

THE EFFECTS OF PRECOMMERCIAL THINNING ON
WATER RELATIONS AND WOOD QUALITY
OF LOBLOLLY PINE

By

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Bachelor of Science

Washington State University

Pullman, Washington

1983

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
Master of Science
July, 1986

Thesis
1986
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PREFACE

This thesis has been written in the form of two separate journal manuscripts, the first article examines the impacts of precommercial thinning on the internal water relations of loblolly pine, the second article discusses the effects of thinning on wood properties of loblolly pine. The articles have been prepared in the format prescribed by the Canadian Journal of Forest Research. Because each article stands alone as a separate manuscript, some duplication was necessary in the Materials and Methods sections of the two articles. I beg the indulgence of my readers for the unavoidable redundancy.

This thesis project, indeed my entire graduate program at Oklahoma State University, has been a rich and rewarding experience. Without a doubt it has been the people I have been associated with at OSU that have made this a very special part of my life. I wish to express my thanks to the following people who have helped me along the way:

Dr. Thomas Hennessey for providing guidance through my study and for providing me with an interesting and challenging thesis project.

The additional members of my committee, Dr. Ron McNew and Dr. Charles Tauer for providing their advice and thoughtful suggestions on my thesis.

Mr. Wayne Stogsdill, Mr. Mickey Rachal, and Mr. Ed Lorenzi, whose assistance made the fieldwork possible, and whose collective sense of humor made it almost enjoyable.

Mr. Randal Holeman for sharing his computer expertise with me.

Dr. Phillip Dougherty for his imagination, inspiration, and insightful comments and questions.

Weyerhaeuser Company Mid-South Research for their financial and material support, without which this project would not have been possible.

Finally, I must express a special word of thanks to my family, especially my parents, Roland and Margaretha Cregg, and my sister, Dianne Neuerburg, for giving me their love, support, and confidence.

TABLE OF CONTENTS

	Page
PART I	
EFFECTS OF PRECOMMERCIAL THINNING ON WATER RELATIONS OF LOBLOLLY PINE (<u>PINUS TAEDA L.</u>)	1
Abstract	2
Introduction	3
Materials and Methods	6
Results and Discussion	13
Conclusions	32
Bibliography	33
PART II	
EFFECTS OF PRECOMMERCIAL THINNING ON WOOD QUALITY OF LOBLOLLY PINE (<u>PINUS TAEDA L.</u>)	51
Abstract	52
Introduction	54
Materials and Methods	57
Results and Discussion	65
Conclusions	79
Bibliography	81

LIST OF TABLES

Table		Page
PART I		
I.	Stand Characteristics Following Thinning	7
II.	Significant Regression Variables for PXP = SWP and EVAP	16
III.	Significant Regression Variables for XPP = SWP and VPD	18
IV.	Significant Regression Variables for Conductance and Transpiration = SWP, VPD and Q (Data segregated by Q)	23
V.	Significant Regression Variables for Conductance and Transpiration = SWP, VPD and Q (Data segregated by VPD)	24
VI.	Significant Regression Variables for Conductance and Transpiration = SWP, VPD and Q (Data segregated by SWP)	26
VII.	Eagletown Leaf Area Index	27
VIII.	Diameter and Per Tree Basal Area Growth Following Thinning	29
IX.	Diameter and Per Tree Basal Area Growth Following Thinning (Trees > 15 cm dbh)	30

Table	Page
X. Total Basal Area Growth After Thinning	31

PART II

I. Stand Characteristics Following Thinning	59
II. Diameter and Per Tree Basal Area Growth Following Thinning	68
III. Mean Latewood Transition Dates After Thinning ..	69
IV. Mean Latewood Percentage Following Thinning	73
V. Mean Specific Gravity Following Thinning	76
VI. 1985 Mean Tracheid Cell Wall Thickness and Radial Tracheid Diameter	78

LIST OF FIGURES

Figure	Page
PART I	
1. Effect of Basal Area on Soil Moisture Availability	36
2. On Site Precipitation, 1984 and 1985	37
3. Monthly Evaporation and Precipitation from Broken Bow Dam, 27 km North of Study Site	38
4. Mean Predawn Xylem Pressure Potential, 1984 and 1985	39
5. Seasonal Trend of Soil Water Potential at the 15 cm depth, 1984 and 1985	40
6. Seasonal Trend of Soil Water Potential at the 45 cm depth, 1984 and 1985	41
7. Predawn Xylem Pressure Potential Versus Soil Water Potential at 15 and 45 cm depths	42
8. Mean Daily Conductance, 1984 and 1985	43
9. Mean Daily Transpiration Rate, 1984 and 1985	44
10. Diurnal Trends of Q , Transpiration, Conductance, VPD, and XPP, August 16, 1984	45
11. Diurnal Trends of Q , Transpiration, Conductance, VPD, and XPP, August 14, 1985	46
12. Stomatal Conductance Versus Q	47
13. Stomatal Conductance Versus VPD	48
14. Stomatal Conductance Versus XPP	49
15. Cumulative Diameter Growth, 1984 and 1985	50

PART II

1.	On Site Precipitation , 1984 and 1985	84
2.	Monthly Evaporation and Precipitation from Broken Bow Dam, 27 km North of Study Site	85
3.	Seasonal Trend of Soil Water Potential at 15 cm Depth, 1984 and 1985	86
4.	Seasonal Trend of Soil Water Potential at 45 cm Depth, 1984 and 1985	87
5.	Mean Daily Predawn Xylem Pressure Potential, 1984 and 1985	88
6.	Daily Diameter Growth Rate, 1984 and 1985	89
7.	Cumulative Percentage of Trees Past Latewood Transition Date, 1984 and 1985	90
8.	Cumulative Diameter Growth for All Treatments, 1984 and 1985	91

PART I

THE EFFECTS OF PRECOMMERCIAL THINNING ON
WATER RELATIONS OF LOBLOLLY PINE

(PINUS TAEDA L.)

ABSTRACT

A stand of loblolly pine (Pinus taeda L.) planted in 1975 in southeastern Oklahoma was thinned in 1984 to three target basal area levels: 5.8 m²ha⁻¹, 11.5 m²ha⁻¹, and 23 m²ha⁻¹. Xylem pressure potential, soil moisture, stomatal conductance, transpiration, and growth were monitored over two growing seasons following thinning. Predawn xylem pressure potential (PXP) did not vary significantly with thinning. Soil water potential (SWP) and PXP decreased significantly in 1984 relative to 1985. Conductance and transpiration per unit leaf area increased on the thinned trees as compared to unthinned controls in 1984; however, the differences were not statistically significant. Conductance and transpiration were greatest when soil moisture was relatively abundant. Transpiration was related to vapor pressure deficit (VPD), conductance, and soil water potential (SWP). Conductance at low VPD was related to SWP, VPD, and light intensity. At high VPD, conductance was primarily a function of SWP. Diameter growth and per tree basal area growth increased significantly both years after thinning. Rapid understory invasion of the site suggests that growth and water relations response from thinning may be increased by concurrently controlling competition.

INTRODUCTION

Loblolly pine (Pinus taeda L.) is generally considered to be the most important commercial forest tree species in the southern United States (Carter et al. 1984, Brendor et al. 1981). As the migration of the forest products industry to the South continues, forest managers are examining the feasibility of expanding the range of loblolly pine (Woods, 1984), as well as increasing site productivity through genetic selection and silvicultural treatments. The Weyerhaeuser company, for example, has recommended planting fast-growing North Carolina seed sources on 60 percent of its approximately 770,000 hectare holdings in Arkansas and southeastern Oklahoma (Lambeth et al. 1984). One possible management tool for reducing the risk from such off-site plantings is stocking control, whereby soil moisture is budgeted to a fewer number of crop trees.

Several studies have shown that soil moisture availability throughout the growing season is greater on sites with low basal area as compared to high basal area sites (Ray, 1963, Moyle and Zahner, 1954, Zahner and Whitmore, 1960). Zahner and Whitmore (1960) studied a nine year old pine plantation near Crossett, Arkansas that had been thinned to 2.3 m^2ha^{-1} , 7.1 m^2ha^{-1} , and left at 15 m^2ha^{-1} . The lowest stocking level consistently had more

available soil moisture than the intermediate or unthinned treatments (figure 1.).

Although the effects of thinning on soil moisture availability have been well documented, few studies have directly investigated the impact of stocking reduction on internal plant moisture stress and the subsequent changes in stomatal conductance and transpiration. From these investigations it is difficult to generalize about thinning impacts on forest tree water relations. Sucoff and Hong (1974) found that thinning an 18 year-old red pine (Pinus resinosa Ait.) plantation from $36.7 \text{ m}^2\text{ha}^{-1}$ to $27.5 \text{ m}^2\text{ha}^{-1}$ tended to increase needle water potential. However, they noted that the difference was only significant on four out of ten measurement days. Whitehead et al. (1984), in contrast, found thinning a 40 year old stand of Scots pine (Pinus sylvestris L.) decreased needle water potential by as much as 0.3 MPa at midday in August. Whitehead et al. (1984) also demonstrated thinning increased individual tree transpiration rate and leaf area.

Plant water relations play a large role in plant productivity and growth (Kozlowski 1979); therefore, understanding the opportunity for influencing the tree moisture stress through silvicultural practice is of great importance. The objectives of the present study are the following: 1) to determine the impact of precommercially thinning a young loblolly pine plantation on internal tree moisture stress (xylem pressure potential), stomatal

conductance, and transpiration, and 2) to determine the relationships between diameter growth, internal moisture stress, stomatal function, and environmental conditions.

MATERIALS AND METHODS

Site Description

The study was located in southeastern Oklahoma approximately 8 km south of Eagletown, Oklahoma (legal description: Section 9, T7S, R26E, Indian Meridian). The land containing the study site is owned by the Weyerhaeuser Company. The soils on the site are of the Cohab series of the Guyton-Ochlocknee association (USDA SCS, 1974), which is characterized by deep alluvial formed soils and slopes of less than one percent. Soil textures on the site ranged from loams to silty clay loams. The year-round climate of the area is generally mild with hot, often droughty summers. The mean annual temperature of the region is 17° C. and the average annual rainfall is 135 cm. The average length of the growing season (the period between the average date of the last freezing temperature in the Spring and the first 0° C. reading in the Fall) is 240 days (Oklahoma Water Resources Board, 1984).

Following harvest of a pine-hardwood stand in 1975, the site was prescribed burned and double-bedded. The area was subsequently planted with loblolly pine of local origin at a stocking density of approximately 2,500 trees per hectare.

In March 1984, a 1.3 ha area of the stand was selected for study and inventoried. At that time, canopy closure was complete and the overall vigor of the stand was fair to good, although a few trees were infected with Southern fusiform rust (Cronatium fusiforme). The mean basal area of the study portion of the stand was 25.9 m²ha⁻¹.

Treatments

After the inventory, nine 0.1 ha plots were thinned to three target basal areas: BA 25 (25 ft²ac⁻¹, 5.8 m²ha⁻¹), BA 50 (50 ft²ac⁻¹, 11.5 m²ha⁻¹) and BA 100 (unthinned, 100 ft²ac⁻¹, 23 m²ha⁻¹). The actual treatment characteristics following thinning are presented in table I. The plots were arranged in a completely randomized block design. Due to suspected variation in soil texture, the blocks were arranged parallel to the Mountain Fork river, approximately 50 meters east of the study site.

TABLE I
STAND CHARACTERISTICS AFTER THINNING

Treatment	Basal area	Stocking	Mean dbh
	m ² ha ⁻¹	Trees ha ⁻¹	cm
BA25	7.49	379	15.72
BA50	12.70	629	15.09
BA100	33.57	2,025	11.90

Environment

Monthly summaries of weather data for the region were compiled from National Oceanic and Atmospheric Administration records from the U.S. Army Corps of Engineers weather station at Broken Bow Dam, approximately 27 km from the study area. Rainfall was measured on the site with two standard rain gauges.

Soil moisture on the site was monitored using the neutron scattering method (Long and French, 1967). Three 3.8 cm diameter steel access tubes were installed to depth of 1.22 m on each measurement plot. The general location of the tubes within a plot was selected at random; however, the tubes were installed down in the beds and 1.5 m from the closest tree to reduce tube to tube variation in moisture content readings. Volumetric soil moisture content was measured every two weeks from May through November in 1984 and 1985 with depth moisture gauge (Troxler 3300 series). Soil moisture release curves derived from soil samples collected on the site were used to convert volumetric soil moisture content to soil water potential (SWP).

Vapor pressure deficit (VPD) was calculated from relative humidity and air temperature values according the formula presented by Lowe (1976).

Growth

A 0.04 ha measurement plot was located inside each 0.1 ha treatment plot to reduce edge effects. Diameters were measured at breast height on all trees inside the measurement plots at the beginning of the study and at the end of the 1984 and 1985 growing seasons. In addition, dendrometer bands were placed on ten trees selected at random on each measurement plot (Liming, 1957). Changes in stem circumference were measured by reading the vernier scale on the bands at two week intervals in the summer of 1984 and at weekly intervals in the summer of 1985. The circumference measurements were subsequently converted to diameter values for reporting.

Water Relations

On each measurement plot, two of the ten dendrometer-banded trees were selected for the water relations phase of the study. The trees chosen were judged to be representative of the plot trees in diameter, height, crown development, and form. A wooden scaffold was erected on each plot between the two selected trees to access live branches for data collection. The scaffolds were originally 4 m in height and were raised to 7 m in the Spring of 1985.

Xylem pressure potential (XPP) was determined on the two measurement trees on each plot four or five times daily on the measurement days. In 1984, measurement runs were made at predawn, 0900 hr, 1200 hr, and 1500 hr on June 15,

July 19, August 16, and September 15. In 1985, water relations were measured at predawn, 0900 hr, 1200 hr, 1500 hr, and 1800 hr on June 13, July 24, August 14, and October 10. The 1800 hr measurement run was omitted on October 10, 1985; thus, 35 measurement runs were made altogether in the two years.

XFP was measured using the Scholander pressure bomb method as described by Johnson and Nielson (1969) and Hinckley and Ritchie (1975). One fascicle of the previous years' needles was used for each XFP determination on a given tree.

Stomatal conductance and transpiration were measured on the same dates and at the same times, except predawn, as the XFP measurements. Conductance and transpiration were measured with a Li-cor 1600 steady-state porometer on needles from the same shoots used for the XFP determination. Porometer measurements were conducted as described in the Li-cor 1600 manual (Li-cor, 1984). Prior to clamping the porometer chamber head onto the sample needles, the 'Hum set' was set to ambient humidity. For 1984 data collection, two fascicles of needles were placed lengthwise into a 116 cm³ cylindrical chamber. The needles were arranged so as not to overlap. The porometer was null balanced to the set humidity and the following parameters were recorded: transpiration, conductance, relative humidity, air temperature, leaf temperature, air flow, and photon flux density. The same procedure was repeated for data

collection in 1985 except that only one fascicle of needles was placed into a 4 cm² chamber head. The leaf area of the needles placed into the chamber was calculated using the volume displacement method described by Johnson (1984).

Biomass/Leaf Area Sampling

Ten sample points were selected on each plot using a stratified random sample in September, 1985. Three samples were taken at each point: understory hardwoods, herbs, and grasses.

Hardwoods were sampled by tallying the number of stems in each of seven diameter (ground level) classes in a 4.05 m² circular plot. Herbs and grasses were sampled by clipping and bagging all stems and foliage in 1 m² quadrat at each sample point. The herb and grass samples were later oven-dried at 70° C. to a constant weight.

Additional samples of the vegetation were collected to develop specific leaf area calibrations. The specific leaf areas were used to determine total leaf area from the herbaceous and grass weights and hardwood stem tallies. The subsamples were measured with a Li-cor 3000 leaf area meter. Leaf area per gram oven dry weight was determined for the BA 25, BA 50, and BA 100 herbaceous and grass samples. Leaf area per stem was calculated for each size class of hardwood stem.

Analysis

Treatment means for water relations parameters were tested using the SAS Analysis of Variance procedure (SAS 1985). Treatment means were compared using the Block*Treatment interaction as the error term. Linear contrasts were used to compare 1, BA25 versus BA50 and 2, BA25 and BA50 versus BA100. Regression models of PXP, XPP, conductance, and transpiration were developed from the water relations, soil moisture, and climatic data sets. Regressions were generated by SAS GLM procedure using Treatment as a class variable. Initial regressions runs included all independent variables and combinations of independent variables (up to second order interactions) that could logically have an effect on the dependent variable. Nonsignificant variables (type I or type II $P > F > 0.1$) were deleted and the regression was rerun until all remaining variables were significant at 0.1 level.

RESULTS AND DISCUSSION

Plant and Soil Water Potential

Seasonal Trends

Climatic differences between the two study years, depicted in figures 2 and 3, had a profound impact on internal tree moisture stress as measured by xylem pressure potential. The summer of 1984 was relatively wet. Rainfall totaled 74.6 cm on the site from the end of May through the end of October (figure 2). In contrast, only 25.6 cm of precipitation was recorded during the same period in 1985. A total of ten rainfall events of 3 cm or more occurred between May and October of 1984, while only four storms of the same intensity occurred in that period in 1985. Pan evaporation (evaporation from a free water surface) exceeded rainfall from May until October in 1985, whereas monthly rainfall deficits occurred only in June and August of 1984 (figure 3).

