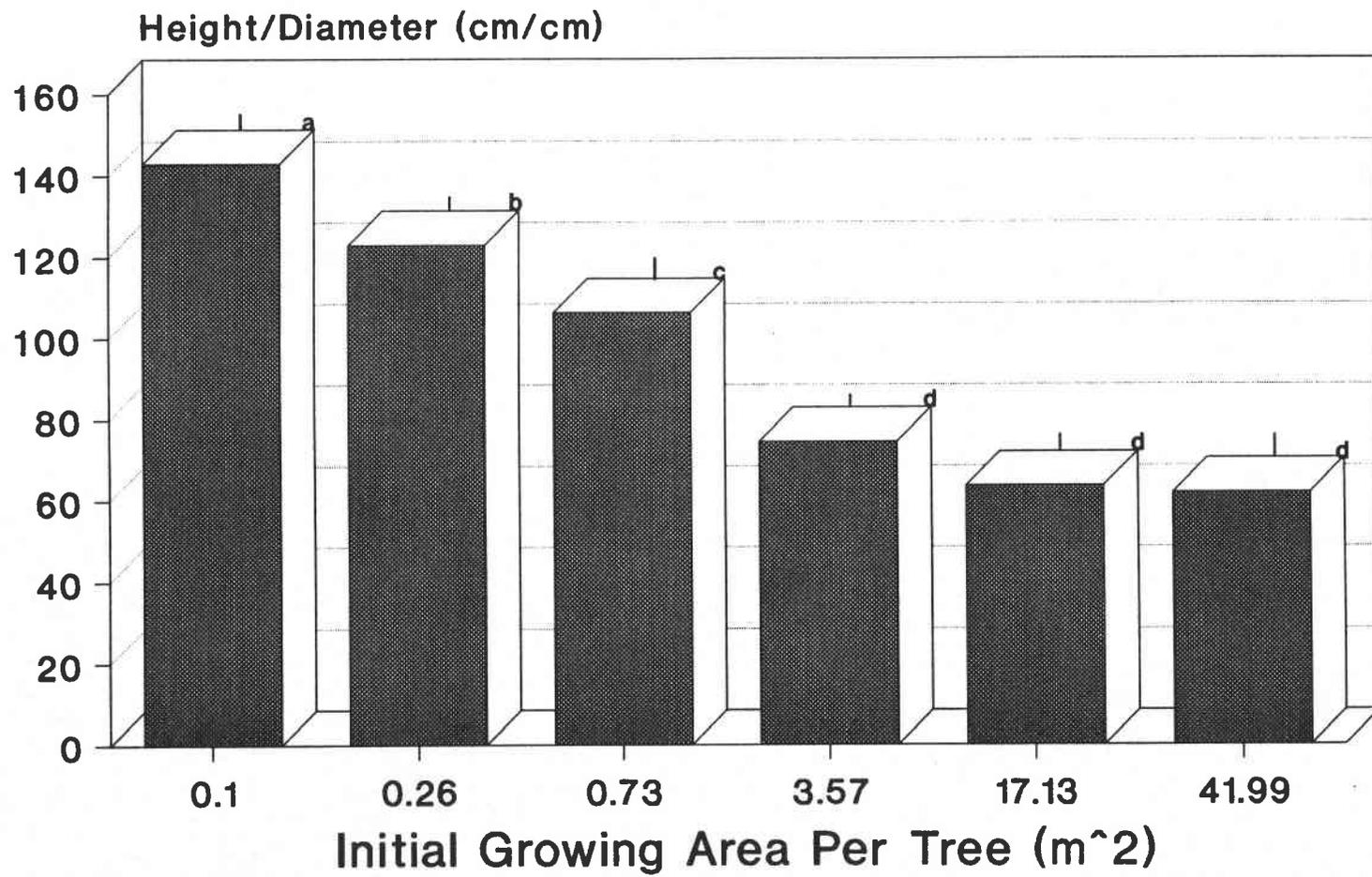


Figure 4.

Figure 5. Mean initial aboveground biomass and aboveground biomass growth of sample trees. Biomass was calculated using allometric equations based on basal diameter and height measurements.

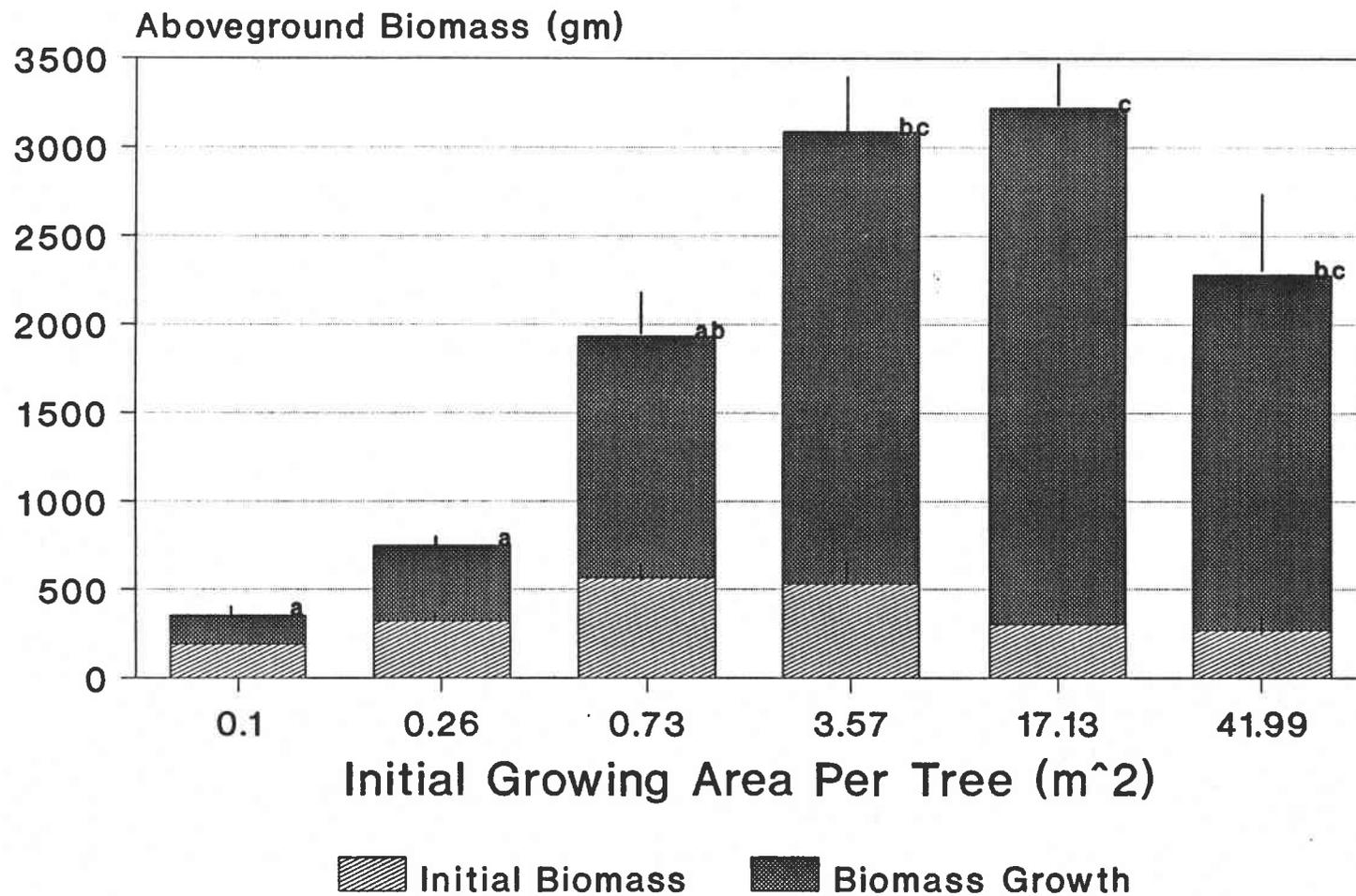


Figure 5.

Figure 6. Mean relative growth rate of aboveground biomass of sample trees. Relative growth rate calculated as: $RGR = (X_2 - X_1) / X_1$ where X_1 = Initial Biomass and X_2 = End Biomass.