Mean predawn xylem pressure potentials (PXP) were significantly lower ($p=0.0005$) on the three late summer measurement dates in 1985 than on the other sample dates (figure 4). Plant moisture stress was greatest (most negative PXP) during the late summer months of 1985 when evaporation consistently exceeded precipitation and soil

moisture availability was low (figures 2 and 3). The lowest mean treatment PXP recorded in 1984 was -0.61 MPa on the control plots in July. In 1985 the minimum PXP was -1.01 MPa in October on the control plots. PXP was consistently lower in 1985 than 1984, for all measurement dates except mid-June.

The thinning treatments had only a slight effect on diurnal xylem pressure potential (XPP) as compared to the control. Using a linear contrast of BA25 and BA50 versus BA100, significant differences were indicated on only five of the 35 measurement periods. Of those five periods, XPP was highest on the unthinned plots twice. Significant differences between the thinned treatments occurred only once, in the midmorning on August 15, 1984. Even without considering the significance of the variation, no consistent pattern of thinning effects was apparent in the XPP data.

Soil water potential (SWP), in contrast, varied considerably across the thinning treatments (figures 5 & 6). Soil moisture was greatest on the thinned plots in a pattern consistent with the results of Moyle and Zahner (1954), Bay (1963), and Langdon and Trousdell (1977). In 1984 soil moisture was depleted slowly at the beginning of the summer, recharged slightly with mid-summer rains, then declined slowly until the fall rains. In the summer of 1985 soil water potential declined slowly at first and then more rapidly during a 40 day drought period in July and August.

While the seasonal trend of PXP tended to follow the trend of SWP, the treatment variation did not. Sucoff and Hong (1974) found a similar response to thinning in Red pine in Minnesota. In their experiment soil moisture availability was always greater on the thinned plots, but PXP was significantly greater on the thinned plots on only four of ten measurement days. In a comparison of thinned and unthinned P. sylvestris trees, Whitehead et al. (1984) showed that PXP was generally lower on the thinned trees throughout the growing season, especially at midday.

Although PXP gives a base level of tree moisture stress, it is not always equivalent to soil water potential, as is sometimes assumed. Figure 6 is a scatterplot of all plot means of PXP versus SWP at the 45 cm depth. The 1:1 line shows that PXP was consistently lower than SWP₄₅.

Kelliher et al. (1984) reported a similar phenomenon in Douglas fir. They found total twig water potential was similar to SWP when SWP was less than -0.4 MPa, but that twig water potential was less than SWP at SWP greater than -0.4 MPa. The investigators concluded that the resistance to water flow from the soil to the twig accounted for the difference in SWP and PXP when SWP was high.

Regression Analysis

In addition to the impact of moisture availability on plant stress, the evaporative demand of the atmosphere also plays an key role. A series of regression models were

developed of PXP as a function of SWP at various depths and the average pan evaporation of the five days before the PXP measurement. A summary of these regressions is shown as table II. Table II lists the most significant variables, their associated F value (from Type II sum of squares), and the R^2 for the regression at each depth. SWP was the most

TABLE II
SIGNIFICANT REGRESSION VARIABLES
FOR PXP = SWP AND EVAPORATION

Depth	Independent Variable	F	R^2	n
15 cm	SWP	107.1	0.89	72
	EVAP ²	37.3		
	SWP*EVAP	35.6		
	EVAP	28.5		
	SWP ²	20.3		
45 cm	SWP	104.9	0.76	
	EVAP ²	21.5		
	EVAP	14.2		
	SWP*TRT	12.9		
76 cm	SWP	95.1	0.73	
	EVAP ²	23.9		
	EVAP	15.8		
	SWP*TRT	9.4		
107 cm	SWP	78.9	0.73	
	EVAP ²	23.8		
	SWP*TRT	17.3		
	EVAP	15.8		

SWP = Soil water potential at indicated depth.

EVAP = Mean daily pan evaporation for 5 days previous to PXP measurement.

F from type II sum of squares

significant factor influencing PXP at all depths. As depth of the SWP measurement increased the strength of the relationship decreased ($R^2 = 0.89$ at 15 cm as compared to $R^2 = 0.73$ at 107 cm). Also, as depth increased the relative significance of evaporation terms in the regression increased. These results indicate that soil moisture readings from the 15 cm depth are most appropriate for estimating tree moisture stress. It should be stressed, however, that the soil moisture values in this study were measured in access tubes located in 30 cm planting beds. For unbedded sites the appropriate depth reading would most likely range down to 45 cm (Hennessey and Dougherty, personal communication).

The relationship of diurnal XPP to SWP and evaporative in 1984 and 1985 reflects the climatic differences in the two years. Table III presents the significant ($P > F = 0.01$) variables and corresponding type II sum of squares F values for regressions of SWP and VPD on XPP. In both years VPD was the most important factor determining XPP. In 1985, however, SWP was more significant in determining XPP than in 1984.

TABLE III
SIGNIFICANT REGRESSION VARIABLES
FOR XPP = SWP AND VPD

Year	Independent Variable	F	R ²	n
1984	VPD	77.3	0.85	105
	VPD ²	16.4		
	SWP	7.0		
1985	VPD	62.8	0.72	127
	SWP	40.6		
	VPD ²	25.8		
	SWP ²	13.0		

SWP = Soil water potential at 15 cm depth.

VPD = Vapor pressure deficit.

F from type II sum of squares.

Stomatal Conductance and Transpiration

Seasonal and Daily Trends

Conductance and transpiration rate were generally greater in trees on the thinned treatments than trees from the control plots (figures 8 & 9) in 1984. In 1984 mean daily conductance (average of 900, 1200, and 1500 hr measurements) was greatest on the BA25 plots in mid-June (cond = 0.194 cm s⁻¹), and was lowest on the BA100 treatment in mid-July (cond = 0.059 cm s⁻¹). Conductance and transpiration were similar across across the treatments in 1985 when water relations were measured on exposed upper crown branches. In 1985 mean daily conductance was highest

in mid-July on the BA50 treatment (cond = 0.193 cm s^{-1}), and lowest on the BA25 treatment in October (cond = 0.035 cm s^{-1}). The greatest mean daily transpiration rate was 5.49 micrograms of $\text{H}_2\text{O cm}^{-2} \text{ s}^{-1}$ in mid-June in 1985 on the BA25 treatment, the lowest transpiration rate was 0.723 micrograms of $\text{H}_2\text{O cm}^{-2} \text{ s}^{-1}$ in October of 1985 on the BA25 trees.

Figures 10 and 11 show the diurnal trends of Quantum flux density (Q), conductance, transpiration, vapor pressure deficit (VPD), and XPP on a day of relatively high soil moisture availability and on a day of low soil moisture availability (August 16, 1984: $\text{SWP}_{45} = -0.08 \text{ MPa}$ and August 14, 1985: $\text{SWP}_{45} = -0.28 \text{ MPa}$, respectively).

On both dates transpiration followed a similar daily trend as conductance except for early in the day when VPD was low. Thus it appears that for the early part of the day the low evaporative demand of the air limited transpiration. At higher levels of VPD, transpiration was more closely coupled to conductance.

As indicated by figures 10 and 11, conductance appeared to be influenced by Q , XPP, and VPD. Tan et al. (1977) showed that stomatal conductance in Douglas-fir was mainly related to soil water potential and VPD. In addition, Kaufmann (1976) has noted that Quantum level influenced the relationship between conductance and VPD in Engelmann spruce (*Picea engelmannii* Engel.). According to Kaufmann, conductance decreased at high VPD and stomatal closure was

more complete at high VPD associated with low light intensity. Kaufmann also noted that conductance declined with decreasing leaf water potential. This latter trend has been noted by several authors (Sands and Nambiar 1984, Pezeshki and Hinckley 1982, Hallgren 1977, Tan et al. 1977).

Boundary Line Analysis

The environmental factors controlling stomatal conductance are complex and not completely understood. Pezeshki and Hinckley (1982) have shown that boundary line analysis (Webb, 1972) can be useful in examining conductance-environmental relationships. All the boundary line analyses performed in this study used only the 1985 data because of extreme treatment variations in light intensities in the 1984 data.

Figure 12 shows a scatterplot of the response of conductance to Q when SWP was high and VPD was low (SWP > -0.14 MPa, VPD < 26). This figure indicates that conductance increased with increasing Q up to approximately 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Presumably, beyond this point Q would not limit stomatal conductance. Beadle et al. (1985) demonstrated a similar trend in Scots pine. Although Beadle et al. did not attempt to determine a boundary line response from their data, it appears that maximum conductance in Scots pine was reached at lower light intensities than the loblolly pines studied here. Kaufmann (1976) found that Engelmann spruce seedlings reached maximum conductance at very low light

intensities ($Q < 100 \text{ microE s}^{-1}\text{m}^{-2}$) when VPD was low. Pezeshki and Hinckley (1982) examined the stomatal response of black cottonwood (Populus trichocarpa Torr. and Gray) and red alder (Alnus rubra Bong.) to light intensity and determined the response differed between morning and afternoon measurements. In the afternoon, maximum conductance for both species was achieved at $Q < 100 \text{ microE s}^{-1}\text{m}^{-2}$. In the morning, conductance increased with Q up to approximately $400 \text{ microE s}^{-1}\text{m}^{-2}$.

Variation in conductance in relation to VPD is represented in figure 13. VPD did not appear to limit conductance at $\text{VPD} < 26 \text{ mbar}$. As VPD increased above 26 mbar, however, conductance dropped off rapidly. The response of conductance to VPD depicted in figure 12 is similar to the response of cottonwood stomata described by Pezeshki and Hinckley (1982). In their experiment the threshold value of VPD associated with decreasing conductance was 30 mbar. As indicated in figures 8 and 9, XPP was closely coupled to VPD. Thus, the decline in conductance at high VPD may be related to stomatal closure associated with decreasing XPP.

To examine the effects of decreasing XPP on stomatal conductance a scatterplot of conductance versus XPP was developed (figure 14). Figure 14 shows that over a wide range of xylem pressure potential values, XPP had little effect in limiting conductance. Conductance was reduced when $\text{XPP} < -1.6 \text{ MPa}$. Apparently at xylem pressure potential

less than -1.6 MPa the needle guard cells are no longer able to maintain sufficient turgor pressure to keep the stomates open and conductance is therefore reduced.

Regression Analysis

To gain a greater understanding of the relative importance of Q , VPD, and moisture availability in determining conductance and transpiration rate, the water relations data was further analyzed using multiple linear regression (SAS, 1985). It must be stated here that the objective of these regressions was not to develop predictive models of the response variables, but rather to determine which environmental variables had the most significant impact on the dependent variable.

At low levels of Q , conductance and transpiration were significantly related to SWP (table IV). In addition, conductance was increased with increased light level and transpiration increased with increasing VPD. At higher levels of Q ($Q > 500$), the light saturation point for stomatal opening was reached as variation in Q did not significantly ($P = 0.05$) impact stomatal conductance.

Under conditions of low evaporative demand (VPD < 26 millibars), conductance was primarily related to Q (table V). Transpiration under these conditions was driven by VPD, SWP, and Q . The influence of Q on transpiration is most likely related to the increase in conductance

associated with increased Q . At higher evaporative demand levels ($VPD > 26$ millibars), both conductance and transpiration were limited by soil moisture availability.

TABLE IV
SIGNIFICANT REGRESSION VARIABLES
CONDUCTANCE AND TRANSPIRATION
= SWP, VPD, AND Q

Range	Independent Variable	F	R ²	n
$Q < 500 \text{ microE m}^2\text{s}^{-1}$				64
Dependent Variable:				
Conductance	SWP	15.4	0.41	
	SWP ²	11.9		
	Q	7.4		
Transpiration	SWP	23.3	0.48	
	SWP ²	21.6		
	VPD	9.5		
	TRT	7.6		
$Q > 500 \text{ microE m}^2\text{s}^{-1}$				63
Conductance	SWP	18.4	0.55	
	VPD ²	11.7		
	SWP*VPD	7.6		
Transpiration	SWP	42.8	0.56	
	SWP ²	20.7		
	VPD	8.7		

SWP = Soil water potential at 15 cm depth.

VPD = Vapor pressure deficit.

Q = Quantum flux density

F from type II sum of squares.

TABLE V
SIGNIFICANT REGRESSION VARIABLES
CONDUCTANCE AND TRANSPIRATION
= SWP, VPD, AND Q

Range	Independent Variable	F	R ²	n
VPD < 26 millibars				72
Dependent variable:				
Conductance	Q	18.6	0.49	
	SWP	9.4		
	Q*VPD	6.9		
Transpiration	VPD	10.9	0.50	
	SWP ²	9.3		
	Q	8.0		
VPD > 26 millibars				55
Conductance	SWP	29.3	0.70	
	SWP ²	23.9		
Transpiration	SWP	32.1	0.65	
	SWP ²	27.0		

SWP = Soil water potential at 15 cm depth.
VPD = Vapor pressure deficit.
Q = Photon flux density.
F from type II sum of squares.

The strongest regression relationships were developed from the water relations data set of SWP < 0.14 MPa. When soil moisture tension was high, SWP was the most significant factor limiting conductance and transpiration. Surprisingly Q had a significant impact on transpiration but not on conductance in this range of SWP. An increase in VPD

surrounding the needles or a decrease in boundary layer resistance associated with changes in leaf surface temperature due to light absorption may be responsible for this phenomenon. The decrease in transpiration and conductance due to declining SWP fits the expected pattern since less water would be available to be transpired and the resultant decrease in plant water potential would limit conductance. When soil moisture availability was greater (SWP > -0.14 MPa), transpiration was driven primarily by VPD. SWP and Q had the most significant impacts on conductance in this range.

The thinning treatments had a significant impact on conductance and transpiration when soil moisture was not limiting. Whitehead et al. (1984) discovered a similar trend in a thinning experiment with P. sylvestris. In their experiment they found that per tree transpiration rate was over three times higher on trees on plots thinned to $27 \text{ m}^2\text{ha}^{-1}$ as compared to trees at the control stocking level of $58 \text{ m}^2\text{ha}^{-1}$. In contrast, Black et al. (1980) observed that the transpiration rate of Douglas fir trees thinned to 840 trees ha^{-1} was very similar to the transpiration rate of trees on the unthinned control (1840 trees ha^{-1}). Black et al. reasoned that increased understory vegetation, primarily salal (Gaultherion salal), on the thinned was responsible for extracting soil moisture, thus limiting the amount of water available for transpiration by the residual stand.

TABLE VI
SIGNIFICANT REGRESSION VARIABLES
CONDUCTANCE AND TRANSPIRATION
= SWP, VPD, AND Q

Range	Independent Variable	F	R ²	n
SWP > -0.14 MPa				98
Dependent variable:				
Conductance	SWP	31.4	0.53	
	Q	25.9		
	Q*VPD	7.0		
Transpiration	VPD	24.1	0.68	
	SWP*VPD	13.1		
	Q*TRT	13.1		
	Q	12.8		
SWP < -0.14 MPa				27
Conductance	SWP ²	19.5	0.79	
	SWP	9.0		
	SWP*TRT	6.7		
	TRT	6.9		
Transpiration	SWP ²	17.9	0.70	
	Q	11.1		
	SWP*Q	9.7		
	SWP*TRT	9.3		
	TRT	9.1		

SWP = Soil water potential at 15 cm depth.
VPD = Vapor pressure deficit. Q = Photon flux density
F from type II sum of squares.

In the present study, a substantial increase in understory vegetation followed the thinning of the treatment

plots. Table VII presents the relative amounts of understory leaf area present one year after thinning. Both herbaceous plants, primarily dewberry (Rubus trivialis), greenbriar (Smilax spp.), and sumac (Rhus spp.) and hardwoods including sycamore (Plantanus occidentalis L.), sweetgum (Liquidambar styraciflua L.) and oaks (Quercus spp.) rapidly invaded the site following thinning. Although no attempt was made to quantify water use by the understory in this experiment, undoubtedly this understory vegetation had a detrimental impact on stand water availability on the thinned plots.

TABLE VII
EAGLETOWN LEAF AREA INDEX
1985

Treatment	Grass	Herbaceous	Woody	Total
BA25	0.063	1.275	0.252	1.590
BA50	0.040	0.588	0.176	0.804
BA100	0.002	0.047	0.211	0.260

Carter et al. (1983) examined the impacts of competing vegetation on the moisture status of 5 year-old loblolly pine trees. By removing woody and non-woody

vegetation from circular plots around individual pine trees and then measuring PXP during a dry summer, the researchers determined that complete removal of competition consistently reduced predawn moisture stress. In addition, Carter et al. also compared the effects of woody and non-woody vegetation and concluded that each could be effective in increasing pine moisture stress.

Clason (1984) has investigated the impacts of understory removal on diameter growth of loblolly pine. His work demonstrated that hardwood removal can significantly increase the diameter growth of loblolly pine following thinning.

These results and the results of the present study suggest that improvements in water relations and growth from thinning may be enhanced by coupling stocking reductions with competition control.

Growth

Both thinning treatments dramatically increased diameter and per tree basal area growth in the two seasons after the treatments were applied (figure 15). As indicated in table VIII, diameter and per tree basal area growth were significantly greater on the BA25 and BA50 treatments than on the control plots in 1984. The second season following thinning showed an even greater segregation among the treatments as per tree growth was significantly higher on the BA25 plots than the BA50 plots.

The growth results presented in table VII are biased by the fact that larger trees remained on thinned plots than on the control plots. To remove this bias, diameter and per tree basal area growth of trees greater than 15 cm were compared (table IX). Table IX indicates that thinning increased bole growth in addition to the effects of the larger residual tree diameters.

Diameter growth rate in both years and on all treatments was greatly influenced by soil moisture supply and the evaporative demand of the air. Diameter growth rate was greatest when SWP₄₅ was greater than -0.3 Mpa.

TABLE VIII
DIAMETER AND PER TREE BASAL AREA GROWTH
FOLLOWING THINNING

Treatment	Diameter growth		BA/tree growth	
	1984	1985	1984	1985
BA25	1.892a	1.732a	49.05ab	49.86a
BA50	1.806a	1.475b	46.40ab	41.82b
BA100	1.209c	0.826d	27.73c	20.64d

means followed by the same letter are not significantly different at the 0.05 significance level, each mean is the average of 30 trees.

TABLE IX
DIAMETER AND PER TREE BASAL AREA GROWTH
OF TREES GREATER THAN 15 CM DBH

Treatment	Diameter growth		BA/tree growth	
	1984	1985	1984	1985
BA25	1.95a	1.76a	51.73a	51.40a
BA50	1.89a	1.51b	50.27a	43.21a
BA100	1.44b	1.03c	36.97b	28.11b

means followed by the same letter are not significantly at 0.05 level.

Regression analysis revealed that 65 percent of the variation in diameter growth rate was attributable to variation in SWP. However, when daily evaporation was added to the equation over 80 percent of the growth rate variation was explained.

This relationship emphasizes the importance of the rate of water loss from the site, as well as plant moisture stress, in determining growth rate. Moehring and Ralston (1967) found that diameter growth was reduced when soil moisture loss was rapid, regardless of the amount of soil moisture available. Similarly, McClurkin (1961) determined that diameter growth rates of shortleaf pine (Pinus echinata) decreased during periods of rapid soil depletion.

Although treatment differences in per tree basal area growth shown in tables VIII and IX were quite large, total

basal area growth was greatest on the unthinned control plots in both study years (Table X). While on the surface this may suggest greater returns from the unthinned plantation, it must be remembered that increased per tree growth rates mean merchantable trees from a shorter rotation length. Thus the net present value of a thinned stand is increased and carrying costs are decreased. Inevitably the economic aspects of the thinning decision must be evaluated on a case basis.

TABLE X.
TOTAL BASAL AREA GROWTH AFTER THINNING

Treatment	1984	1985
BA25	1.88	1.89
BA50	2.92	2.63
BA100	5.62	4.18

Growth in m^2ha^{-1} .

CONCLUSION

Precommercial thinning of a ten year-old loblolly pine stand in southeastern Oklahoma did not have a significant impact on internal tree moisture stress. Soil water potential was consistently higher on the thinned plots than on the unthinned control. Predawn and diurnal xylem pressure potential were not significantly effected by thinning. Conductance and transpiration per unit leaf area were higher on trees on the thinned treatments in 1984. When VPD was low, conductance was related to SWP, VPD and light intensity. At high VPD, transpiration and conductance were related to SWP. Diurnal XPP was primarily a function of SWP and VPD. Diameter and per tree basal area growth were significantly greater on the thinned plots than on the unthinned controls. The results suggest that PXP was not increased by thinning, despite the treatment increase in SWP, due to increased crown exposure to light and wind resulting in increased transpirational losses. A dramatic increase in understory vegetation following thinning indicates that water relations and growth responses from thinning may be enhanced by brush control measures.

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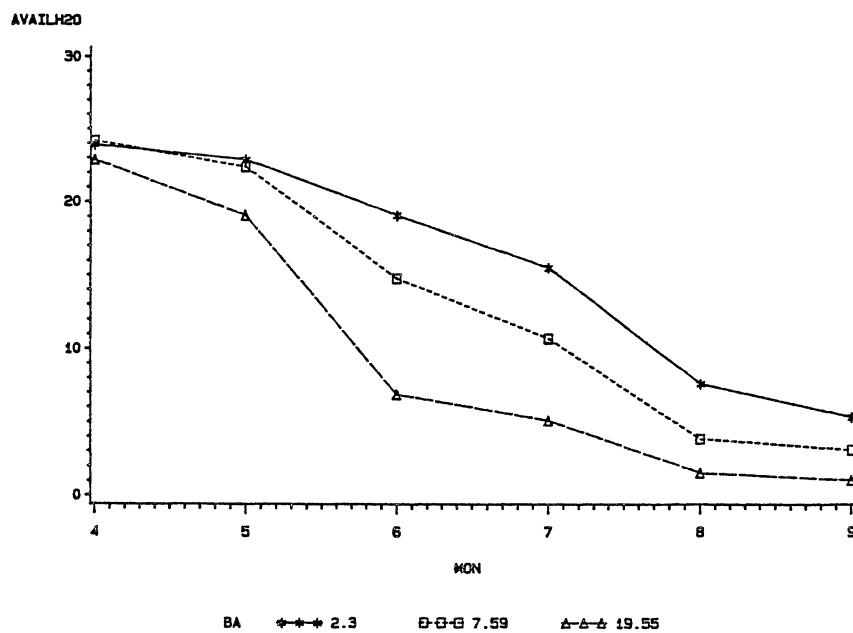


Figure 1. Effect of Stand Basal Area on Soil Moisture Availability. AVAILH2O = Available H₂O in cm, MON = Month (i.e. 6 = June). Adapted from Zahner and Whitmore (1960).

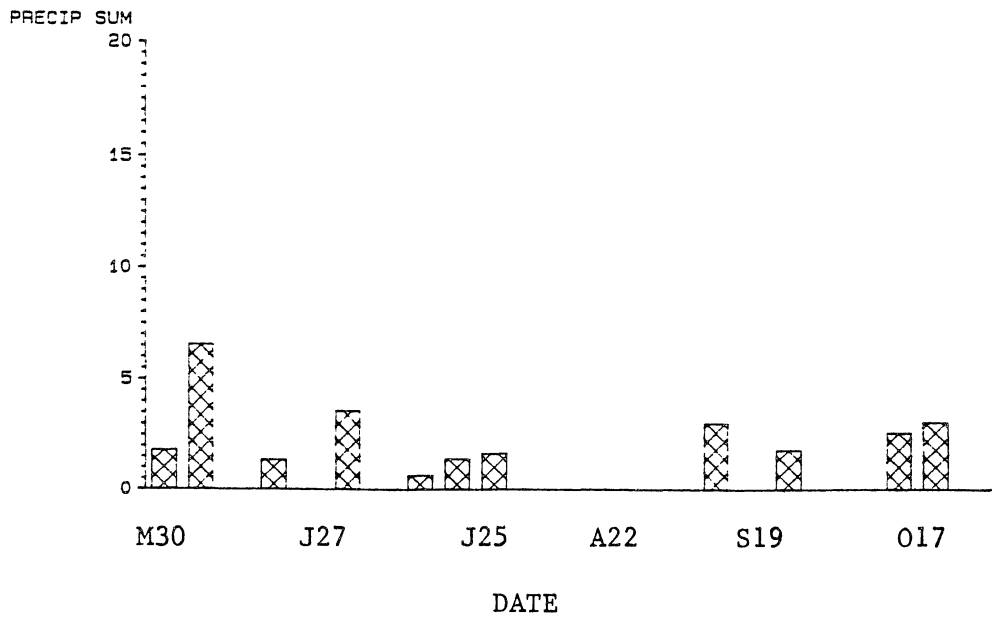
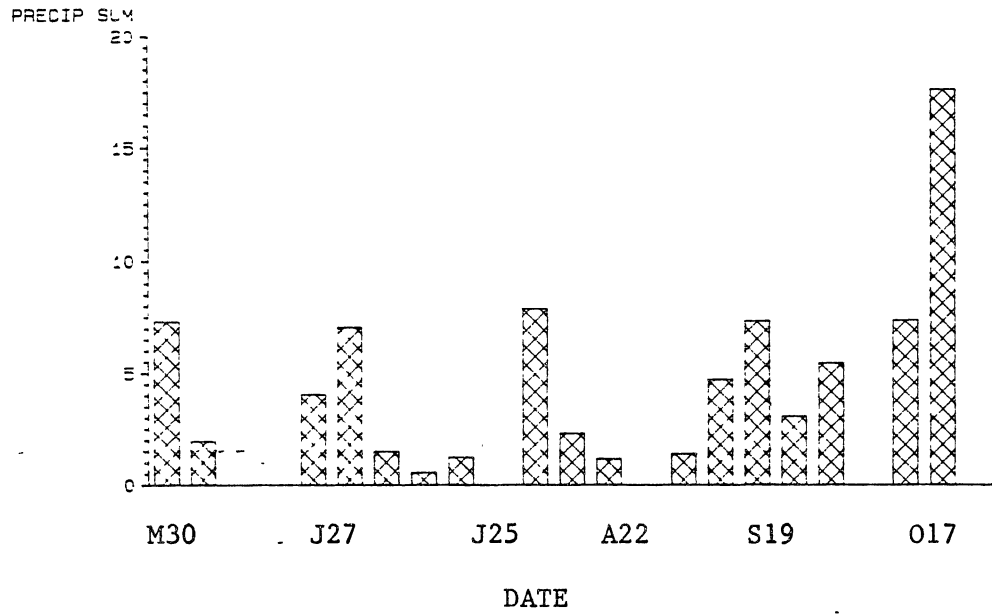


Figure 2. On Site Precipitation in cm, 1984 and 1985.

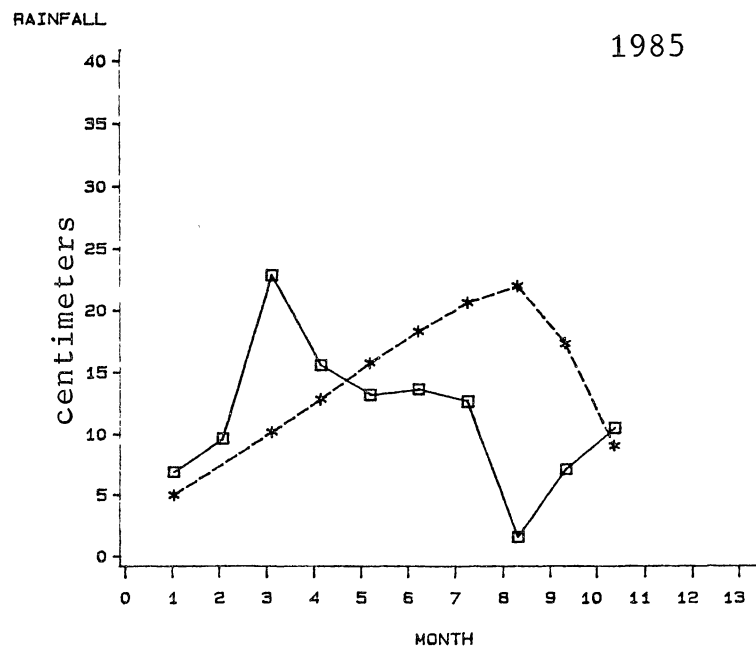
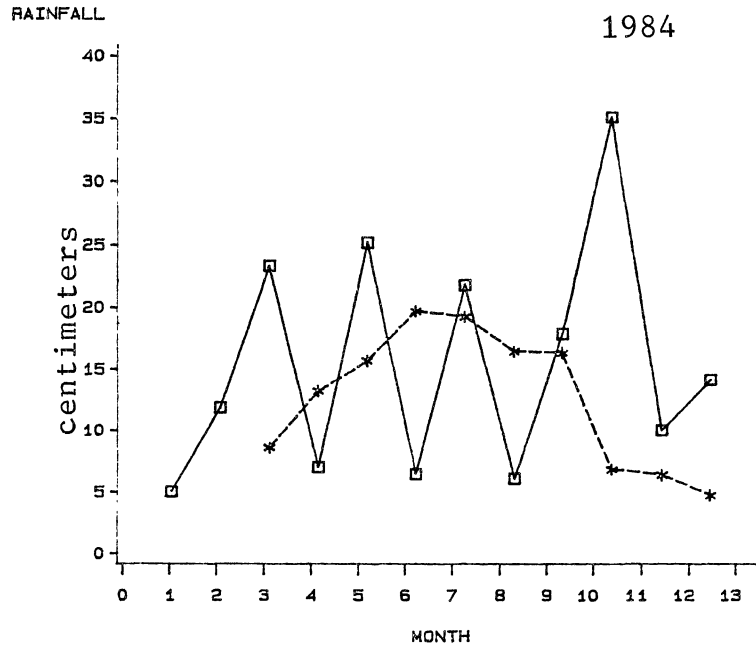


Figure 3. Monthly Rainfall and Pan Evaporation from Broken Bow Dam, 27 km North of Study Site. Solid line = Rainfall, Dashed line = Evaporation.

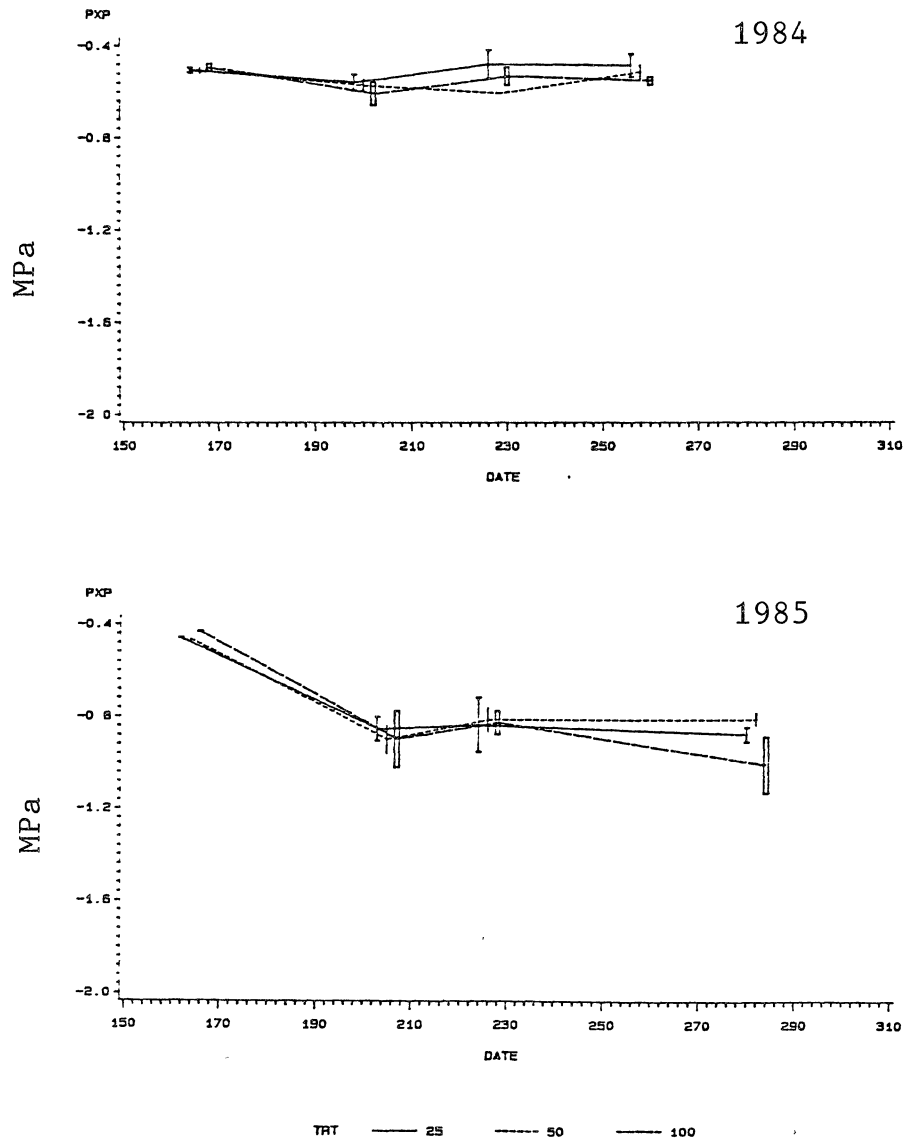


Figure 4. Mean Predawn Xylem Pressure Potential(PXP), 1984 and 1985. Each bar represents 95% C.I. for each mean.