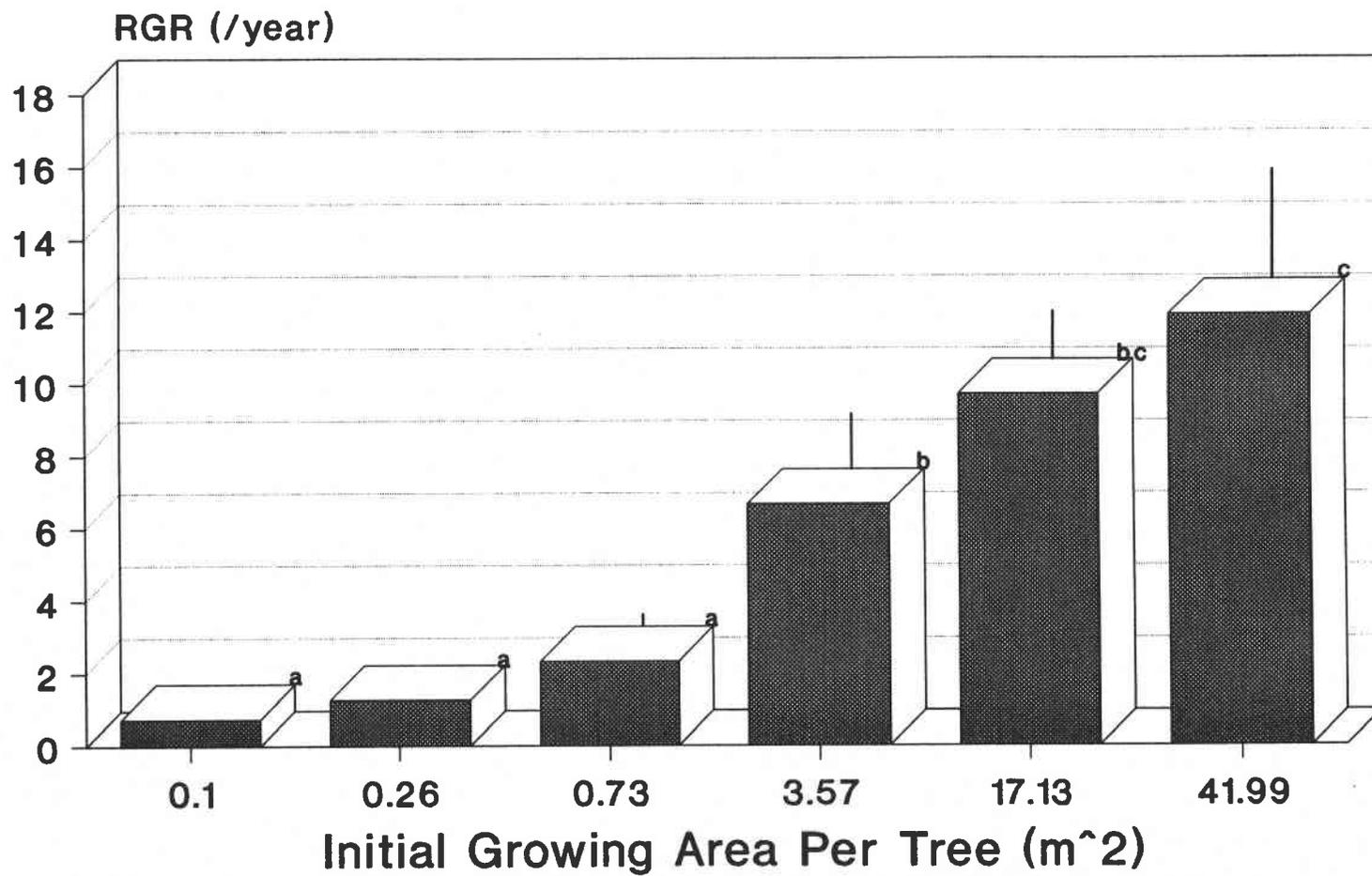
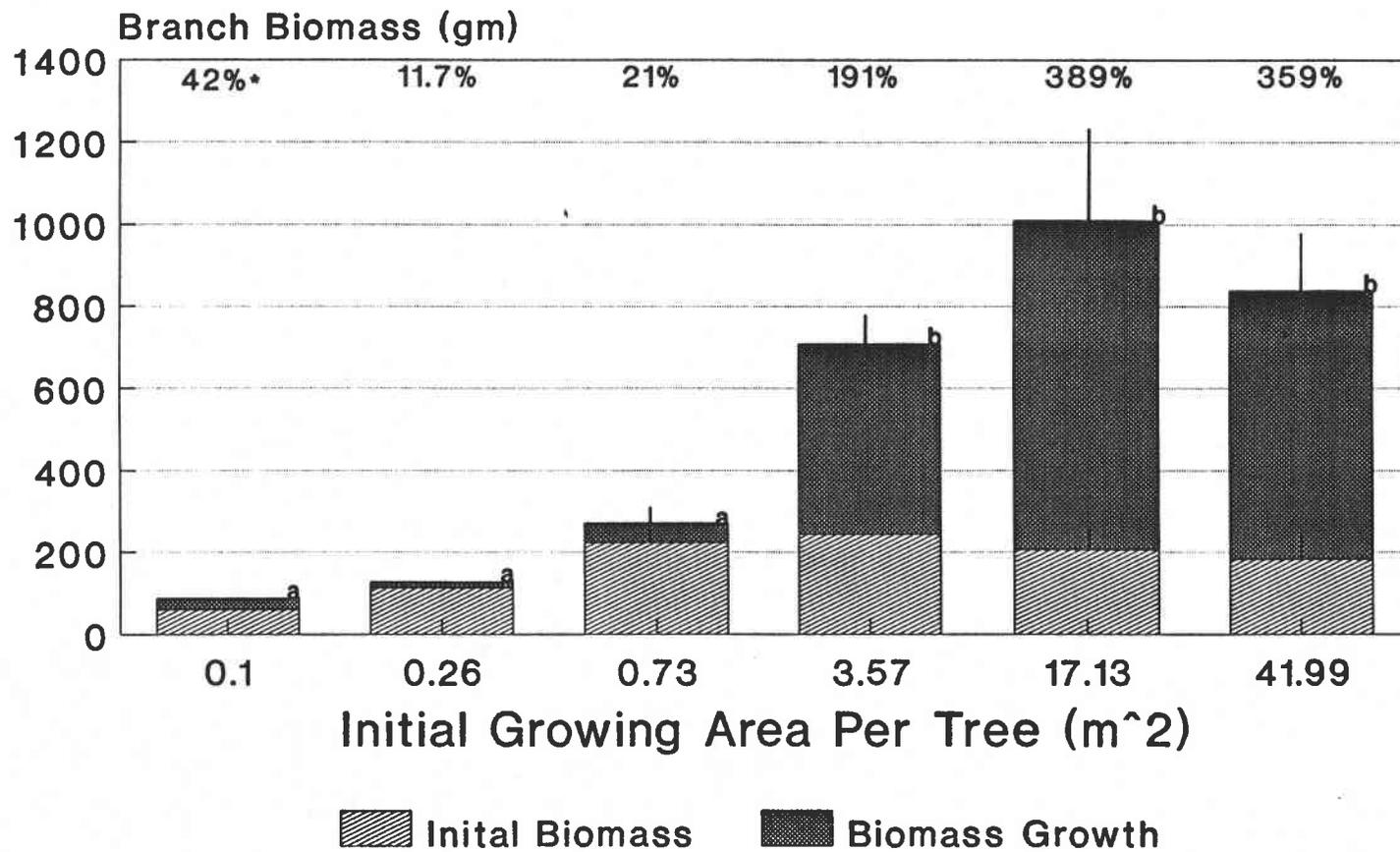


Figure 6.

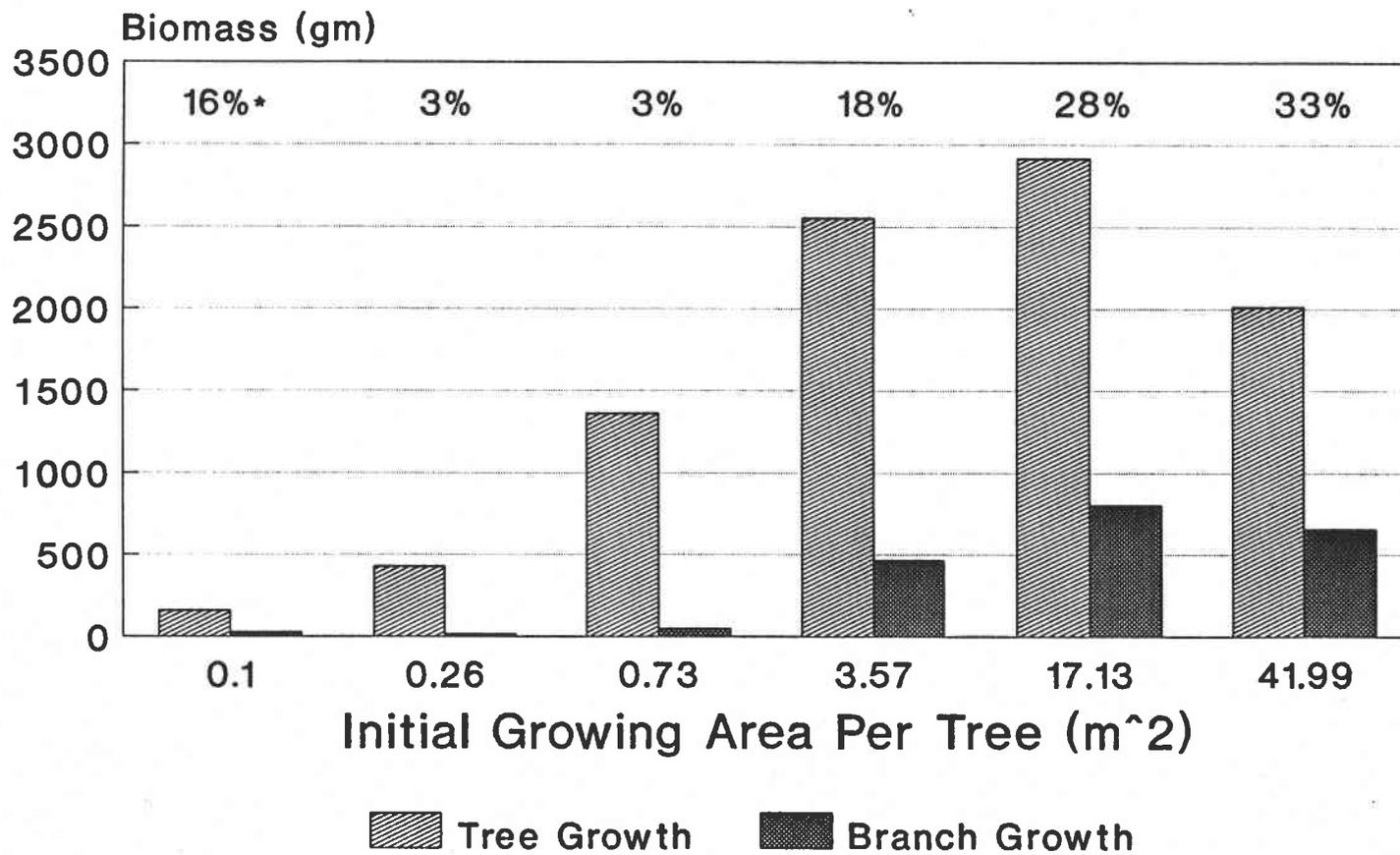
Figure 7. Mean initial branch biomass and mean net branch biomass growth of sample trees. Branch biomass is calculated using allometric equations based on basal diameter and length of the branch. Branch mortality is calculated as the loss of biomass associated with any decrease in size of the branch.



* % increase in biomass

Figure 7.

Figure 8. Mean net aboveground biomass growth and mean net branch growth of sample trees.



* Branch/Tree (gm/gm)

Figure 8.

Figure 9. Mean branch mortality and mean gross branch growth of sample trees. Mortality and gross growth represent yearly values.