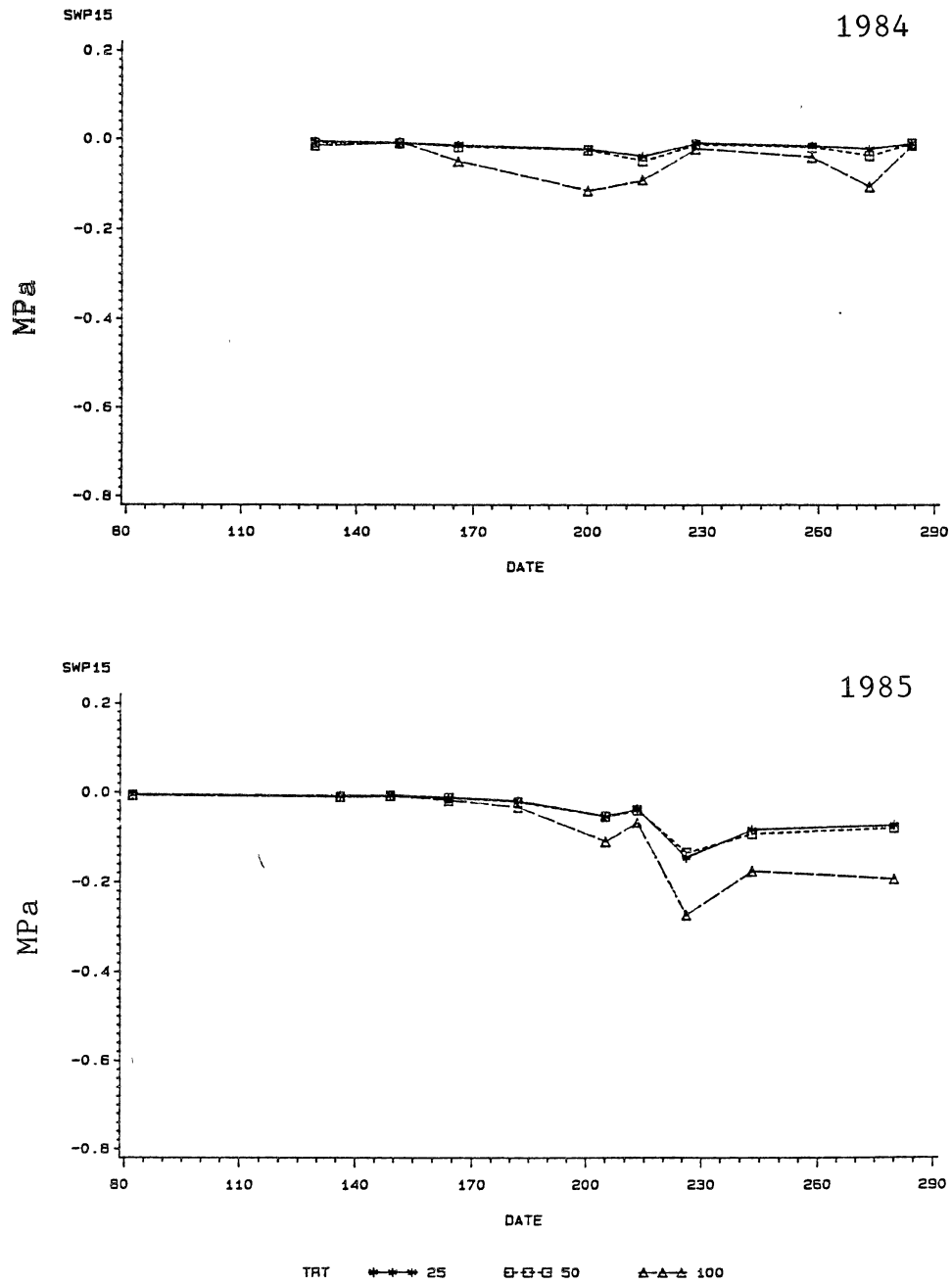


Figure 5. Seasonal Trend of Soil Water Potential at the 15 cm depth, 1984 and 1985.

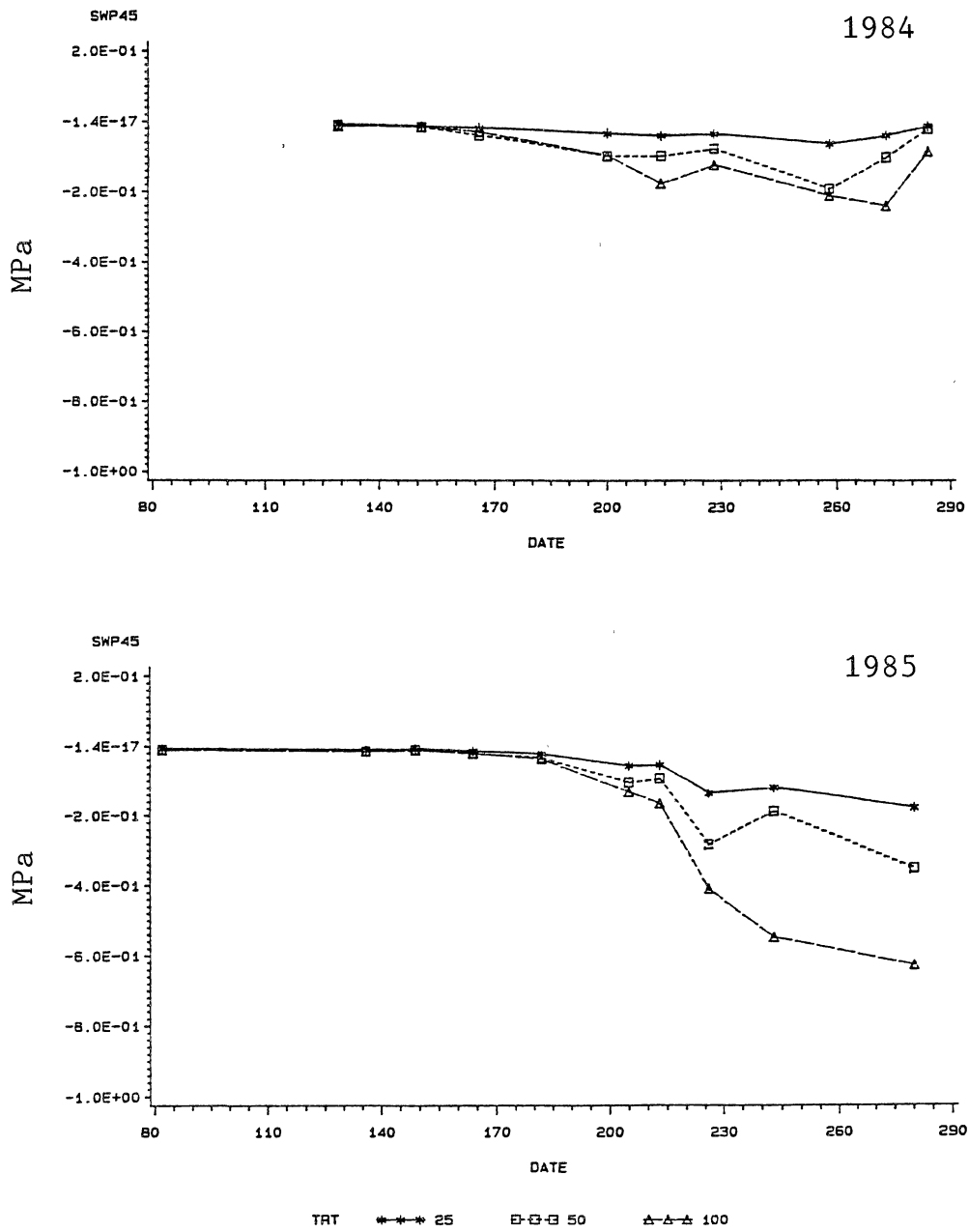


Figure 6. Seasonal Trend of Soil Water Potential at the 45 cm depth, 1984 and 1985.

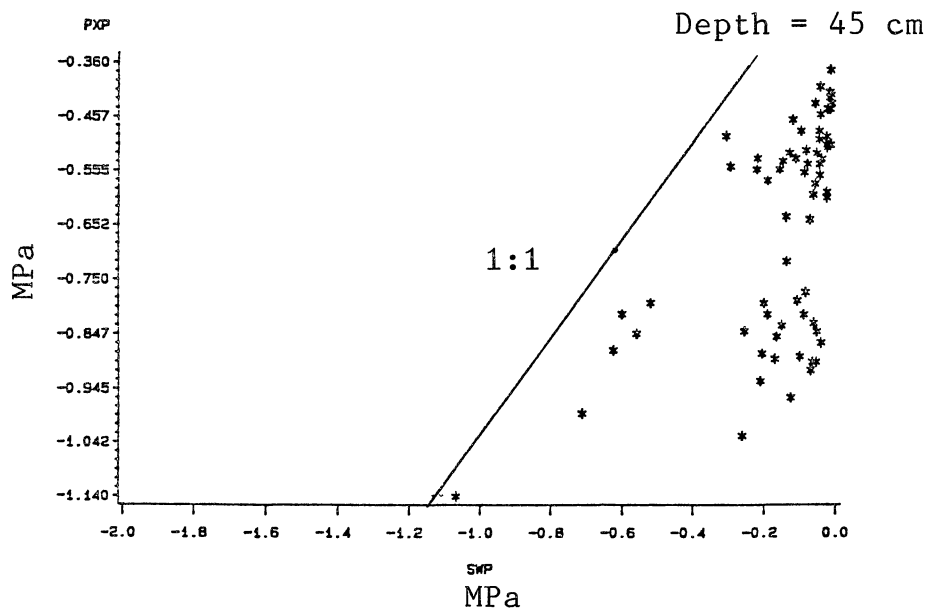
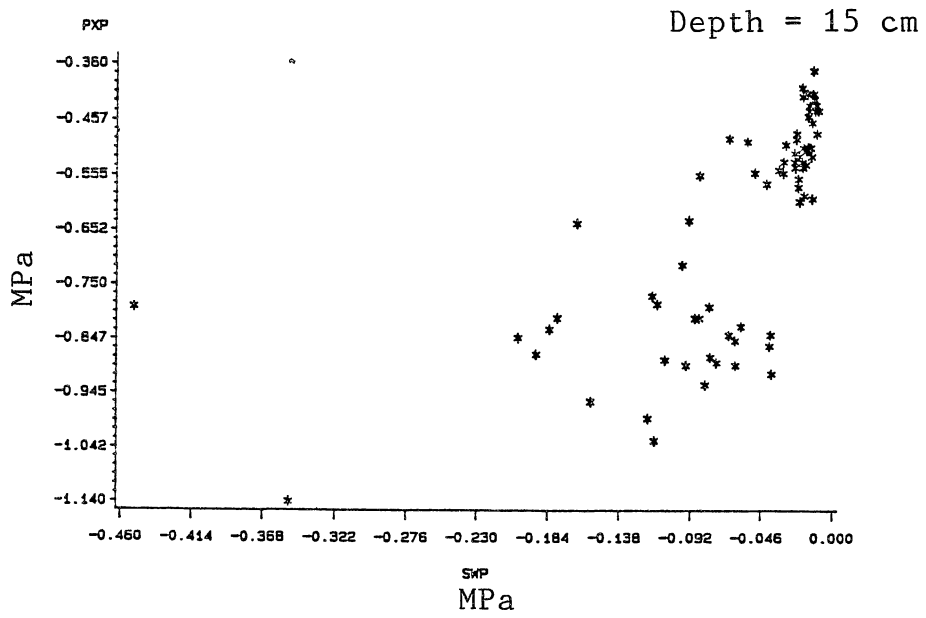


Figure 7. Predawn Xylem Pressure Potential Versus Soil Water Potential at 15 and 45 cm Depths

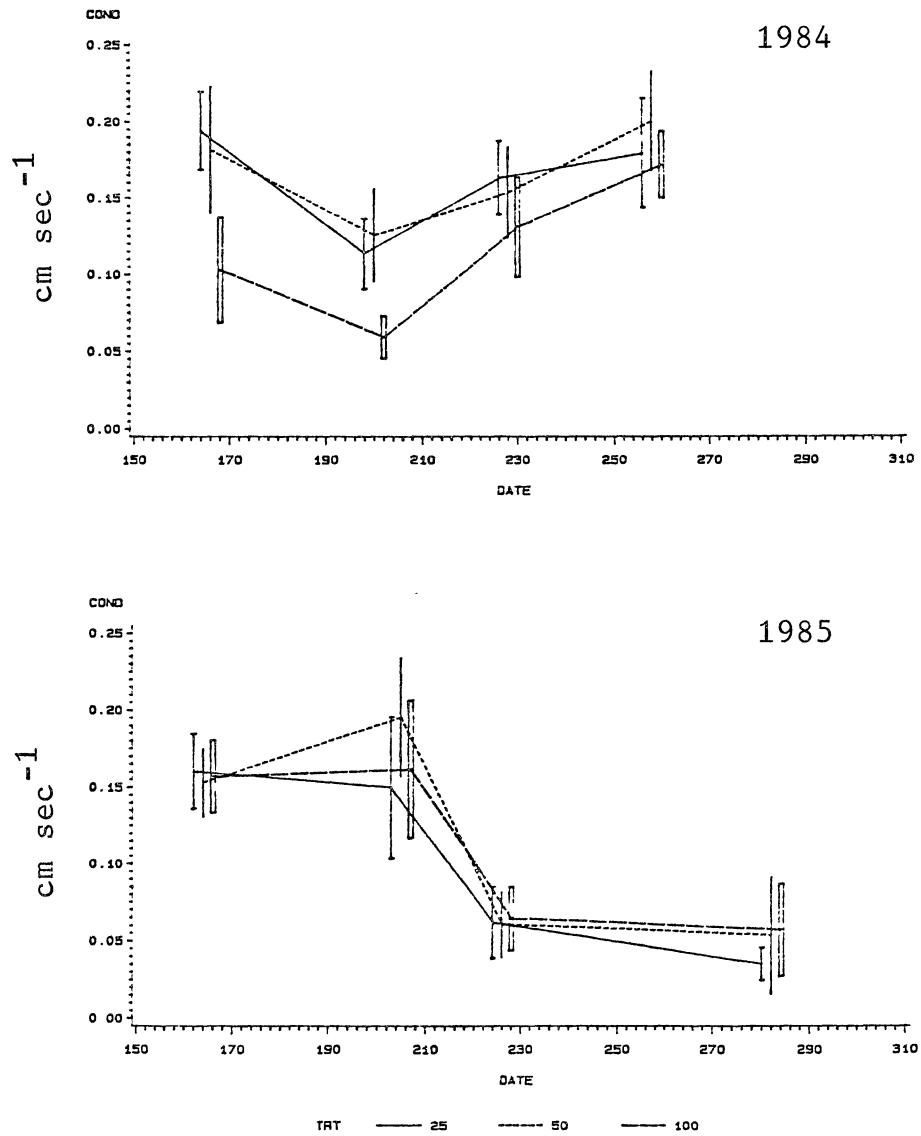


Figure 8. Mean Daily Conductance (average of 0900, 1200, and 1500 hr measurements), 1984 and 1985. Each bar represents 95% C.I. for each mean.

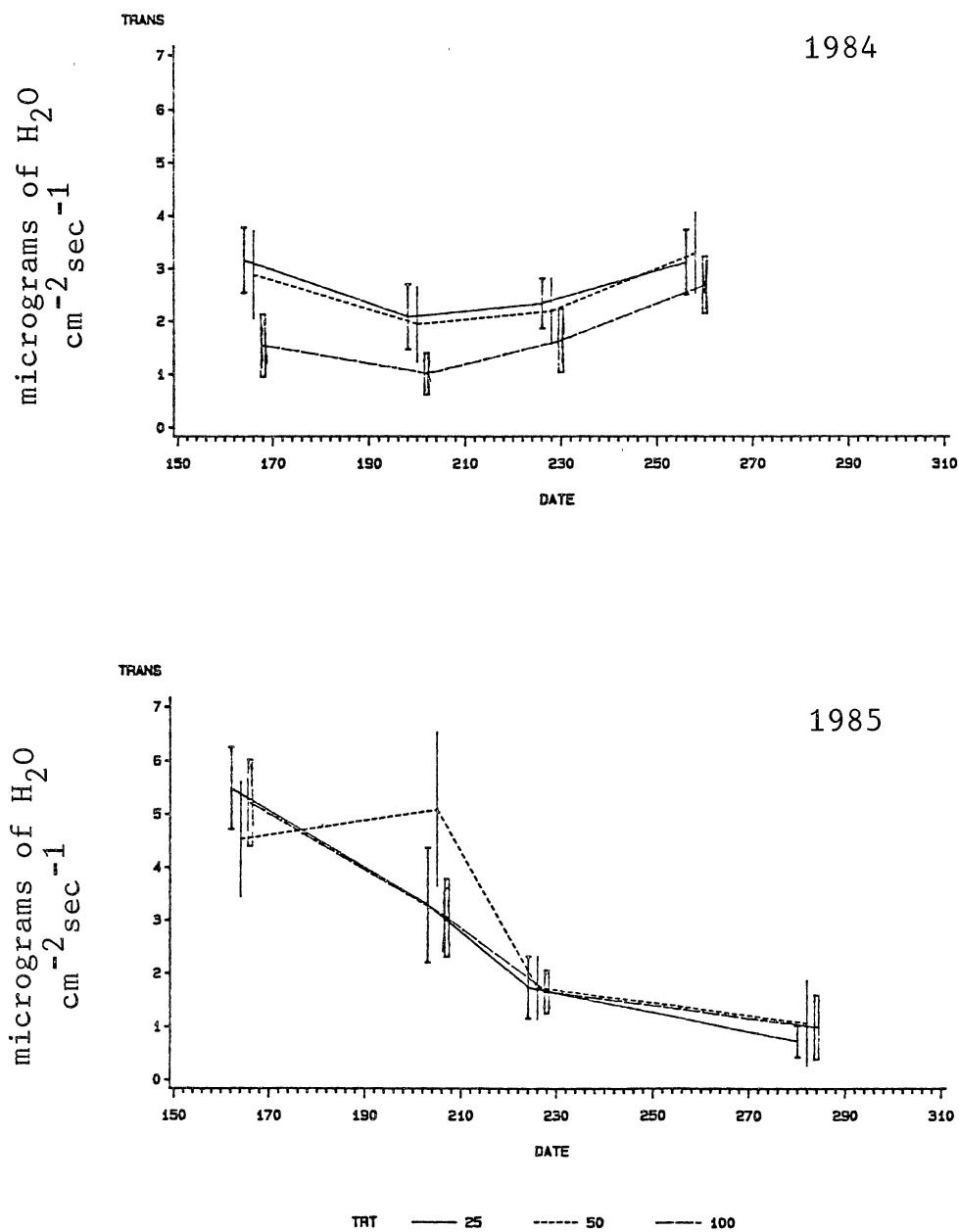


Figure 9. Mean Daily Transpiration Rate (average of 0900, 1200, and 1500 measurements), 1984 and 1985. Each bar represents 95% C.I. for each mean.