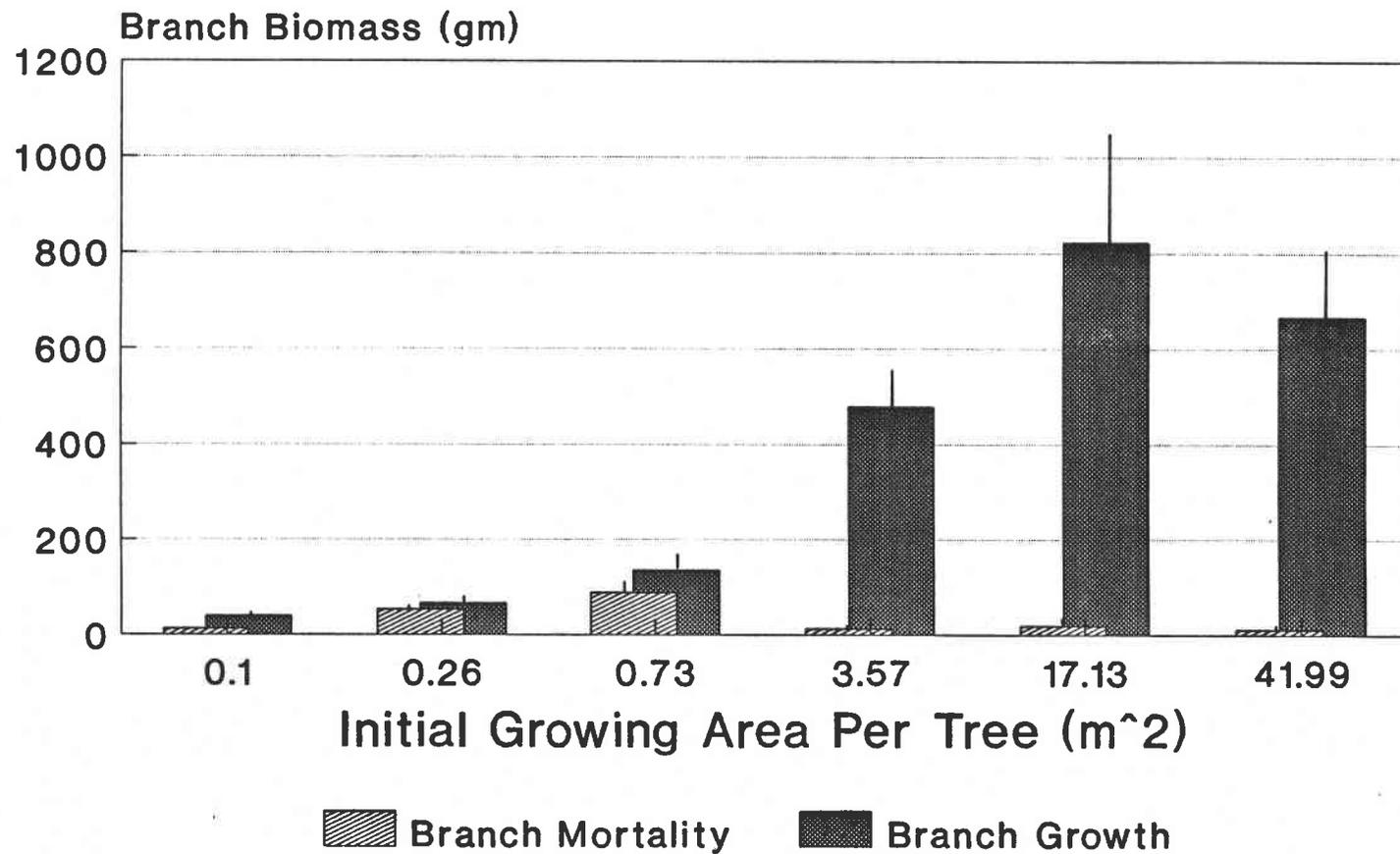


Figure 9.

Figure 10. Mean net branch biomass growth of the lower, mid, and upper sections of sample tree crowns. Each tree was divided into 1/3 sections based on initial height to place branches in the lower, mid, and upper sections of the crown.

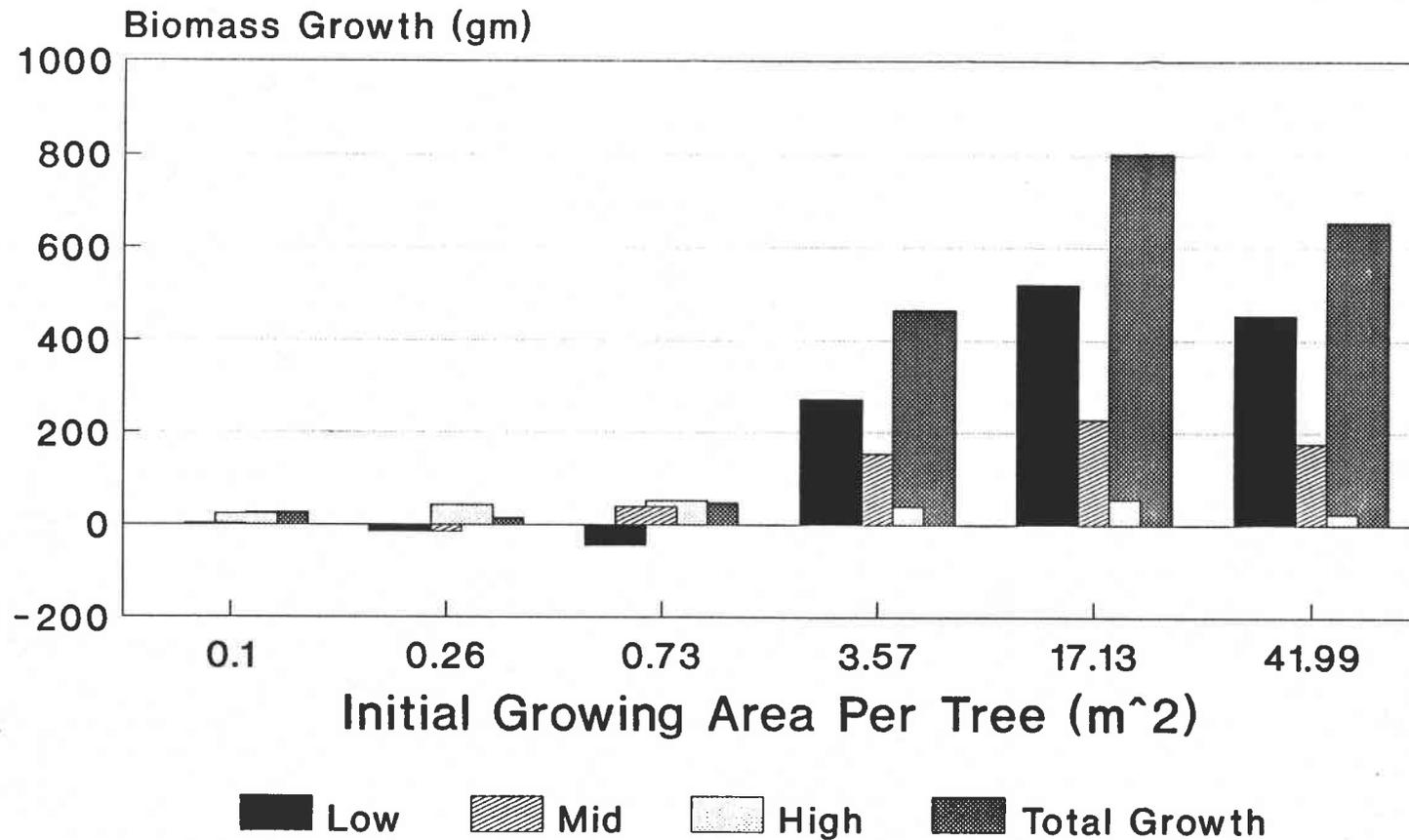


Figure 10.

Figure 11. Mean branch mortality and mean gross branch growth in the lower section of sample trees.

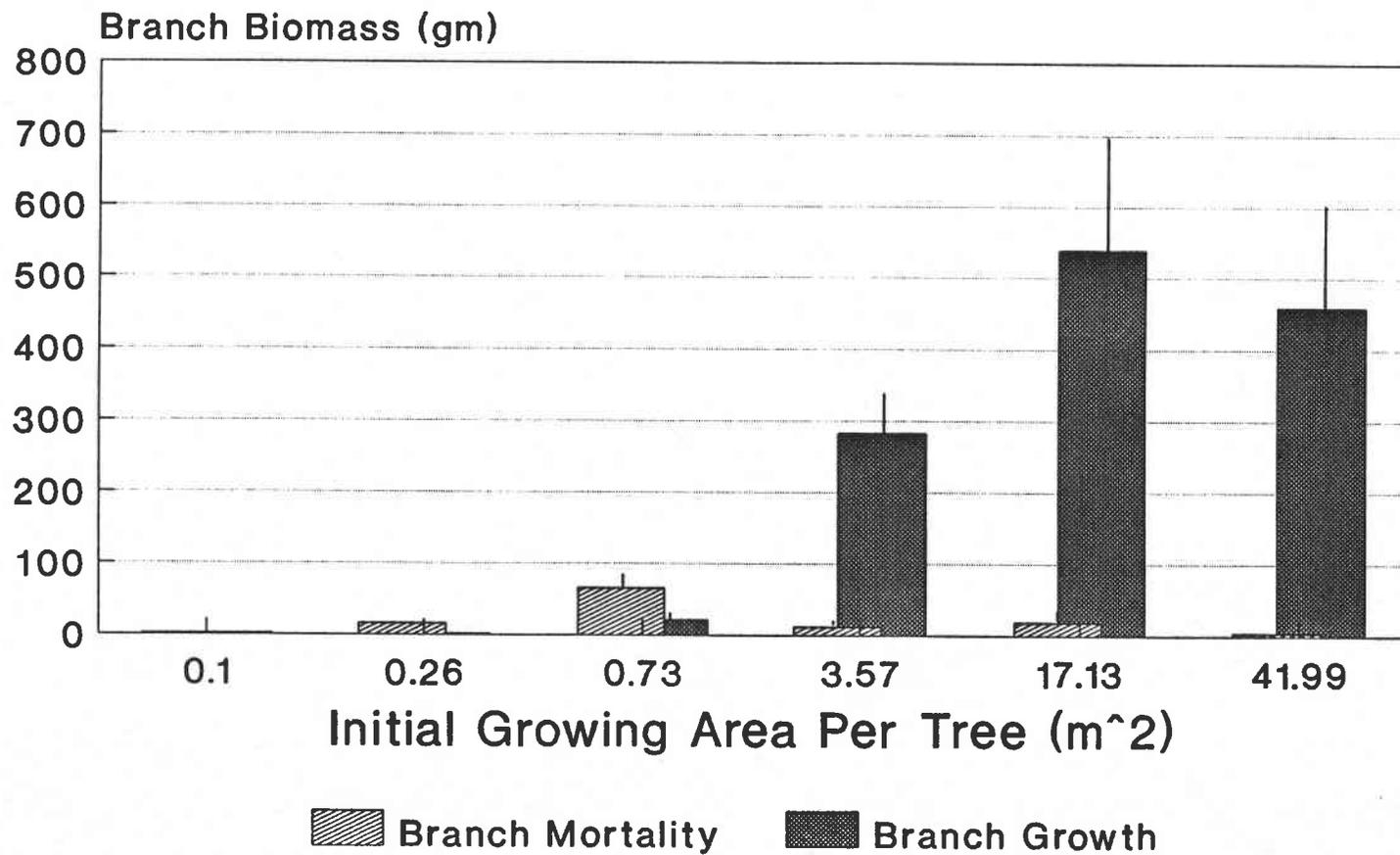


Figure 11.

Figure 12. Mean maximum leaf area of the lower, mid, and upper sections of sample trees. Leaf area is calculated using allometric equations based on basal diameter, length, tree spacing, and crown position of the branch. Maximum leaf area is leaf area attained at the end of the season.

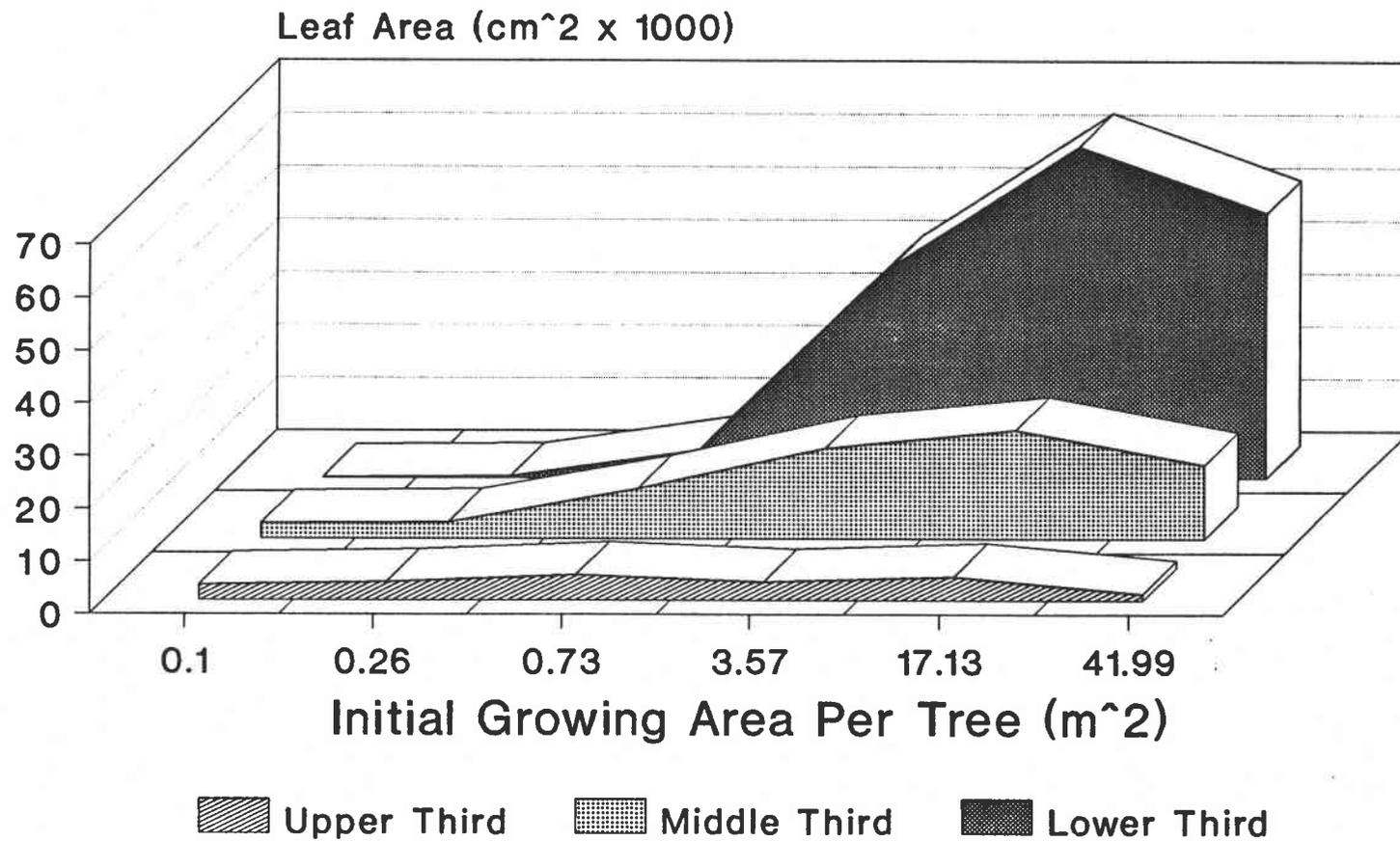


Figure 12.

Figure 13. Mean canopy depth of sample trees. Canopy depth is calculated as the distance from the top of the tree crown to the lowest living branch.

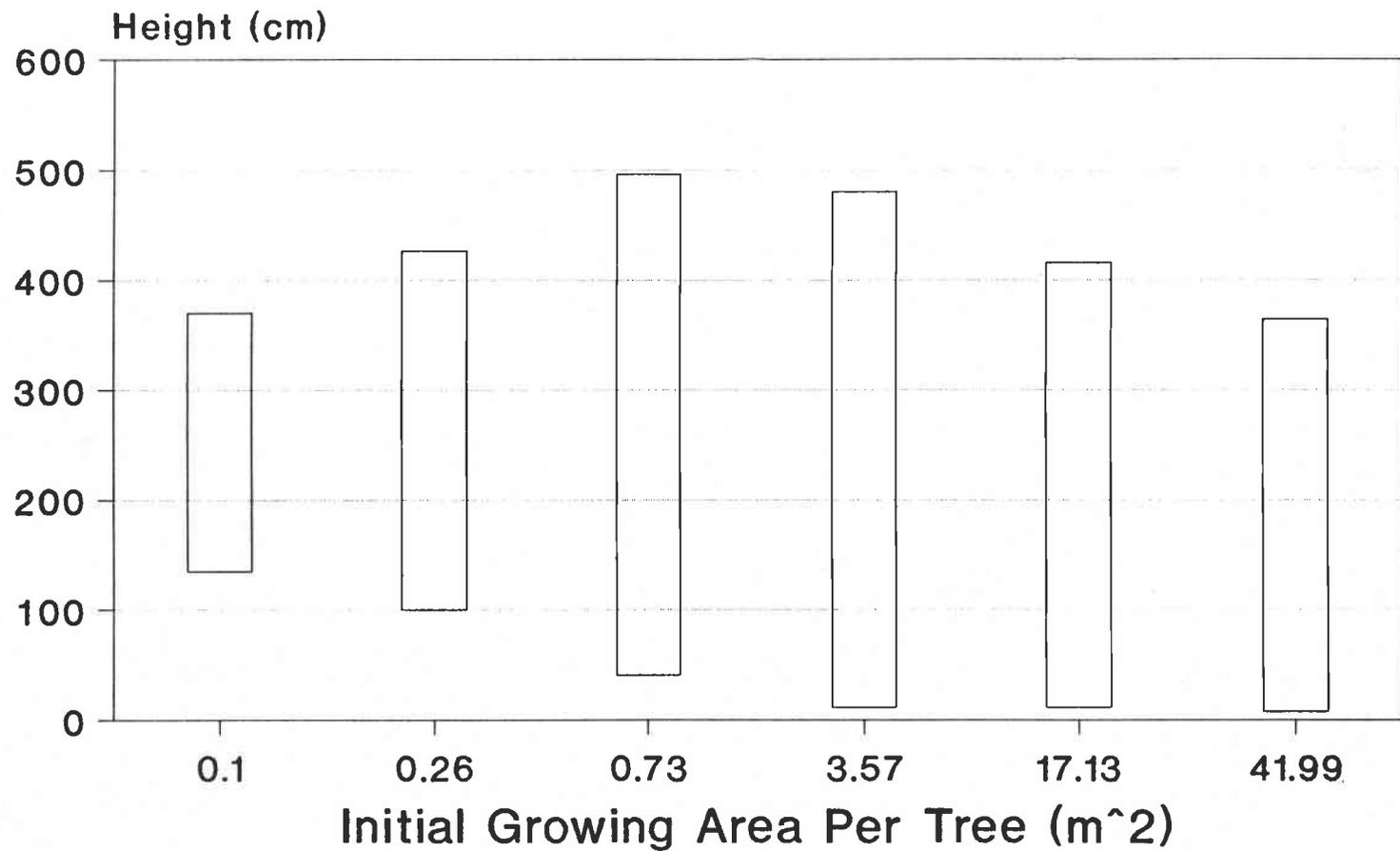


Figure 13.

Figure 14. Mean maximum leaf area index of sample trees. Leaf area index is calculated as the leaf area per tree divided by the initial growing area per tree.

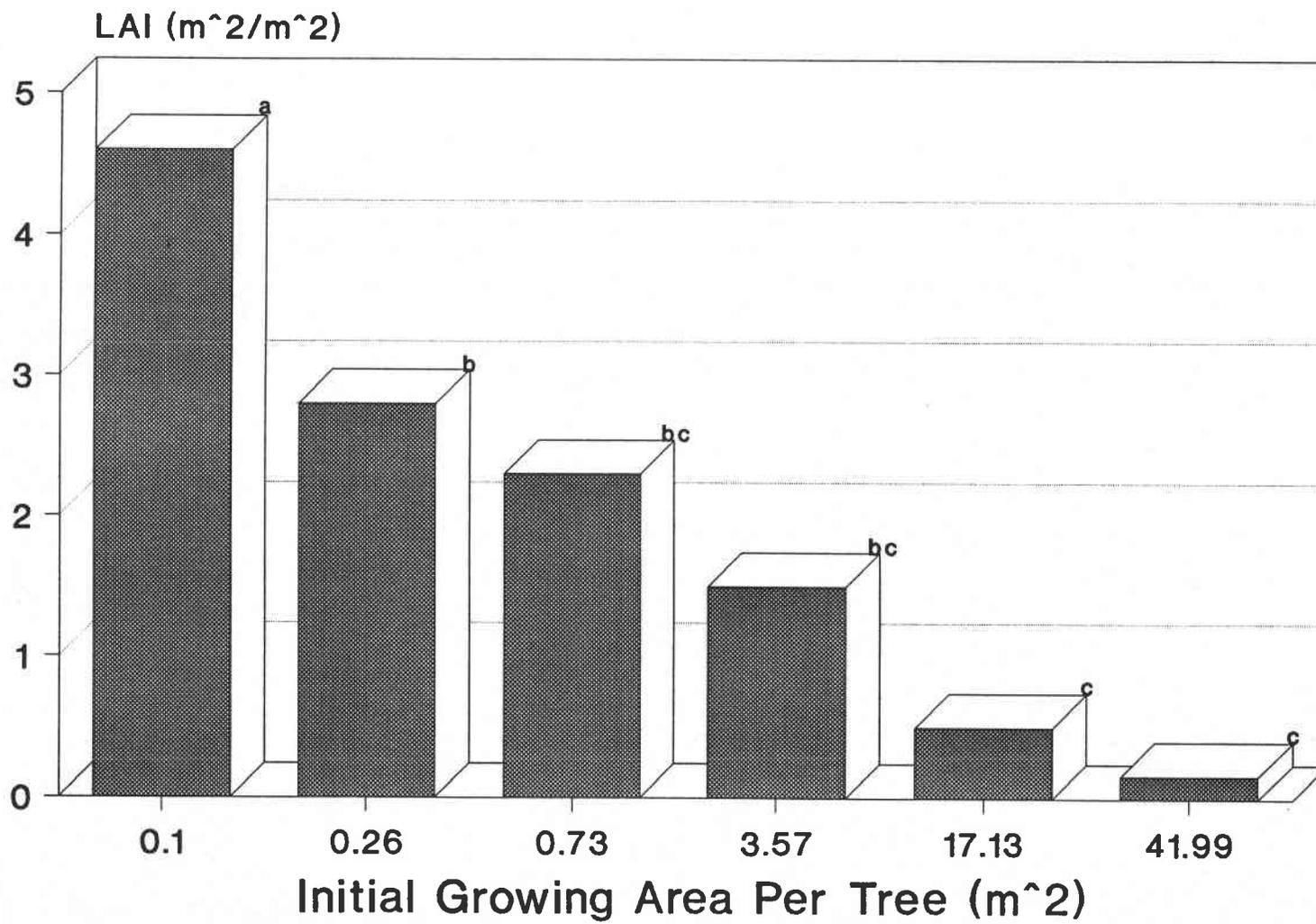


Figure 14.