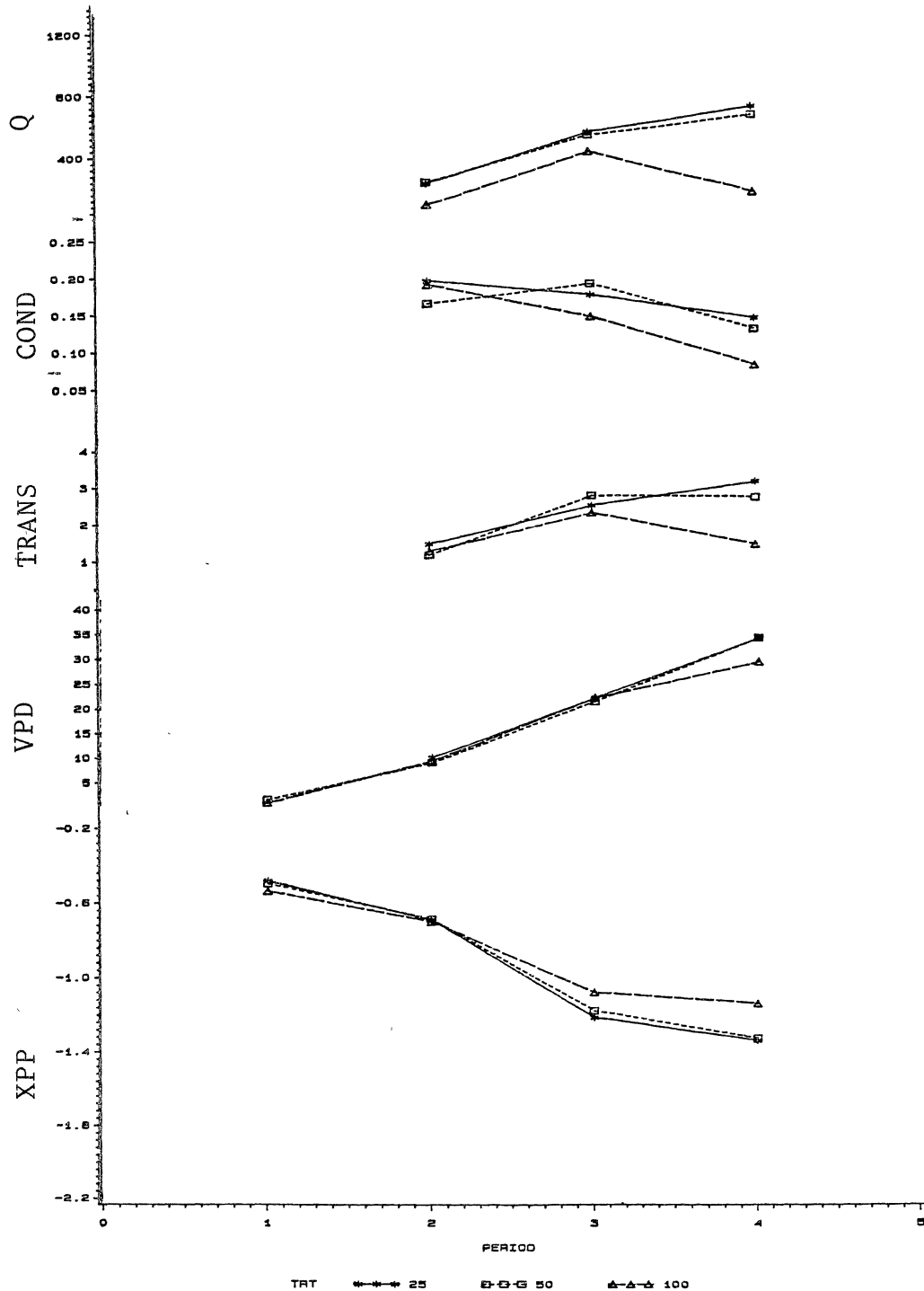


Figure 10. Diurnal trends of Q, Transpiration, Conductance, VPD, and XPP, August 16, 1984. Q in $\mu\text{E m}^{-2}\text{sec}^{-1}$, Transpiration in $\mu\text{g H}_2\text{O cm}^{-2}\text{sec}^{-1}$, Conductance in cm sec^{-1} , VPD in millibars, XPP in MPa.

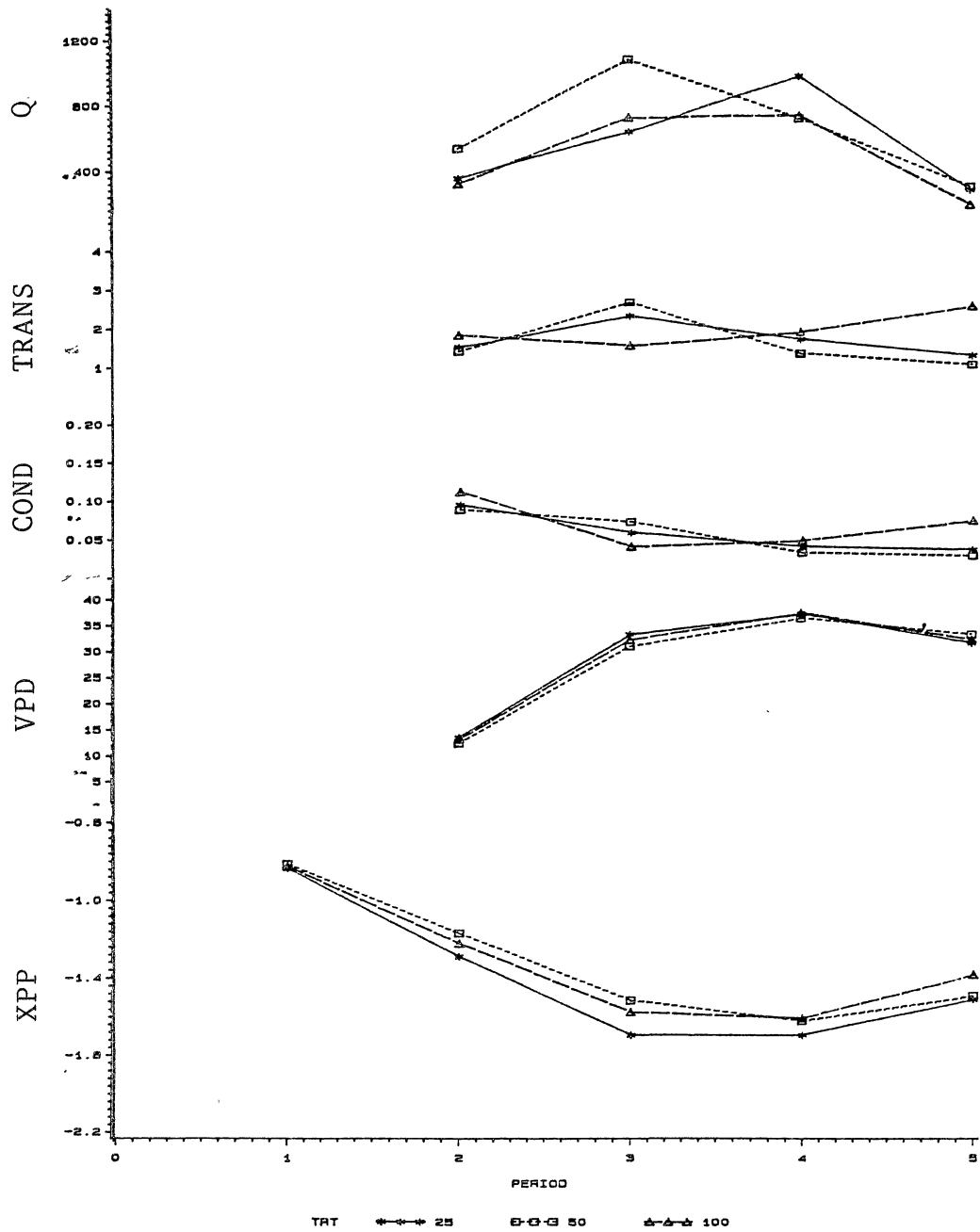


Figure 11. Diurnal Trends of Q, Transpiration, Conductance, VPD, and XPP, August 14, 1985. Q in $\text{microE m}^{-2} \text{sec}^{-1}$, Transpiration in $\text{micrograms of H}_2\text{O cm}^{-2} \text{sec}^{-1}$, Conductance in cm sec^{-1} , VPD in millibars, XPP in MPa.

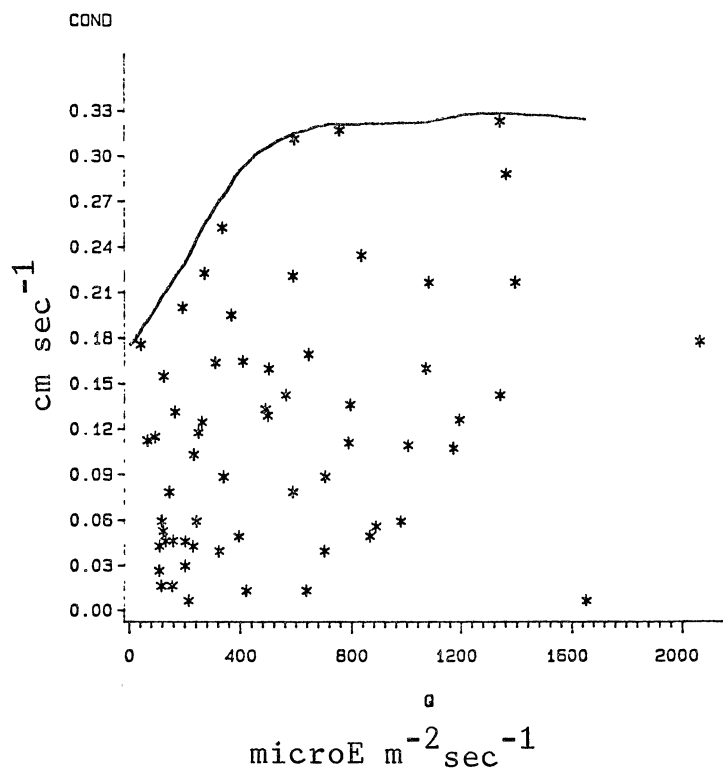


Figure 12. Stomatal Conductance Versus Q. (VPD less 26 millibars and SWP₆ greater than -0.14 MPa).

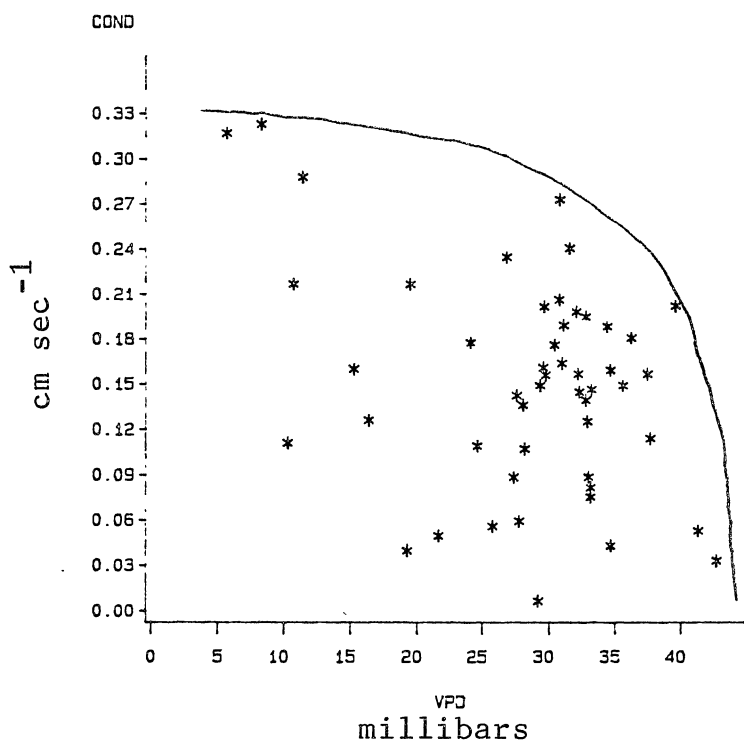


Figure 13. Stomatal Conductance Versus VPD.
(Q greater than $500 \text{ microE m}^{-2} \text{ sec}^{-1}$ and
 SWP_6 greater than -0.14 MPa).

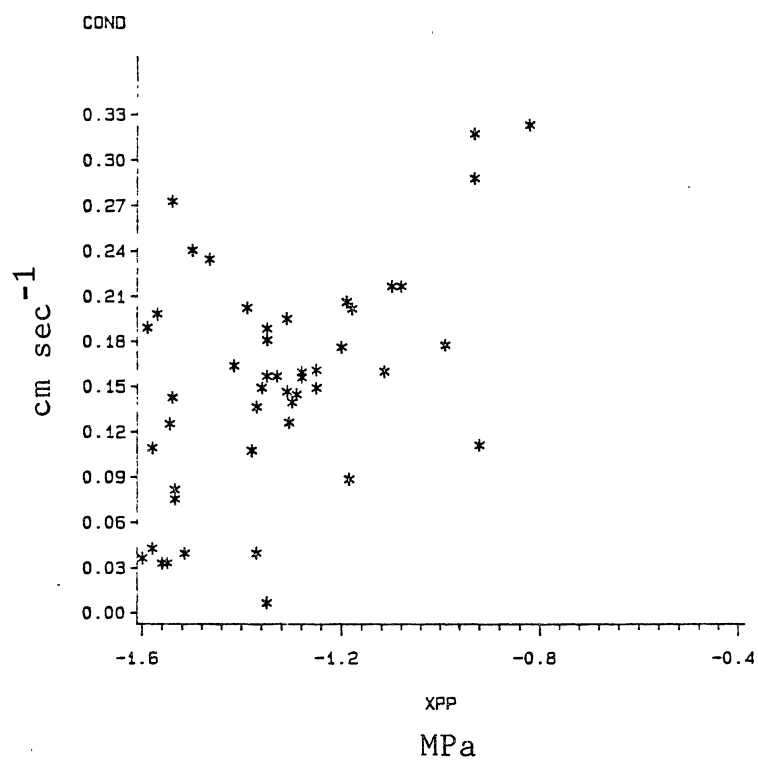
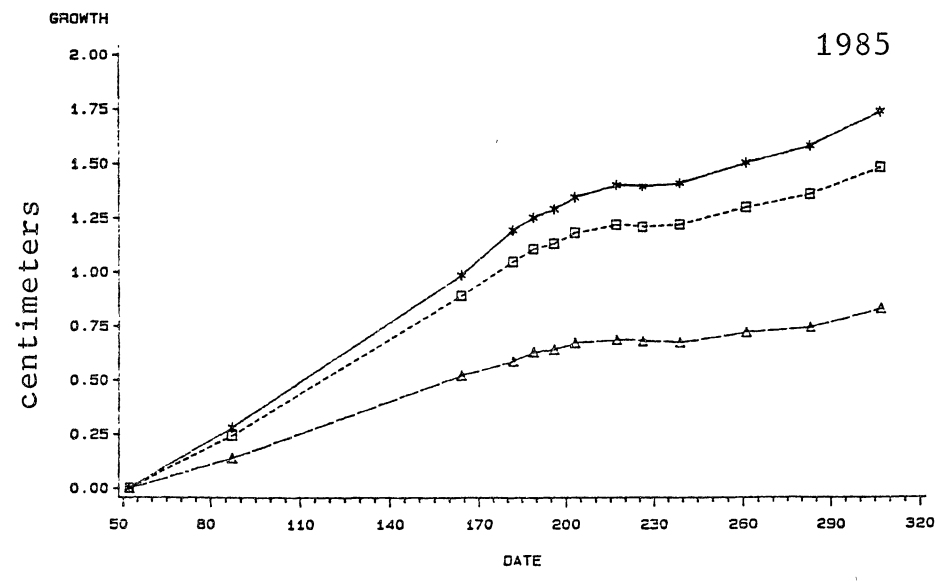
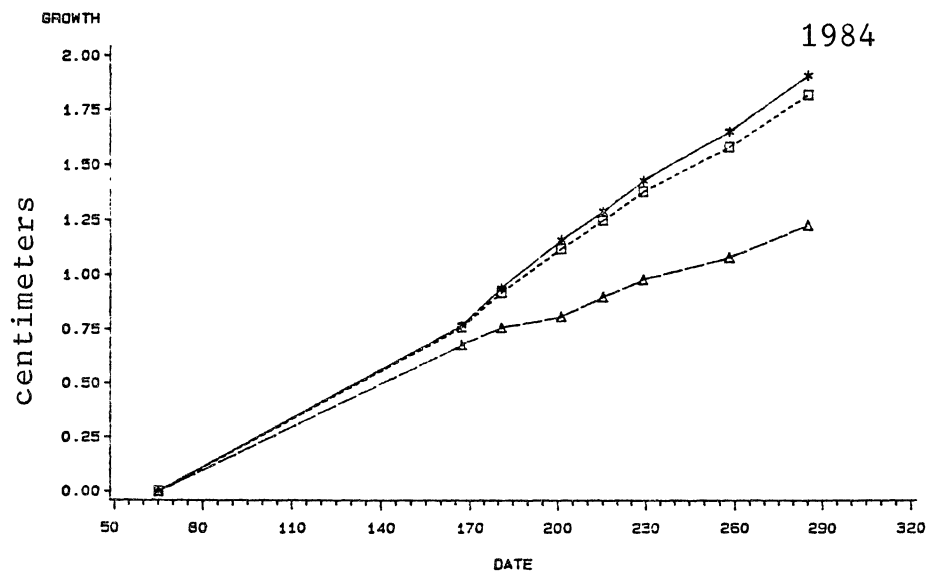


Figure 14. Stomatal Conductance Versus XPP. (Q greater than 500 $\mu\text{E m}^{-2}\text{sec}^{-1}$ and SWP_6 greater than -0.14 MPa).



TRT *-*-* 25 - - - - 50 - - - - 100

Figure 15. Cumulative Diameter Growth, 1984 and 1985. Each point represents mean of 30 trees.