Figure 15. Mean leaf weight ratio (LWR) and mean net assimilation rate (NAR) of sample trees. LAR is calculated using the end of season leaf area and biomass of each tree. NAR is calculated using the end of season leaf area and seasonal yearly biomass growth of each tree.

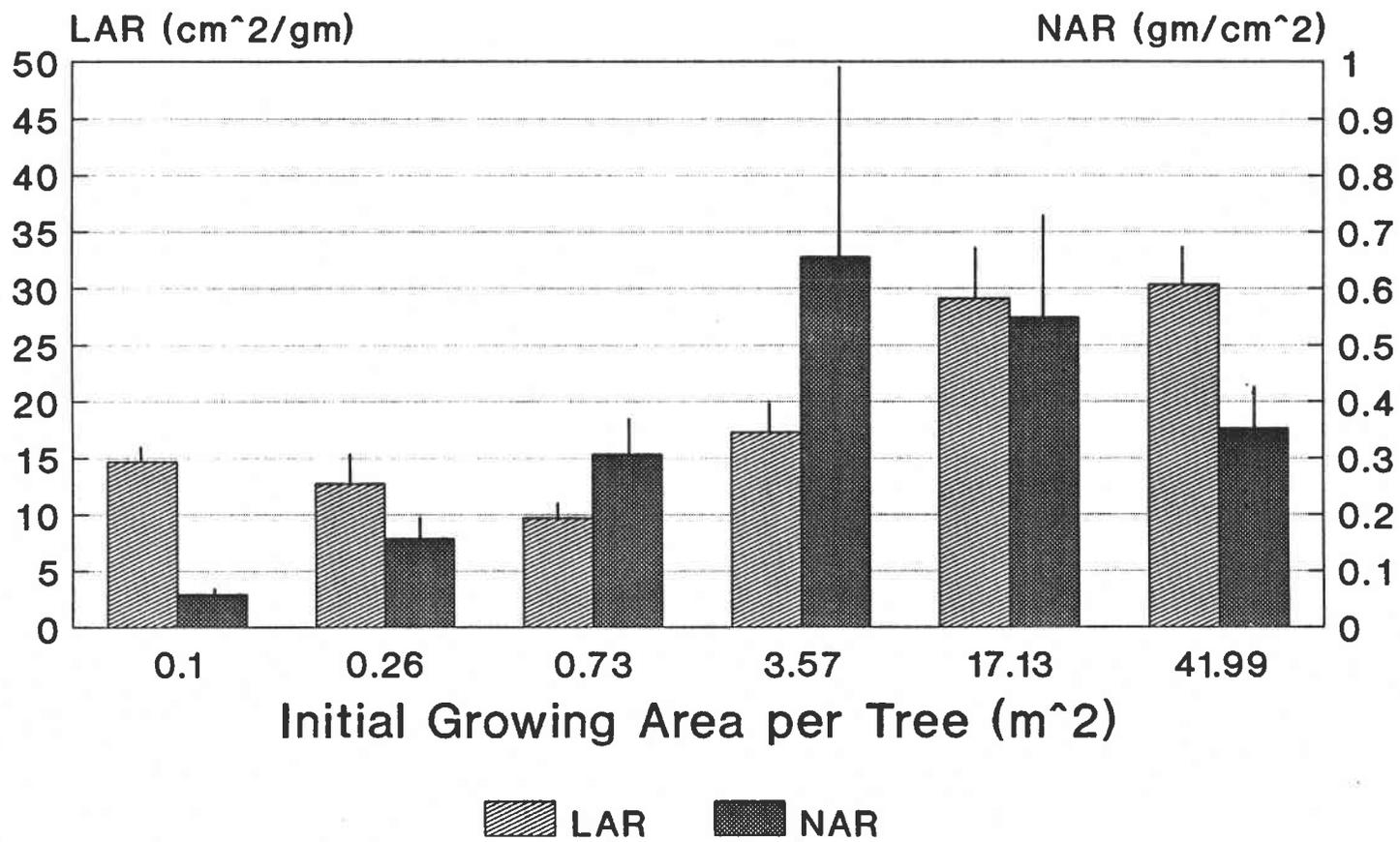


Figure 15.

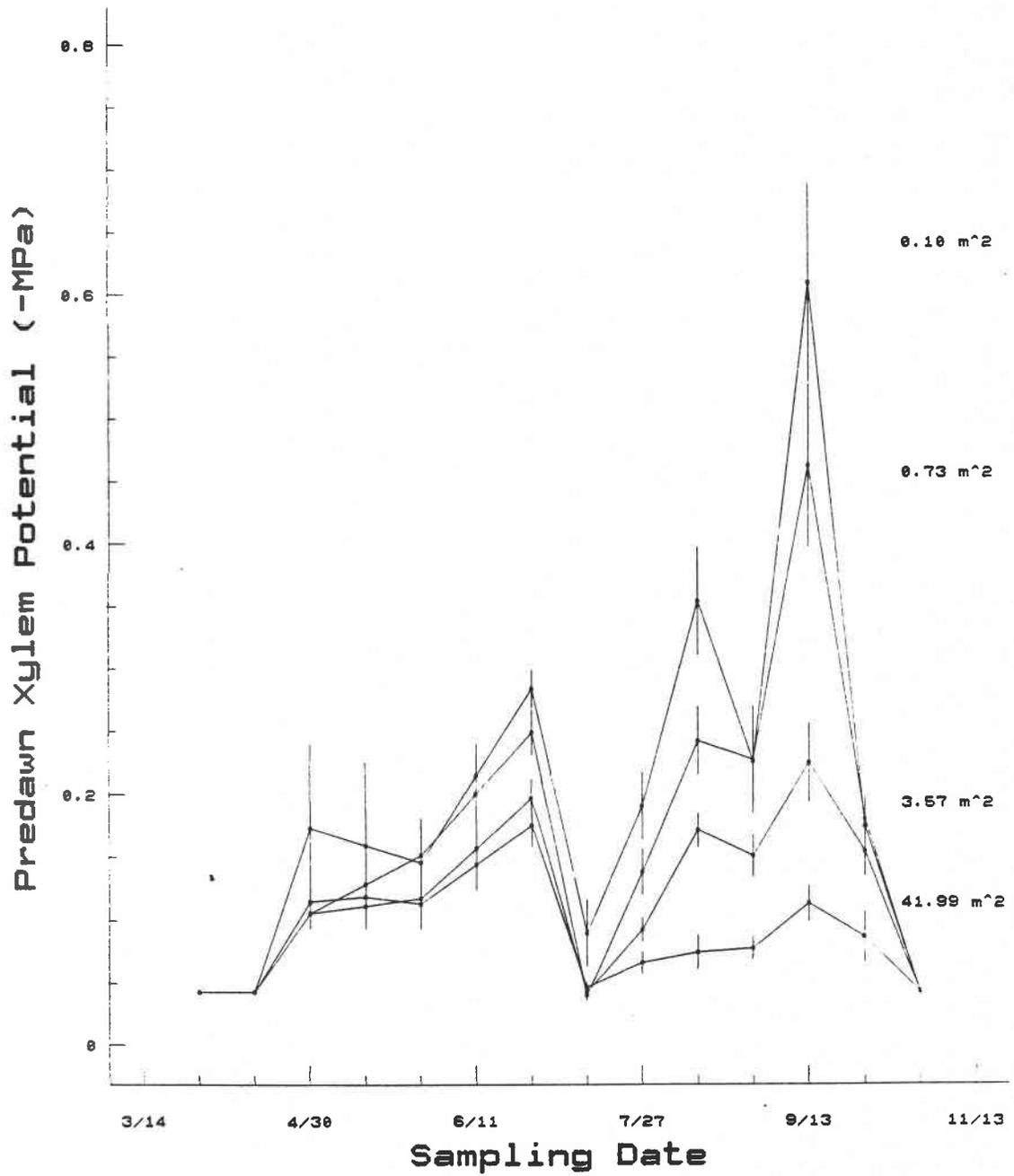


Figure 16. Plot of predawn plant water potential vs. time during the season.

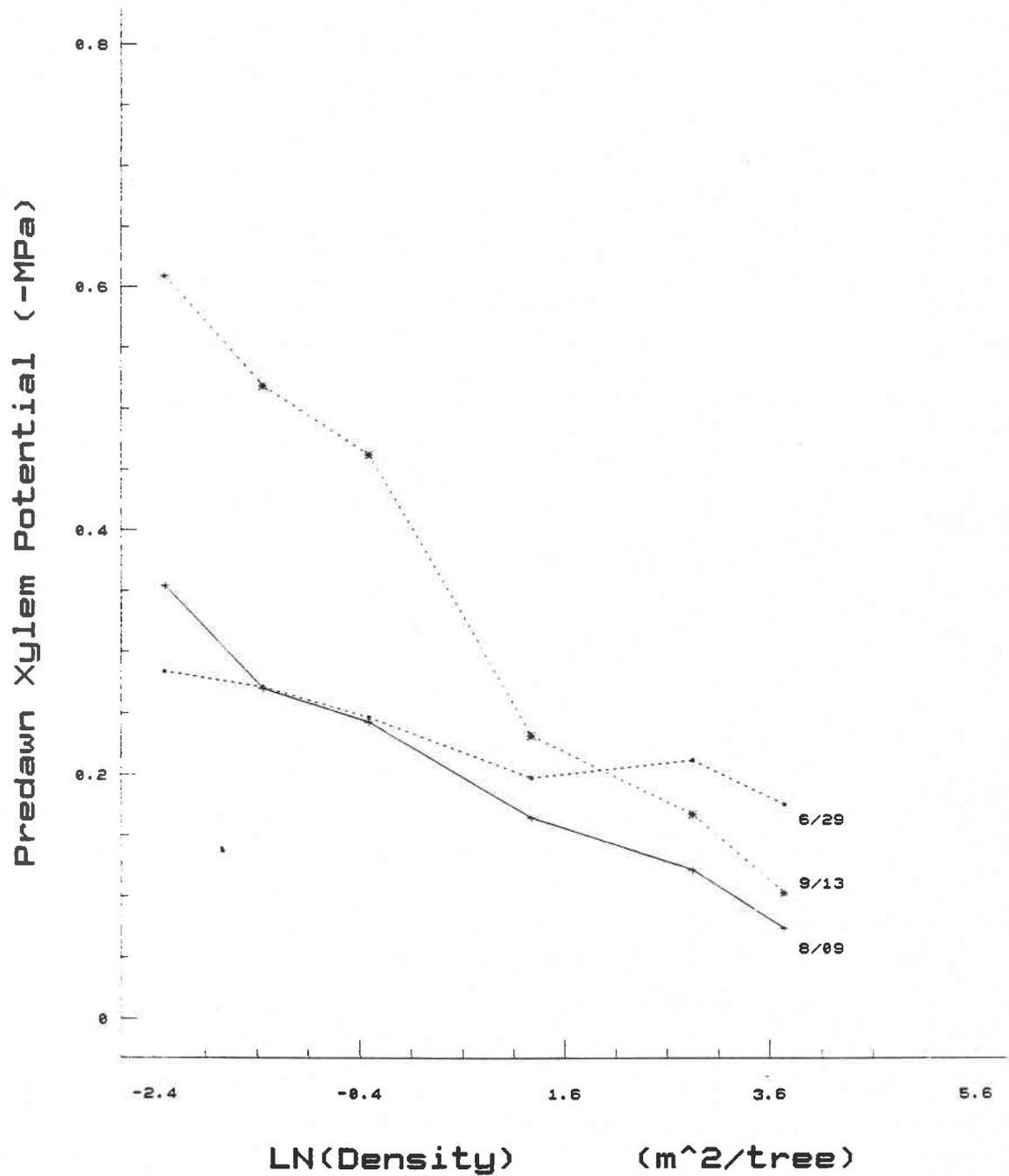


Figure 17. Plot of water potential vs. Ln (Density) on June 29, August 9, and September 13.

Figure 18abc. (a) Plot of aboveground biomass relative growth rate vs. predawn water potential on June 29, 1989. (b) Plot of aboveground biomass relative growth rate vs. predawn water potential on August 9, 1989. (c) Plot of aboveground biomass relative growth rate vs. predawn water potential on September 13. Predawn xylem potential measured using a pressure bomb between 0300-0500.

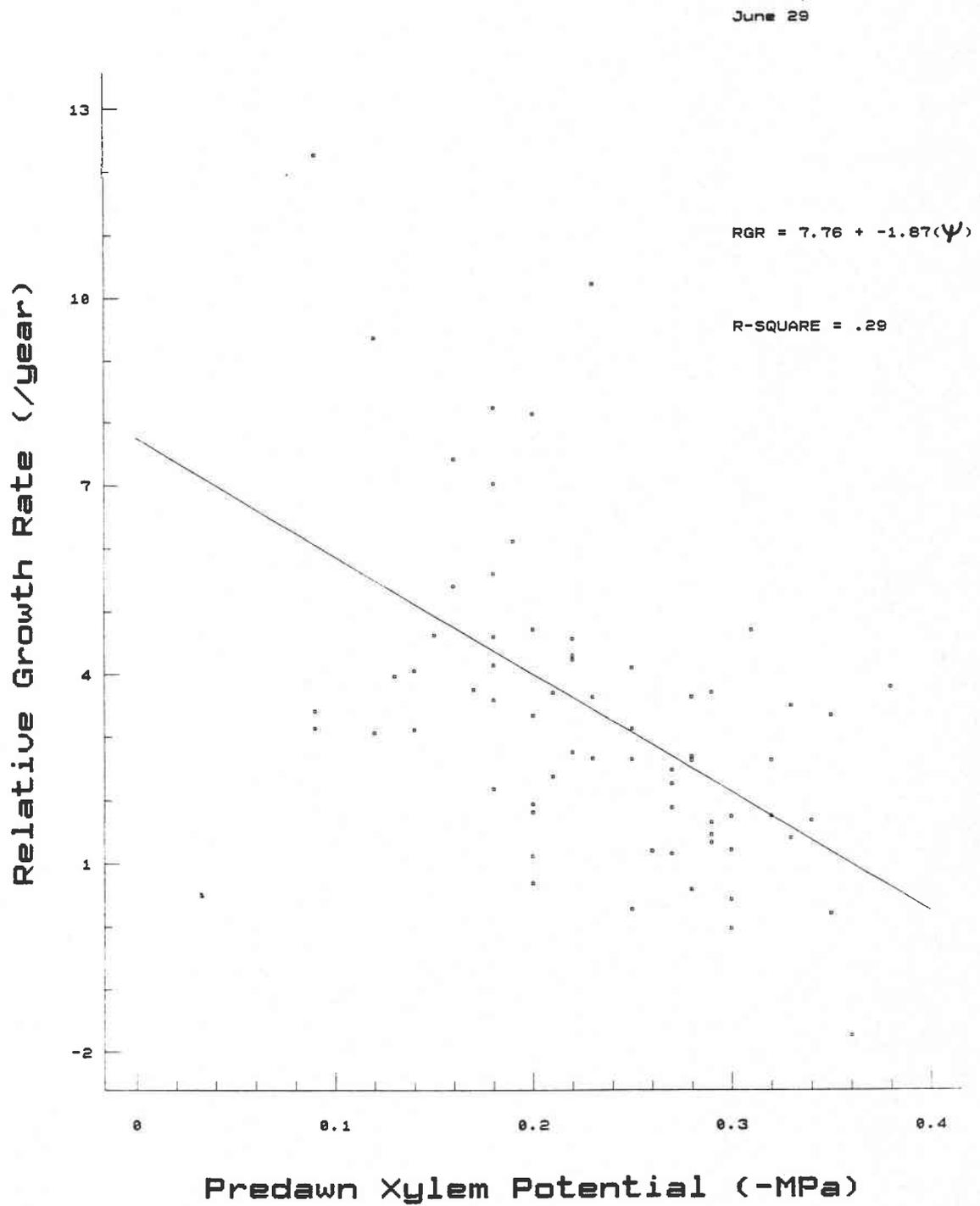


Figure 18a.

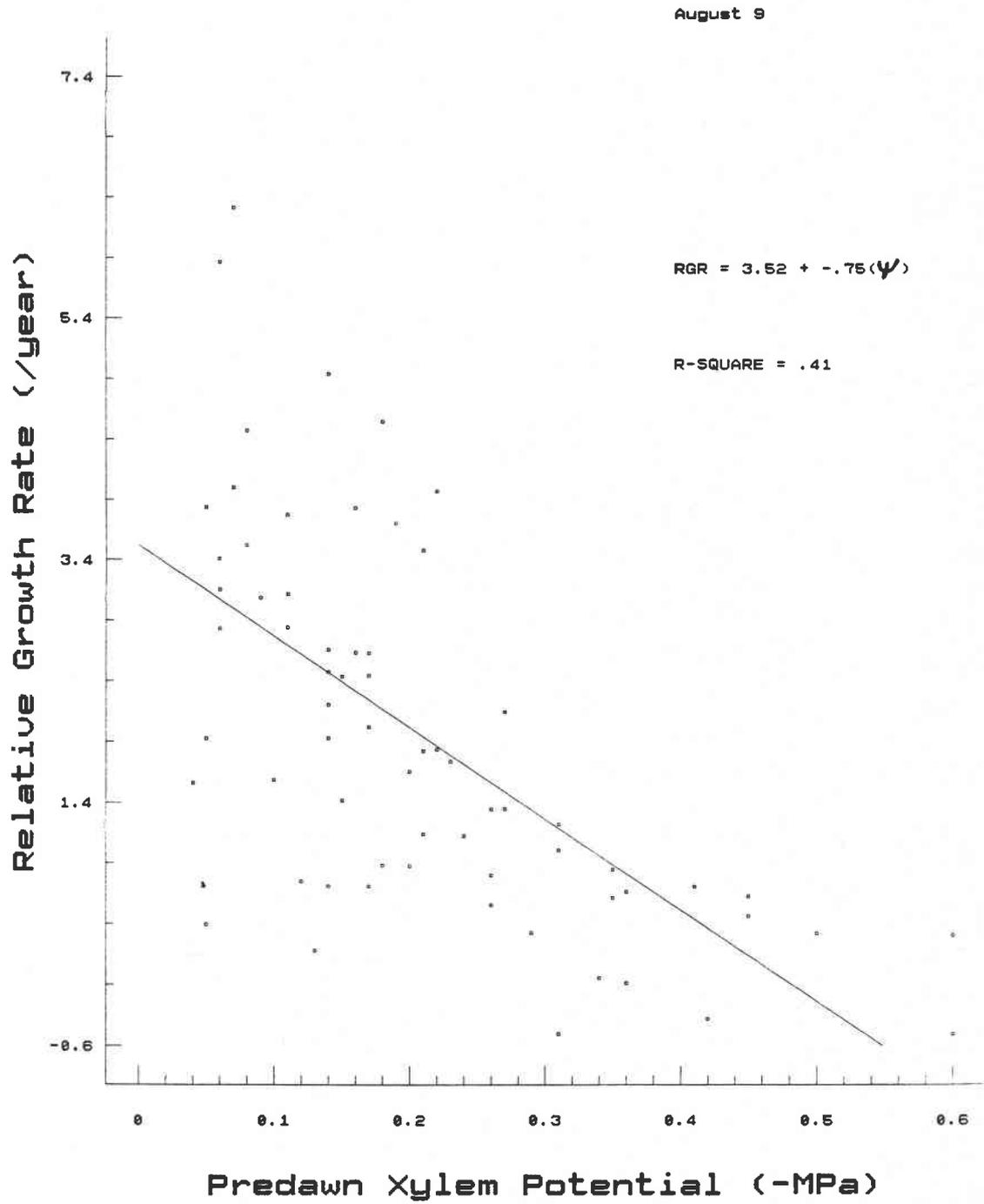


Figure 18b.