PART II

THE EFFECTS OF PRECOMMERCIAL THINNING ON
WOOD QUALITY OF LOBLOLLY PINE
(PINUS TAEDA L.)

ABSTRACT

A ten year old stand of loblolly pine (Pinus taeda L.) in southeastern Oklahoma was thinned to three target basal area levels: $5.8 \text{ m}^2\text{ha}^{-1}$, $11.5 \text{ m}^2\text{ha}^{-1}$, and $23 \text{ m}^2\text{ha}^{-1}$ (control). Specific gravity, latewood percentage, date of transition from earlywood to latewood, growth, and climate variables were measured for the two years after thinning. Climatic variation in the two years caused a greater variation in wood properties than the thinning treatments. In 1984, a relatively wet year, wood was produced with a later date of latewood transition, higher latewood percentage, and higher specific gravity than in 1985, a year of low summer rainfall. The date of transition from earlywood to latewood occurred 10 to 14 days sooner on the unthinned plots in both years. Latewood percentage and specific gravity were not significantly effected by thinning. Increased late season growth rates compensated for a later transition date on the thinned treatments resulting in no net change in latewood percentage relative to the unthinned controls. Transition date was related to predawn moisture stress and evaporative demand. Specific gravity was related to latewood percentage and tree diameter. Diameter growth and per tree basal area growth were significantly greater on the thinned treatments both

years after thinning. The results indicate that diameter growth can be increased by thinning without reducing wood density.

INTRODUCTION

Growing trees faster to meet anticipated future demand has long been a goal of both private and public forest managers. Recently, however, foresters are becoming increasingly concerned about the possible impacts of faster diameter growth rates on the quality of wood produced from forest plantations.

Senft et al. (1985) present statistics which show that the increasing proportion of juvenile wood (wood produced within 7 to 11 annual rings of the pith) in lumber is beginning to create problems for the construction industry. These problems include increased lumber shrinkage, bending, warping, and beam failure. In addition to the impacts on solid wood products, the increase in proportion of juvenile wood in trees harvested from shorter rotations also reduces pulp yields (Zobel and Blair, 1974).

In loblolly pine (Pinus taeda L.) latewood percentage and specific gravity tend to increase with age, that is, from the pith outward (Loo-Dinkins et al., 1984, Panshin and deZeeuw, 1980, Zobel and McElwee, 1958). The primary strength properties of wood such as modulus of rupture (bending load to failure), modulus of elasticity (ratio of stress to strain), and maximum crushing strength are all

directly related to specific gravity (Panshin and deZeeuw, 1980). As growth rates are increased and rotation lengths shortened through intensive silvicultural management, the ratio of juvenile to mature wood in trees harvested will tend to increase.

Genotypic variation greatly impacts the specific gravity and strength properties of wood and genetic selection is one avenue being explored to increase the specific gravity of plantation-grown loblolly pine (Loo-Dinkins et al., 1984, Pearson and Gilmore, 1980). However it is also important to recognize and understand the influence of environmental conditions, particularly as modified by silvicultural prescriptions, on wood properties.

The present study will examine the effects of precommercial thinning on young loblolly pine trees under plantation management in southeastern Oklahoma. Thinning may radically alter the microenvironment of the trees remaining in the residual stand. Variations in light interception, soil moisture, mineral nutrition, and understory vegetation may contribute to changes in growth and wood formation following stocking reduction.

The objectives of the this study are the following: 1) to determine the impacts of thinning and site variables on the date of transition from earlywood to latewood, 2) to determine the effects of thinning on latewood percentage and

specific gravity, and 3) to examine the relationship between growth rate, environmental and physiological variables, and wood quality.

MATERIALS AND METHODS

Site Description

The study was located in southeastern Oklahoma approximately 8 km south of Eagletown, Oklahoma (legal description: Section 9, T7S, R26E, Indian Meridian). The land containing the study site is owned by the Weyerhaeuser Company. The soils on the site are of the Cohab series of the Guyton-Ochlocknee association (USDA SCS, 1974), which is characterized by deep alluvial formed soils and slopes of less than one percent. Soil textures on the site ranged from loams to silty clay loams. The year-round climate of the area is generally mild with hot, often droughty summers. The mean annual temperature of the region is 17° C. and the average annual rainfall is 135 cm. The average length of the growing season (the period between the average date of the last freezing temperature in the Spring and the first 0° C. reading in the Fall) is 240 days (Oklahoma Water Resources Board, 1984).

Following harvest of the previous stand, a pine-hardwood mixture, in 1975 the site was site-prep burned and double-bedded. The area was subsequently planted with local seed source loblolly pine seedlings at a stocking density of approximately 2,500 trees per hectare.

In March 1984, a 1.3 ha area of the stand was selected for study and inventoried. At that time canopy closure was complete and the overall vigor of the stand was fair to good, although a few trees were infected with Southern fusiform rust (Cronatium fusiforme). The mean basal area of the study portion of the stand was $25.9 \text{ m}^2\text{ha}^{-1}$.

Treatments

After the inventory, nine 0.1 ha plots were thinned to three target basal areas: BA 25 ($25 \text{ ft}^2\text{ac}^{-1}$, $5.8 \text{ m}^2\text{ha}^{-1}$), BA 50 ($50 \text{ ft}^2\text{ac}^{-1}$, $11.5 \text{ m}^2\text{ha}^{-1}$) and BA 100 (unthinned, $100 \text{ ft}^2\text{ac}^{-1}$, $23 \text{ m}^2\text{ha}^{-1}$). The stand characteristics following thinning for each treatment are listed in table I. The plots were arranged in a completely randomized block design. Due to suspected variations in soil textures, the blocks were arranged parallel to the Mountain Fork river, approximately 50 meters east of the study site.

Environment

Monthly summaries of weather data for the region were compiled from National Oceanic and Atmospheric Administration records from the U.S. Army Corps of Engineers weather station at Broken Bow Dam, approximately 27 km from the study area. Rainfall was monitored on the site with two standard rain gauges.

TABLE I
STAND CHARACTERISTICS AFTER THINNING

Treatment	Basal area	Stocking	Mean dbh
	m ² ha ⁻¹	Trees ha ⁻¹	cm
BA25	7.49	379	15.72
BA50	12.70	629	15.09
BA100	33.57	2,025	11.90

all measurements from March, 1984.

Soil moisture on the site was monitored using the neutron scattering method (Long and French, 1967). Three 3.8 cm diameter steel access tubes were installed to depth of 1.22 m on each measurement plot. Volumetric soil moisture content was measured every two weeks from May through November in 1984 and 1985 with depth moisture gauge (Troxler 3300). Soil moisture release curves derived from soil samples collected on the site were used to convert volumetric soil moisture content to soil water potential (SWP).

Growth

A 0.04 ha measurement plot was located inside each 0.1 ha treatment plot to reduce edge effects. Diameters were measured at breast height on all trees inside the measurement plots at the beginning of the study and at the

end of the 1984 and 1985 growing seasons. In addition, dendrometer bands were placed on ten trees selected at random on each measurement plot (Liming, 1957). Changes in stem circumference were measured by reading the vernier scale on the bands at two week intervals in the summer of 1984 and at weekly intervals in the summer of 1985. The circumference measurements were subsequently converted to diameters for reporting.

Wood core analysis

Increment core samples, 4 mm in diameter, were extracted at breast height (1.5 m) from the outer annual ring of five of the ten dendrometer-banded trees on each plot at the end of the 1984 and 1985 growing seasons. These cores were analyzed to determine ring latewood percentage, specific gravity, and tracheids diameter and wall thickness.

Latewood percentage for each sample was estimated by examining the core under a magnifying light and measuring the amount of earlywood, latewood, and ring width to the nearest 0.5 cm with calipers. Loblolly pine, like most southern pines generally has an abrupt transition from earlywood to latewood (Panshin and deZeeuw, 1980); thus, measuring the width of each band is relatively straightforward. However, in a few cases the delineation from earlywood to latewood was not clear and these cores were hand-sectioned, mounted on slides, and examined microscopically at 100x magnification. Mork's 1928

definition of latewood cells as described by Kozlowski (1971) was used as the criterion for distinguishing earlywood from latewood.

The specific gravity of each core was determined by the maximum moisture content method (Smith, 1959). The cores were saturated by boiling in 12 ml individual collection vials and then allowed to cool to room temperature. Once saturated, the cores were individually weighed and then oven dried at 72° C. for 48 hours and reweighed. The saturated weight and the oven-dry weight were entered into equation 1 to calculate the unextracted specific gravity of each sample on a green weight basis.

$$\text{Green specific gravity} = \frac{1}{\frac{s - d}{d} + \frac{1}{g}} \quad (1)$$

Where: s = saturated core weight
 d = oven dry core weight
 g = 1.53 = the density of solid wood substance

A subsample of the 1985 year-end cores from each treatment were selected at random for tracheid dimension analysis. The cores were hand-sectioned and cross-sectional mounts were examined at 200x magnification with a light microscope. Ten points on each slide were randomly located with the zero end of an eyepiece micrometer (5 points in the earlywood band and 5 points in the latewood band). The radial cell diameter and radial wall thickness of the two tracheids nearest the end of the micrometer were recorded.

The date of transition from thin-walled earlywood cells to thicker-walled latewood cells was estimated by microscopic examination of increment cores extracted periodically in the summer. The cores for transition date determination were extracted at two week intervals from mid-June to the beginning of August in 1984 and at weekly intervals from July through the beginning of August in 1985. The cores were saturated as described earlier and stored in 12 ml vials with 50 percent ethanol as a preservative. The cores were hand-sectioned and mounted on slides. Core sections for each tree were examined sequentially in the order collected. The presence or absence of latewood was noted for each slide. Again, the abrupt nature of the transition aided in the identification of this point. If a slide examination revealed that a tree had begun latewood production, the width of the latewood band was measured and recorded. The width of the latewood band was compared to the diameter growth rate of the tree to determine the number of days of latewood production. The days of latewood production was then subtracted from the core extraction date to calculate the date of transition from earlywood to latewood.

Biomass/Leaf Area Sampling

Ten sample points were selected on each measurement plot using a stratified random sample in September, 1985. Three samples were taken at each point: understory hardwoods, herbs, and grasses.

Hardwoods were sampled by tallying the number of stems in each of seven diameter (ground level) classes in 4.05 m² circular plot. Herbs and grasses were sampled by clipping and bagging all plants in 1 m² quadrat at each sample point. The herb and grass samples were later oven-dried at 70° C. for three days and weighed.

Subsamples of the vegetation were collected to develop specific leaf area calibrations in order to determine the leaf area index (LAI) from the herbaceous and grass weights and hardwood stem tallies. The subsamples were measured with a Li-cor 3000 leaf area meter. Leaf area per gram oven dry weight was determined for the BA 25, BA 50, and BA 100 herbaceous and grass samples. Leaf area per stem was calculated for each size class of hardwood stem.

Analysis

Treatment means of wood quality variables were compared using the SAS Analysis of Variance procedure. Multiple comparisons of treatment means were made using Duncan's multiple range test. Regressions for latewood transition

date and specific gravity were developed from the wood quality, soil moisture, climatic, and water relations data sets using the SAS GLM procedure (SAS, 1985).

RESULTS AND DISCUSSION

Soil and Plant Water Potential

The Summer and early Fall of 1984 were relatively wet. On-site rainfall totaled 74.6 cm from the end of May to the end of October in 1984, as compared to 25.6 cm for the same period in 1985 (figure 1). A total of ten rainfall events of 3 cm or more occurred between May and October of 1984, while only four storms of the same intensity occurred in that period in 1985. Pan evaporation (evaporation from a free-water surface) exceeded rainfall from May until October in 1985, whereas monthly rainfall deficits occurred only in June and August of 1984 (figure 3).

Given these differences in climate, variation in soil water potential (SWP) and predawn xylem pressure potential (PXP) were to be expected. Soil water potential at the 15 cm and 45 cm depth was significantly lower after mid-August, 1985 than after mid-August, 1984. The seasonal trends of SWP₁₅ and SWP₄₅ for 1984 and 1985 are shown in figures 3 & 4.

As indicated in figures 3 & 4, rootzone SWP varied among the treatments as well as between the study years. The treatment pattern of soil moisture availability shown in figures 3 & 4 is similar to the results of Moyle and Zahner

(1954), Zahner and Whitmore (1960), and McClurkin (1961). These studies demonstrated that thinning increases soil moisture availability for the residual stand.

The seasonal trend of predawn xylem pressure potential also differed significantly between the two study years (figure 5). Plant moisture stress was greatest (most negative PXP) during the late summer months of 1985 when evaporation consistently exceeded precipitation and soil moisture availability was low (figures 2, 3, & 4. In contrast, PXP never declined below -0.6 MPa on any measurement period in 1984, a summer of frequent summer rains.

Despite the large treatment variations in SWP, particularly in 1985, PXP did not vary consistently with the thinning treatments (figure 5). Significant ($p = 0.05$) treatment differences in PXP were indicated in September, 1984 and October, 1985. In June, 1984 moisture stress was significantly lower on the BA100 treatments as compared to the thinned stands. On the other dates mentioned above, stress was highest on the BA100 treatment. No significant differences in PXP were determined between the two thinned treatments.

Bole Growth

Both the BA25 and the BA50 thinning treatments produced significant gains in diameter and per tree basal area growth as compared to the unthinned control (table II).

Significant gains in diameter growth from thinning were apparent in the first season following treatment application. Diameter growth was increased by an average of 0.68 cm on the BA25 plots and by an average of 0.60 cm on the BA50 plots, relative to the BA100 treatment in 1984. In the second season following thinning the pattern of growth variation was the same as the previous year; however, diameter growth on the BA25 treatment was significantly greater than growth on the BA50 treatment. This result is somewhat in contrast with the results of McClurkin (1961). McClurkin found that thinning a 20 year old stand of shortleaf pine (P. echinata Miller) immediately increased soil moisture availability but did not increase diameter growth until the second year following treatment.

Diameter growth rates were generally high throughout the 1984 growing season. Figure 6 shows that growth rates exceeded 0.006 mm per day on the thinned plots from early June to mid-October, 1984. In contrast, diameter growth rates varied widely in 1985. As in 1984, diameter growth rates exceeded 0.006 mm per day on the thinned plots through June, then declined slightly. Growth increased after an early July storm then declined steadily. Stem shrinkage was observed towards the end of a 40 day drought period in July and August.

TABLE II
DIAMETER AND PER TREE BASAL AREA GROWTH
FOLLOWING THINNING

Treatment	Diameter growth		BA/tree growth	
	1984	1985	1984	1985
BA25	1.892a	1.732a	49.05ab	49.86a
BA50	1.806a	1.472b	46.40ab	41.82b
BA100	1.209c	0.0826d	27.73c	20.64d

means followed by the same letter are not significantly different at the 0.05 level, each mean is the average of 30 trees.

Latewood Transition Date.

The climatic differences between the two study years and the thinning treatments both had a significant impact on the date of transition from earlywood to latewood. Analysis of increment cores taken periodically during the the two summers indicated that the mean transition date for all treatments was June 25 in 1985, a relative dry summer, compared to July 17 in 1984, a year of high summer rainfall. Table 3 shows that the trees on the unthinned control plots made the transition a week and one half to two weeks earlier than the trees on the thinned plots.

TABLE III
 MEAN TRANSITION DATES AFTER THINNING
 1984 & 1985

Treatment	1984	1985
BA25	July 19ab	June 27d
BA50	July 21a	June 28cd
BA100	July 8bc	June 18d

means followed by the same letter not significantly different at the 0.05 level.

Figure 7 graphically represents the cumulative percentage of trees past the latewood transition date for 1984 and 1985. The graph shows that latewood initiation began around June 4 in 1985 (julian date 155) versus June 19 in 1984 (julian date 170). Over 90 percent of the sampled trees had initiated summerwood by July 11, 1985, while in 1984 the same percentage of trees past the latewood transition date was not reached until August 3rd.

Regression analysis indicated that transition date was significantly related to predawn moisture stress (equation 2).

(2)

$$TD = -2511.3 - 9471.7(P) - 0.207(BA) + 3889.8(E) - 7754.0(P^2) + 13698.6(P*E) + 11236.9(P^2*E)$$

Where: BA = stand basal area in m^2ha^{-1}
 P = predawn xylem pressure potential in MPa
 E = daily pan evaporation five days previous
 to latewood transition date in cm
 BA = treatment basal area in m^2ha^{-1}
 $R^2 = 0.74$
 $n = 85$
 $SE = 9.11$

Table III demonstrates that the thinning treatments also had a significant effect on transition date timing in 1984. In both years the transition average date of transition occurred ten to fourteen days sooner on the unthinned plots than on the thinned treatments.

Two general theories have been proposed to explain the mechanisms controlling the initiation of summerwood formation (Larson, 1962, Zahner, 1963). Larson (1962) states that environmental factors influence wood formation indirectly through changes in the growth and development of the tree crown. Patterns of wood formation from the pith outward and along the stem point the influence of the crown on xylem production. In loblolly pine wood formed within 7 to 10 rings of the pith is considered juvenile wood (Megraw, 1984). Such wood is formed in close proximity to the crown and is characterized by a high proportion of thin-walled, low density earlywood tracheids. In open-grown trees in which crown recession is delayed, the transition from

juvenile wood to mature wood is gradual and occurs later than in forest grown trees (Larson, 1962). Although the exact nature of the influence of the crown on wood formation is not completely understood, hormonal levels, particularly of indole-3-acetic acid (IAA, an auxin) appear to play a role (Larson, 1962, Wodzicki, 1973). Savidge and Wareing (1984) found axial gradients in IAA in stems of 20 year old lodgepole pine (P. contorta Dougl.). IAA in differentiating xylem showed seasonal variations and indicated a possible regulatory role of auxin in controlling latewood transition (Savidge and Wareing, 1984).