September 13

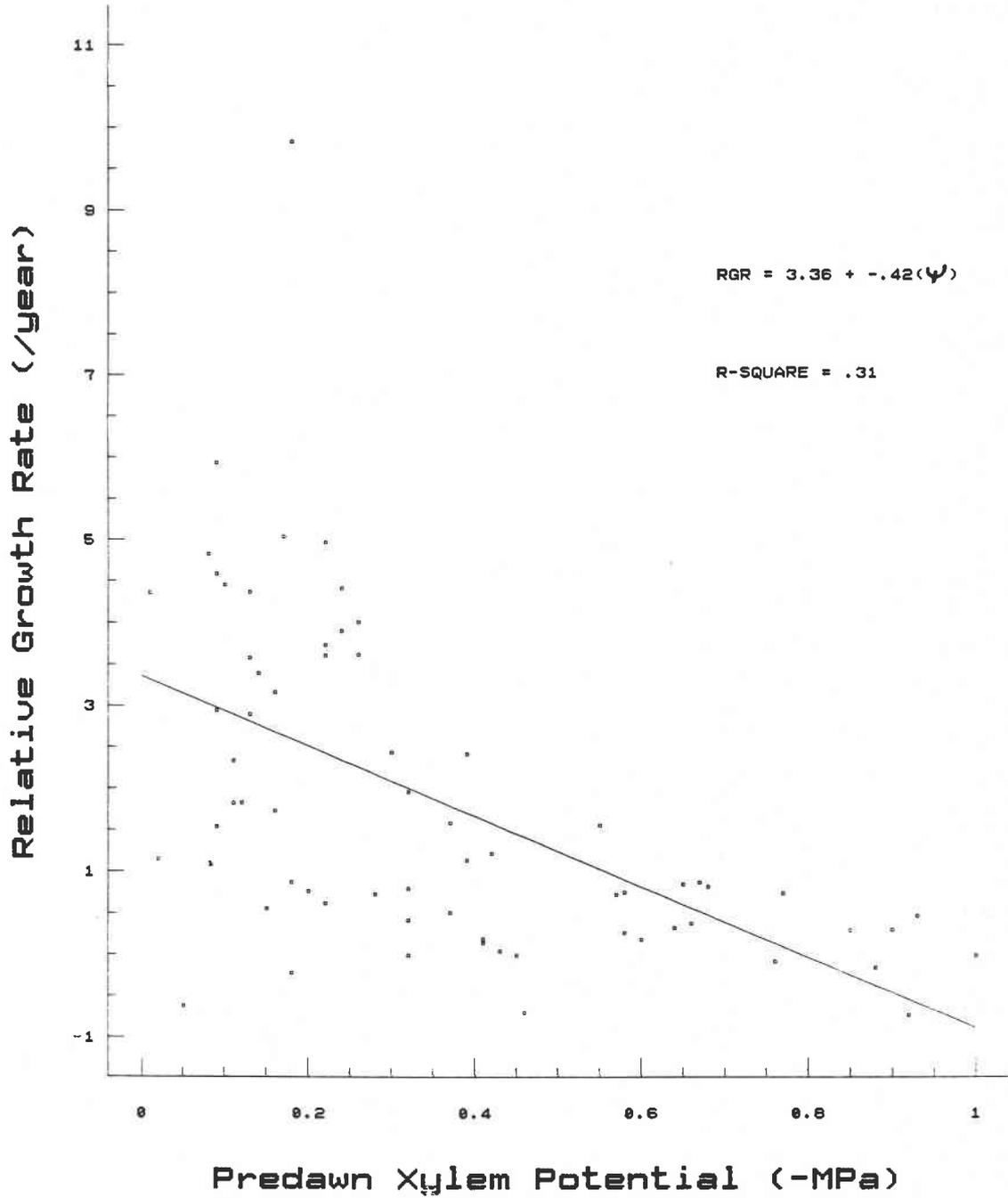


Figure 18c.

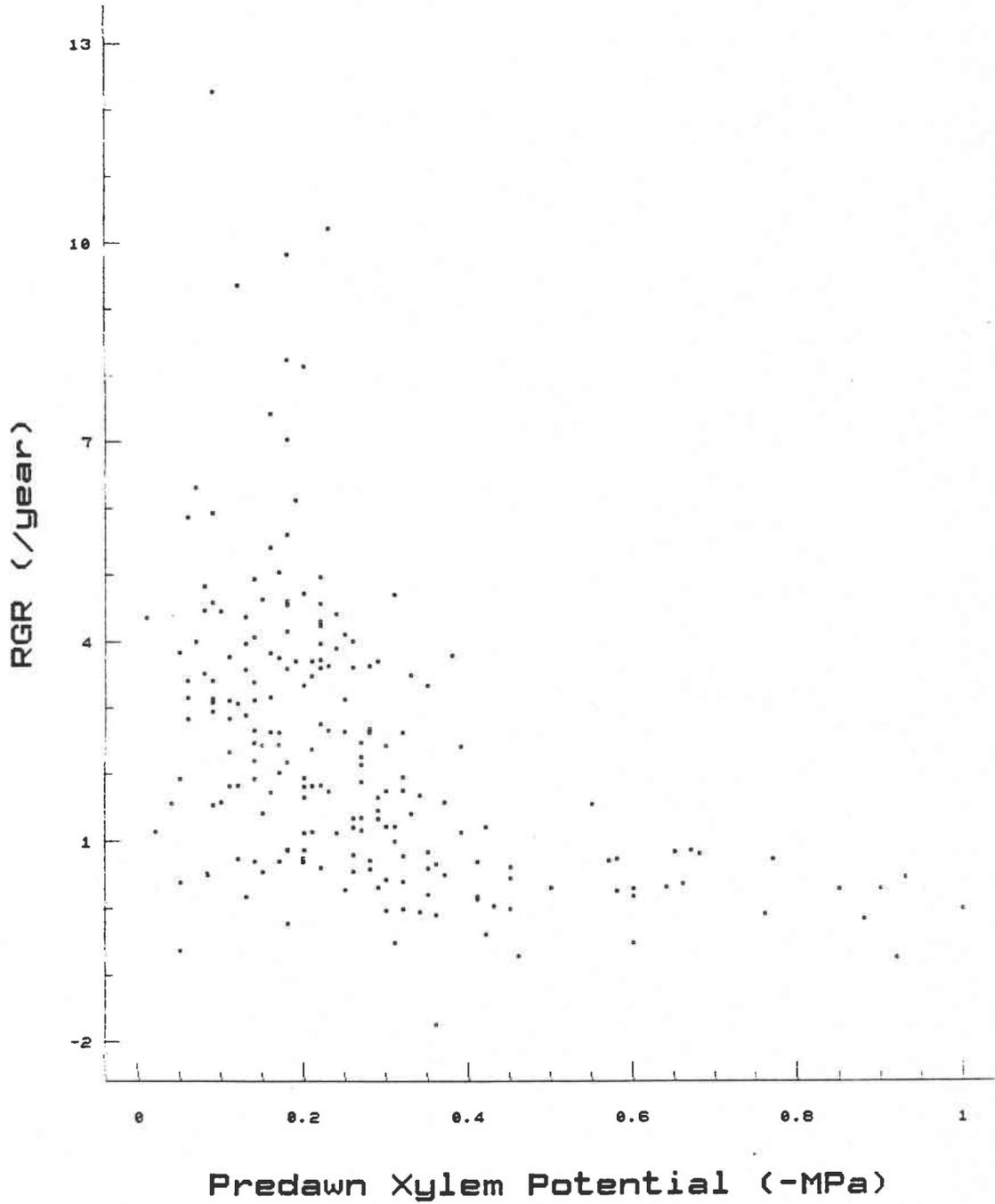


Figure 19. Plot of mean relative growth rate of aboveground biomass vs. predawn plant water potential for June 29, August 9, and September 13.

Figure 20. Height distribution of the 4 trees with the smallest and largest initial heights for 0.10 and 0.26 m² spacings.

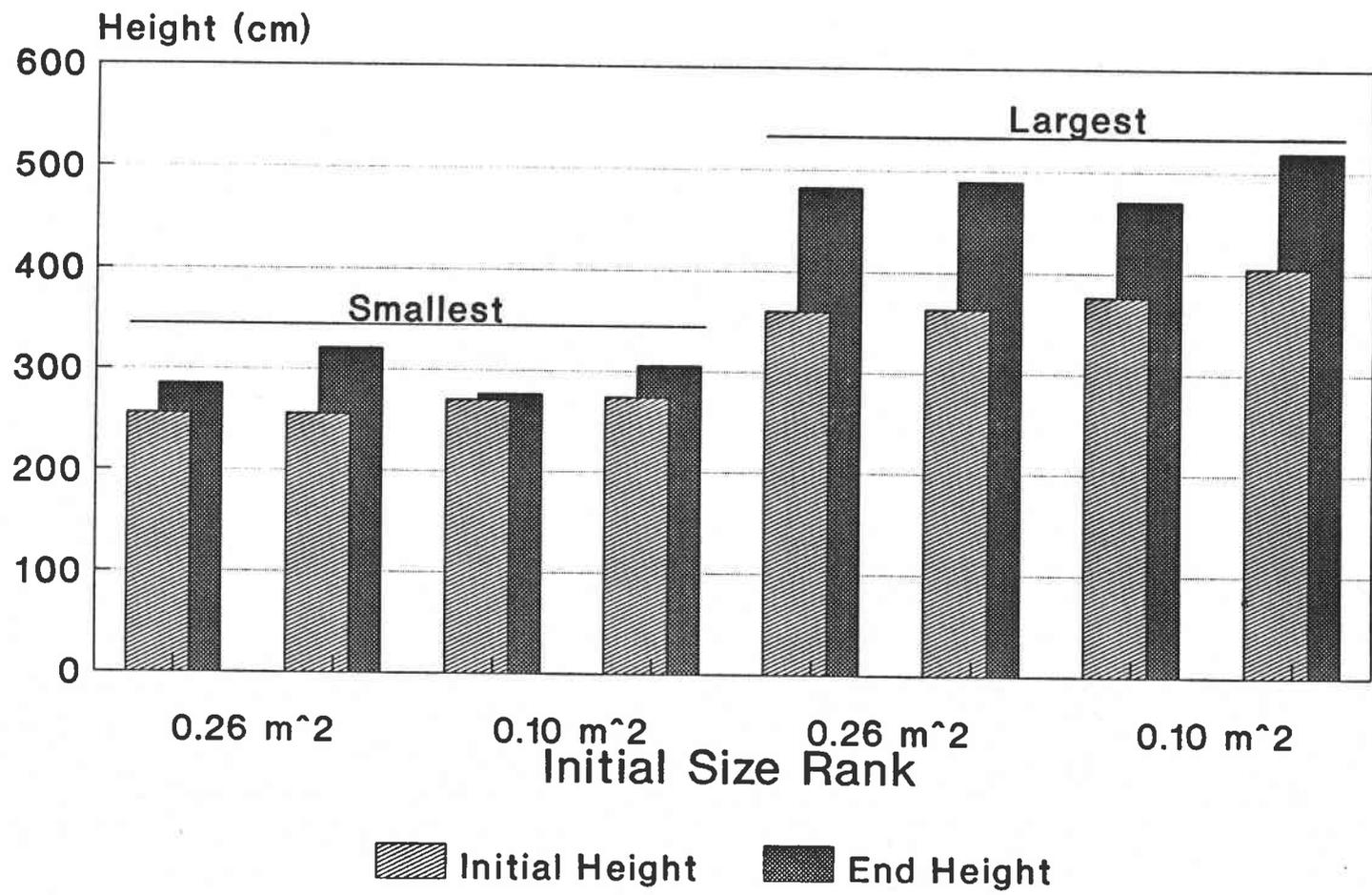


Figure 20.

Figure 21. Aboveground biomass distribution of the 4 trees with the smallest and largest initial heights for 0.10 and 0.26 m² spacings.

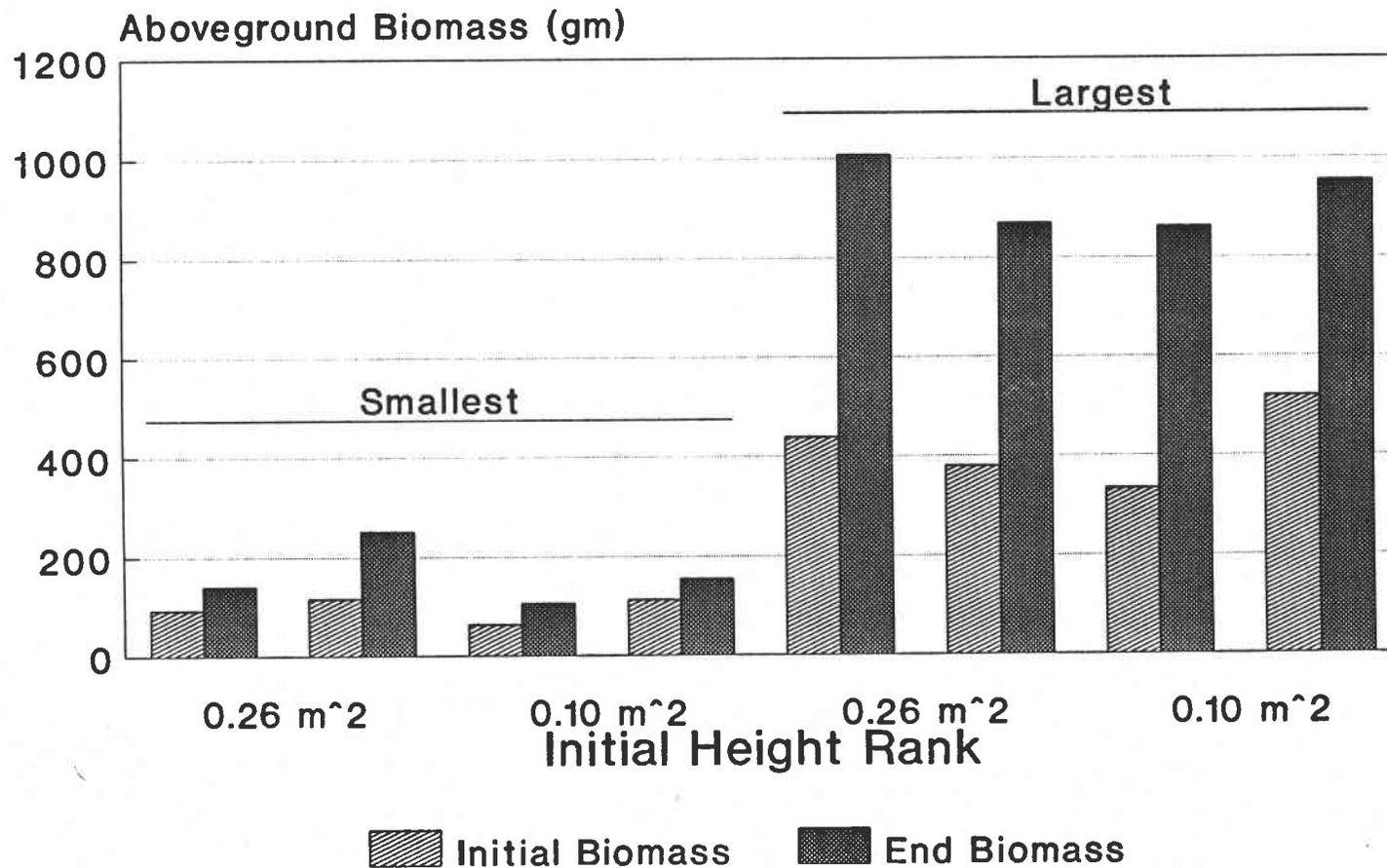


Figure 21.

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APPENDIX

Data values and standard error of sample values for derivation of graphs representing mean values.

Appendix Table 1. Initial basal diameter and basal diameter growth.

Initial Spacing(m ²)	Initial Basal Diam.	Basal Diam. Growth
0.1	22.7(1.1)	3.4(0.7)
0.26	28.0(1.2)	7.0(0.8)
0.73	33.6(2.6)	14.8(2.0)
3.57	36.9(2.8)	28.3(1.7)
17.13	30.8(2.6)	36.4(3.9)
41.99	30.6(3.3)	31.3(3.8)

Appendix Table 2. Mean initial height and mean height growth.

Initial Spacing(m ²)	Initial Height(cm)	Height Growth(cm)
0.1	318.8(12.2)	51.3(9.5)
0.26	325.4(12.0)	101.0(9.3)
0.73	337.5(17.9)	158.8(19.8)
3.57	266.3(14.4)	213.8(14.0)
17.13	224.6(17.9)	191.1(21.1)
41.99	205.0(20.7)	159.1(10.8)

Appendix Table 3. Mean Height/Diameter Ratio.

Initial Spacing(m ²)	Mean Height/Diameter(cm/cm)
0.10	142.9(3.5)
0.26	122.9(3.0)
0.73	106.2(4.9)
3.57	74.4(2.8)
17.13	63.5(3.9)
41.99	61.8(5.0)

Appendix Table 4. Mean Initial Biomass and Mean Biomass Growth.

Initial Spacing(m ²)	Initial Biomass(gm)	Biomass Growth(gm)
0.10	191.6(38.3)	158.0(47.6)
0.26	321.5(38.2)	425.5(63.1)
0.73	566.8(111.8)	1362.5(275.2)
3.57	533.1(136.0)	2552.9(361.8)
17.13	301.7(82.7)	2918.5(698.1)
41.99	270.2(104.6)	2010.8(508.8)

Appendix Table 5. Mean Relative Growth Rate.

Initial Spacing(m ²)	Mean Relative Growth Rate(/year)
0.10	0.73(0.1)
0.26	1.25(0.1)
0.73	2.32(0.3)
3.57	6.66(1.5)
17.13	9.70(1.2)
41.99	11.92(2.8)

Appendix Table 6. Mean initial branch biomass and mean net branch biomass growth.

Initial Spacing(m ²)	Initial Biomass(gm)	Net Biomass Growth(gm)
0.10	60.8(13.0)	25.5(5.2)
0.26	113.8(10.8)	13.4(10.1)
0.73	223.5(32.9)	47.0(38.8)
3.57	313.0(106.2)	464.2(76.0)
17.13	206.4(48.8)	802.5(227.1)
41.99	182.3(57.5)	654.3(138.9)

Appendix Table 7. Mean net aboveground biomass growth and mean net branch growth.

Initial Spacing(m ²)	Tree Growth(gm)	Branch Growth(gm)
0.10	158.0(47.6)	25.5(5.2)
0.26	425.5(63.1)	13.4(10.1)
0.73	1362.5(275.2)	47.0(38.8)
3.57	2552.9(361.8)	464.2(75.9)
17.13	2918.5(698.1)	802.5(227.1)
41.99	2010.8(508.8)	654.3(138.9)

Appendix Table 8. Mean branch mortality and mean gross branch growth

Initial Spacing(m ²)	Branch Mortality(gm)	Branch Growth(gm)
0.10	13.3(4.4)	25.5(5.2)
0.26	52.4(10.1)	13.4(10.1)
0.73	88.7(20.1)	47.0(38.8)
3.57	13.2(4.9)	464.2(75.9)
17.13	18.5(11.2)	802.5(227.1)
41.99	11.1(8.5)	654.3(138.9)

Appendix Table 9. Mean net branch biomass growth of the lower, mid, and upper sections of sample tree crowns.

Initial Spacing(m ²)	Low(gm)	Mid(gm)	Upper(gm)	Total(gm)
0.10	-0.1	2.5	23.1	25.5
0.26	-14.9	-15.2	43.5	13.4
0.73	-45.1	39.3	52.8	47.0
3.57	271.1	153.5	39.6	464.2
17.13	519.7	228.1	54.8	802.4
41.99	454.1	176.8	23.4	654.2

Appendix Table 10. Mean branch mortality and mean gross branch growth in the lower section of sample trees.

Initial Spacing(m ²)	Branch Mortality(gm)	Branch Growth(gm)
0.10	0.8(0.8)	0.7(0.6)
0.26	15.8(4.0)	0.9(0.8)
0.73	65.9(16.2)	20.8(6.6)
3.57	11.8(4.5)	282.9(54.8)
17.13	18.3(11.2)	537.9(159.2)
41.99	3.9(2.4)	458.0(141.1)

Appendix Table 11. Mean maximum leaf area of the lower, mid, and upper section of sample tree crowns.

Initial Spacing(m ²)	Low(cm ²)	Mid(cm ²)	Upper(cm ²)
0.10	117	2943	2913
0.26	335	3237	3476
0.73	5331	9579	4802
3.57	39749	17279	3509
17.13	62890	20785	4545
41.99	50355	14122	1276

Appendix Table 12. Mean canopy depth.

Initial Spacing(m ²)	Crown depth(cm)
0.10	135(19)
0.26	100(22)
0.73	41(11)
3.57	12(2)
17.13	11(2)
41.99	7(2)

Appendix Table 13. Mean maximum leaf area index (LAI).

Initial Spacing(m ²)	LAI(m ² /m ²)
0.10	4.6
0.26	2.8
0.73	2.3
3.57	1.5
17.13	0.5
41.99	0.2