Zahner (1963) has emphasized the direct effects of the environment, particularly moisture stress, in initiating latewood formation. Zahner gives an excellent review of the process of latewood formation and states, "...when water deficits become large the (direct) effects probably override many of the indirect effects." Zahner goes on to hypothesize that high internal moisture deficits act to draw water out of the cambial cells and newly formed tracheids, reducing turgor available for cell expansion and thereby directly limiting their enlargement. Whitmore and Zahner (1967) demonstrated that decreased water potential levels decreased the incorporation of glucose into differentiating xylem cell walls in P. sylvestris L. Thus, cell wall growth was reduced independent of auxin levels (Whitmore and Zahner, 1967).

Our results suggest that both indirect and direct mechanisms were involved in controlling variation in latewood initiation. Variations in SWP, PXP, and evaporation between the two summers were significantly related to variations in transition date. Thus direct, moisture stress-related effects are implicated. The lack of treatment variations in moisture stress levels (figure 5) do not support the direct effects mechanism with regard to within year differences in transition date. However, light intensity patterns and stomatal conductance did vary between the thinned and control treatments (Cregg, unpublished data). These changes may be responsible for altering physiological processes in the crown and directly resulting in variations in latewood formation.

To summarize, it appears that between-year variation in latewood initiation was related to the direct effects of climate and moisture stress, while the within-year variation may be indirectly related to changes in crown function associated with thinning.

Latewood Percentage

Climatic variation between the study years had a greater impact on latewood percentage than the thinning treatments. Table IV shows that the mean latewood percentage for all treatments was approximately 9.5 percent lower in 1985 than 1984. Mean treatment latewood percentage

was highest for the BA100 treatment in both years; however, the difference between the treatments was not statistically significant ($p = 0.05$).

TABLE IV
MEAN LATEWOOD PERCENTAGE BY TREATMENT
1984 & 1985

Treatment	1984	1985
BA25	44.45ab	36.13c
BA50	44.67ab	34.51c
BA100	48.55a	38.78bc

means followed by the same letter not significantly different at 0.05 level.

Figure 8 relates the cumulative growth pattern of all treatments in 1984 and 1985 to changes in latewood percentage. This graph is useful in explaining the apparent discrepancy of the transition date and latewood percentage results. Although the 1985 mean latewood transition date was approximately 23 days earlier than in 1984, the mean percentage of latewood was greater in 1984. After the 1984 transition date, diameter growth continued at a relatively vigorous rate, while growth slowed in 1985 following

latewood initiation (figure 8). Thus, rapid late-season growth offset the later transition date in 1984, resulting in a greater percentage of latewood in the annual ring. Zahner and Whitmore (1964) demonstrated a similar pattern in an experiment with 25 year old red pine. One group of pines was subjected to imposed drought while the other group was irrigated. Trees subjected to drought initiated Mork latewood cell production on July 5; whereas the wet treatment trees began latewood production on July 12. Total latewood cell production was approximately 2 times greater on the irrigated treatment. Brix (1972) found that irrigation of Douglas fir delayed latewood initiation by over two weeks as compared to a natural rainfall control. The delay in latewood transition led to a reduction in latewood percent in the two years he studied.

Studies on the effects of thinning on latewood percentage have produced mixed results. Erickson and Lambert (1958) found thinning reduced latewood percentage to 32 percent for the four years following thinning, compared to 37 percent for the unthinned controls. Brix and Mitchel (1980) found that thinning decreased the latewood percentage of Douglas fir slightly. In the four years after thinning latewood percentage was 35.4 percent , compared to 38.4 percent for the unthinned control. Smith (1968), in contrast, demonstrated that thinning increased the percentage of latewood in the annual rings of loblolly pines thinned at age nine from 28.0 percent (unthinned) to 36.0

percent. Mean ring width was 3.56 mm for the unthinned trees and 9.61 mm for the thinned trees. Van Lear et al. (1977) documented an increase in the summerwood percentage after thinning longleaf pine (P. palustris Mill.). Trees thinned to 11.5 m²/ha averaged 66 and 71 percent latewood in the two years while trees on the unthinned control (33.6 m²/ha) averaged 56 and 64 percent over the same period.

Specific Gravity

Thinning had little effect on specific gravity of samples taken at breast height in either of the study years (table 5). In 1984 no pattern of stand basal area effect on specific gravity was evident; while in 1985 specific gravity was slightly higher on the heavily thinned treatment. The 1984 mean specific gravity for all treatments was 0.463, in 1985 the mean specific gravity for all treatments was 0.428. Both of the above mean values are within the range of specific gravity reported for nine to ten year old loblolly pine (Loo-Dinkins et al., 1984, Talbert and Jett, 1981).

Several regression models were developed to relate specific gravity to tree, stand, and environmental factors. Latewood percentage had the greatest impact on SG of the variables tested ($p > f = 0.0001$).

Larson (1957) undertook a thorough examination of the effects of environmental factors and tree characteristics on

the specific gravity of slash pine (P. elliotii Engelm.). Larson determined that latewood percentage was the single best predictor of ring specific gravity.

TABLE V
SPECIFIC GRAVITY FOLLOWING THINNING
1984 & 1985

Treatment	1984	1985
BA25	0.46ab	0.44abc
BA50	0.47a	0.42c
BA100	0.46a	0.43bc

means followed by the same letter not significantly different at 0.05 level.

Table IV indicates that mean treatment latewood percentage in 1984 and 1985 was highest in trees from the BA100 treatment. However, specific gravity was nearly equal among the treatments 1984 and highest on the BA25 treatment in 1985. Apparently, the thinnings influenced SG in addition to the effects latewood percentage. Although the treatments were not significant in any specific gravity regressions tested, the trees on the thinned plots were somewhat larger and a diameter effect may account for some

of the deviation from the expected latewood percentage-SG relationship (Equation 3).

(3)

$$SG = 0.15 + 0.007(L) + 0.000024(L^2) + 0.013(D) - 0.0004(L*D)$$

Where: L = Latewood percent as a whole number
 D = diameter in cm
 $R^2 = 0.40$
 $n = 75$
 $SE = 0.03$

Another possible explanation for the deviation in the latewood percent-SG pattern is presented by Brix and Mitchell (1980). They found that in the four years after thinning a Douglas fir stand to one-third the original density, cell wall thickness of the earlywood cells were increased from 3.17 microns to 3.50 microns.

A microscopic examination of a subset of the 1985 year-end increment cores used for specific gravity determination revealed a similar trend. Mean treatment cell wall thickness and radial thacheid diameters are presented in table VI.

TABLE VI
 1985 MEAN THACHEID CELL WALL THICKNESS
 AND RADIAL THACHEID DIAMETER

Treatment	Earlywood		Latewood	
	cell wall thickness	radial diameter	cell wall thickness	radial diameter
BA25	3.82b	41.89a	6.74a	25.74a
BA50	4.89a	42.00a	6.87a	23.58a
BA100	3.37c	38.95b	7.13a	24.89a

all values in microns. Means in the same column followed by the same letter are not significantly different at 0.05 level.

The increase in EW cell wall thickness, (and therefore EW density) may, at least partially, counteract the higher latewood percentage found on the BA100 treatment thus resulting in no net difference in specific gravity.

CONCLUSION

Variation in the date of transition from earlywood to latewood in two years of contrasting climate indicates that a direct, moisture stress related mechanism is involved in the initiation of latewood formation. Latewood initiation occurred 10 to 14 days earlier on thinned plots than on unthinned plots in both years suggesting that indirect mechanisms, perhaps associated with crown function, are superimposed over the climate impacts.

Treatment patterns of latewood percentage demonstrate that increased growth rates in the thinned trees can compensate for the later transition date, resulting in little net effect on latewood percentage following thinning. Likewise, thinning did not cause a significant change in specific gravity. Diameter and per tree basal area growth increased significantly after thinning.

For the forest scientist, the results reported here point out the importance of accounting for climatic variation in appraising the effects of silvicultural treatments on wood properties. Comparisons between studies must be made carefully and consideration must be given to stand, climatic, and edaphic factors. In addition, research in this area will continue to be of vital importance.

Identification of the relative importance of the direct and indirect effects of stress in wood formation may prove valuable in manipulating wood properties silviculturally.

For the forester, the results concur with the preponderance of the evidence that faster growth rates per se do not equate to less dense, weaker wood. Increased growth rates will, however, lead to shorter rotation lengths, increasing the proportion of juvenile wood in harvested trees. A possible remedy suggested by our work and that of Larson (1962) would be to postpone precommercial thinning to allow increased natural self-pruning. By reducing the live crown ratio at an early age, the length of juvenile production may be shortened. Once the stand is eventually thinned, the capacity for mature wood expansion will be increased.

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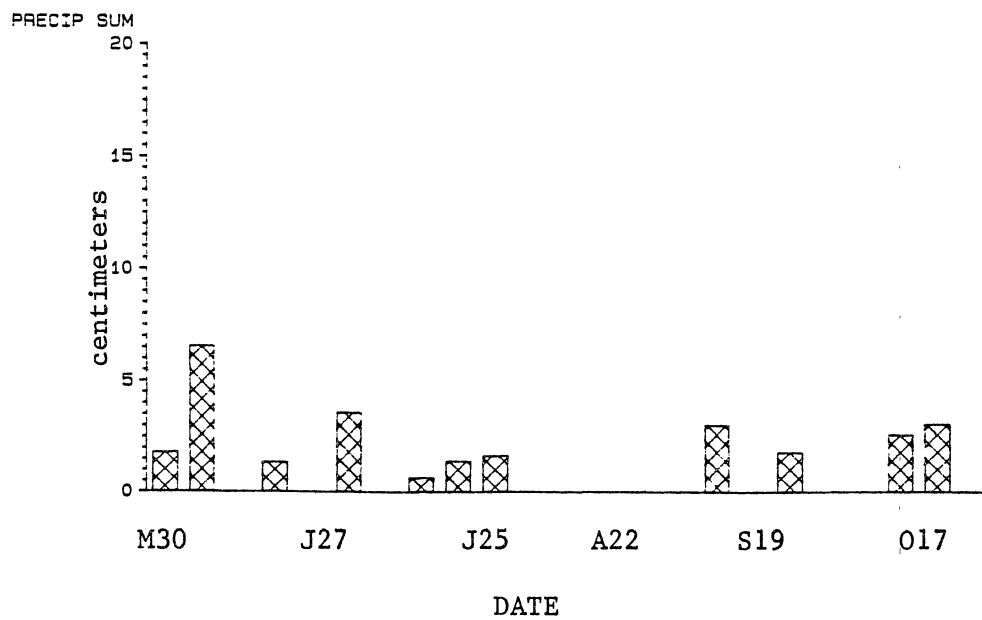
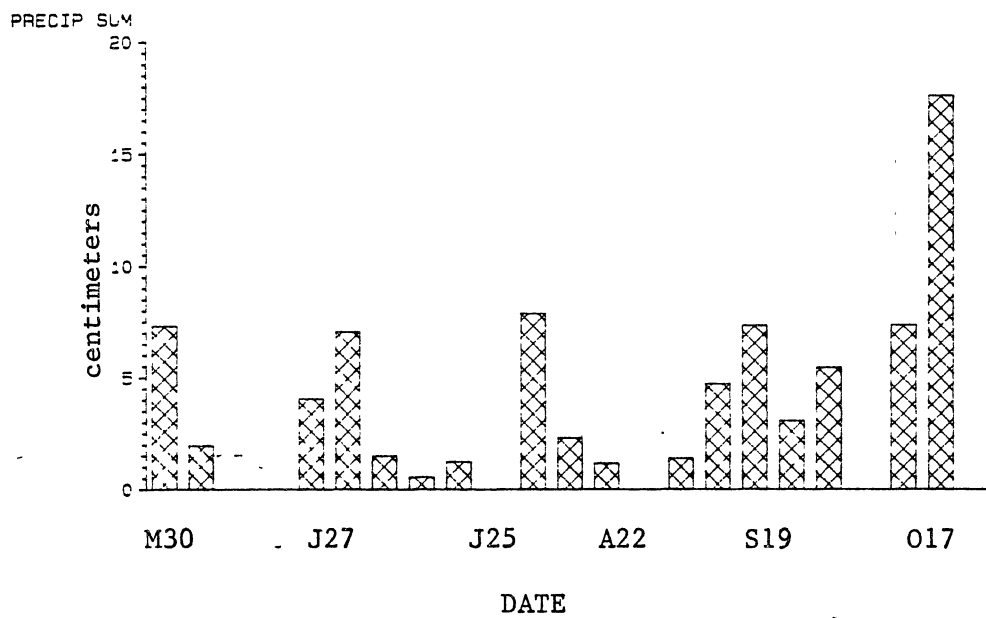


Figure 1. On Site Precipitation in cm, 1984 and 1985.

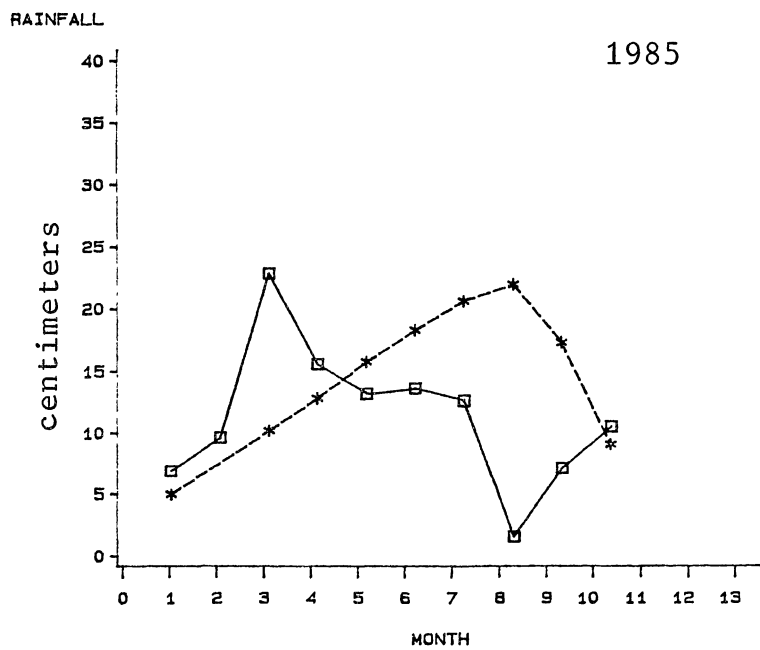
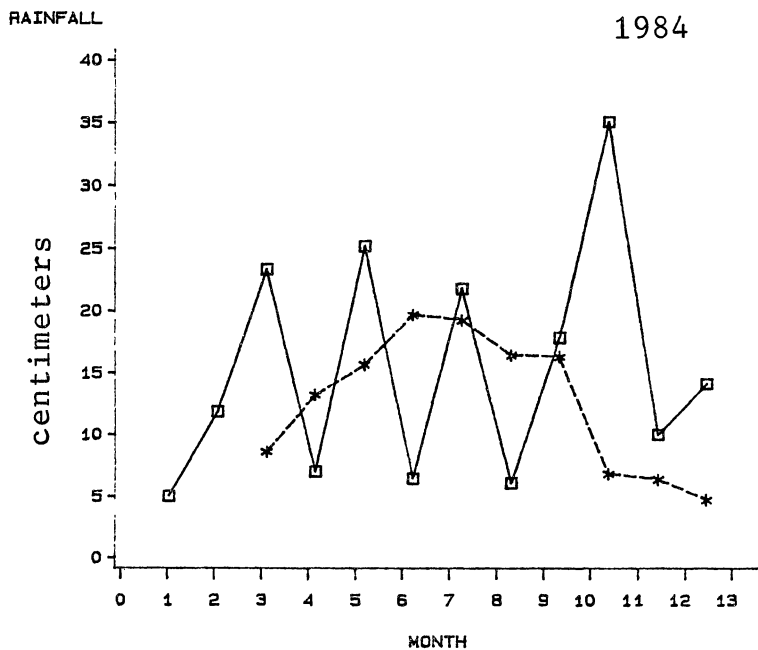


Figure 2. Monthly Rainfall and Pan Evaporation From Broken Bow Dam, 27 km North of Study Site.
 Solid line = Rainfall,
 Dashed line = Evaporation.

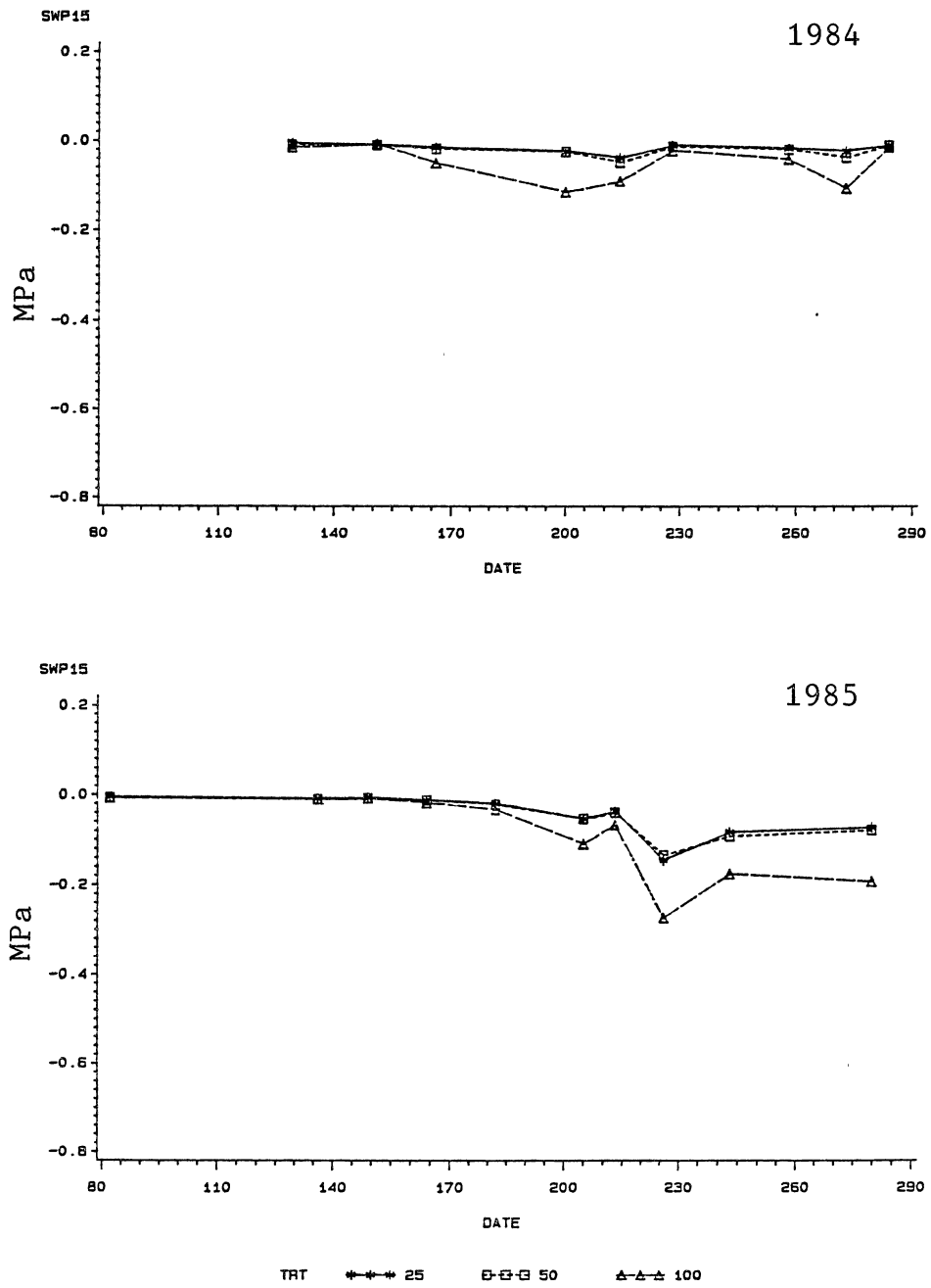


Figure 3. Seasonal Trend of Soil Water Potential at the 15 cm depth, 1984 and 1985.

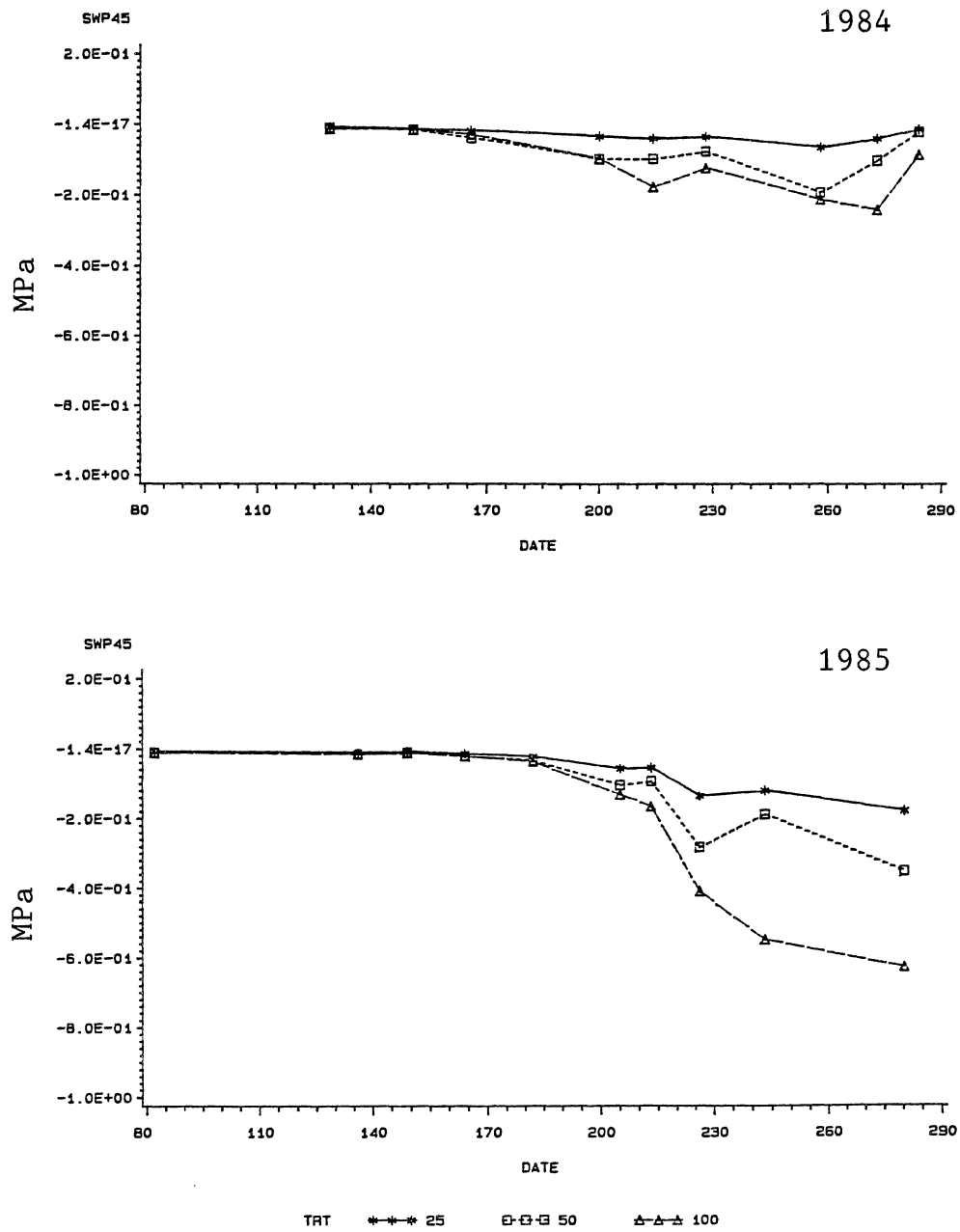


Figure 4. Seasonal Trend of Soil Water Potential at the 45 cm depth, 1984 and 1985.

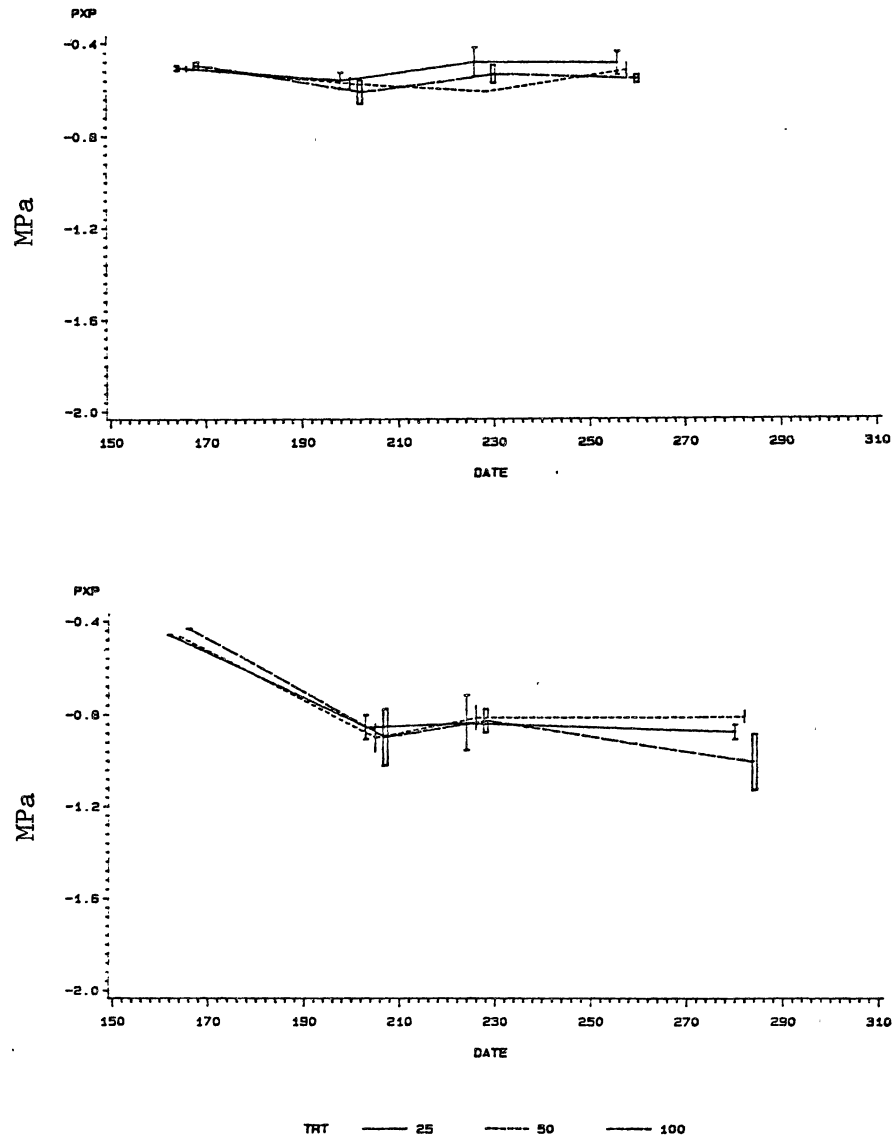


Figure 5. Mean Predawn Xylem Pressure Potential (PXP), 1984 and 1985. Each bar represents 95% C.I. for each mean.

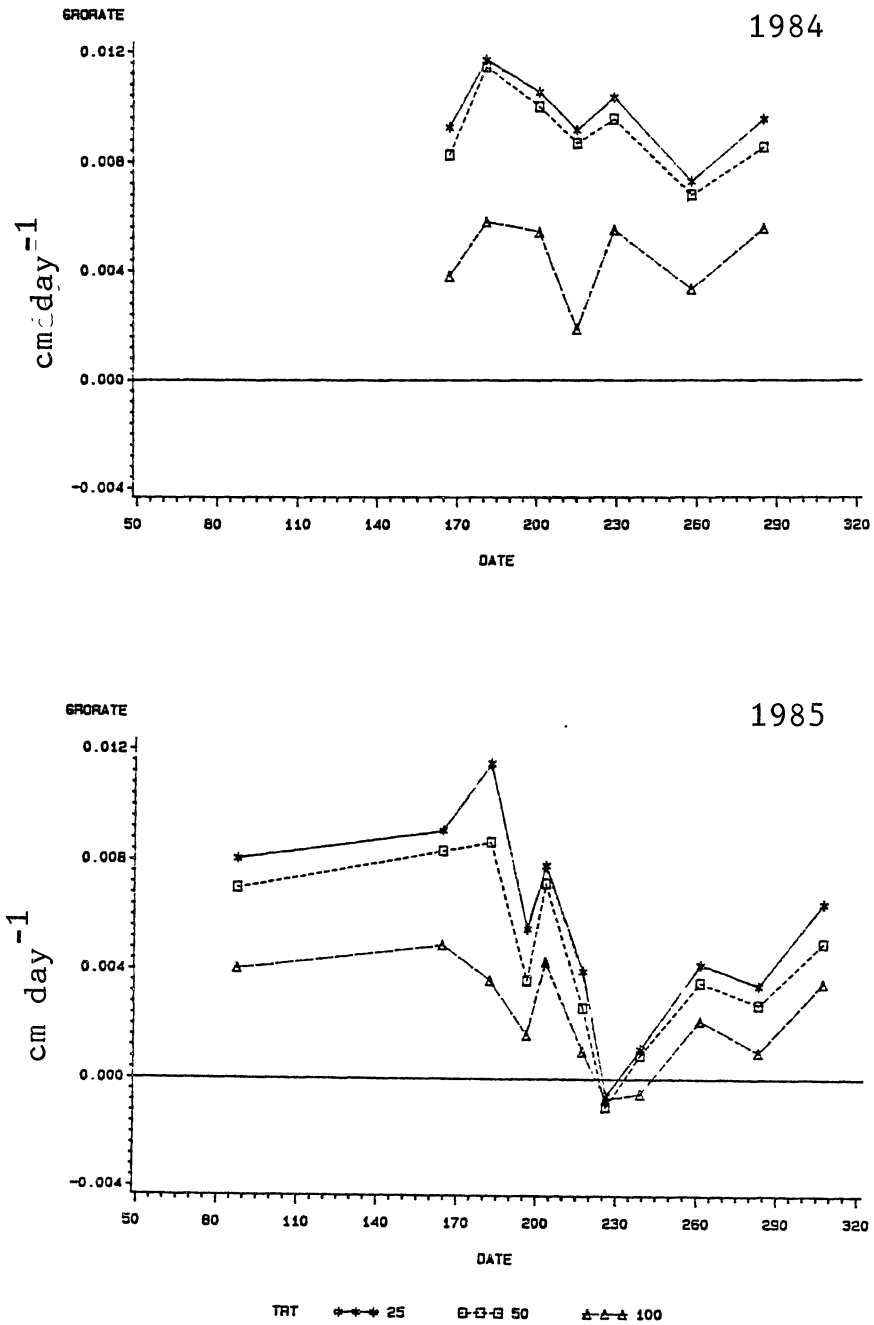


Figure 6. Daily Diameter Growth Rate, 1984 and 1985.

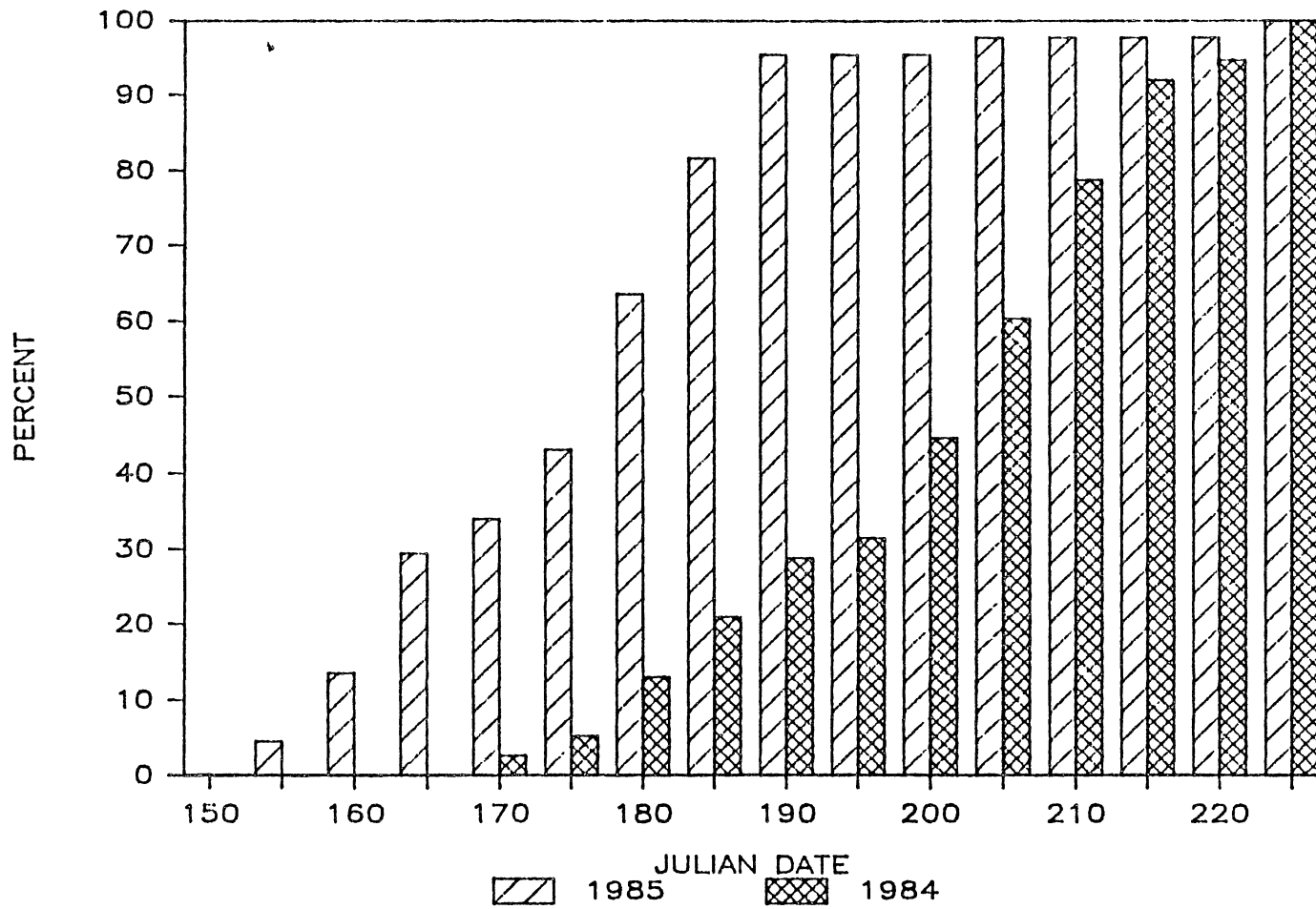
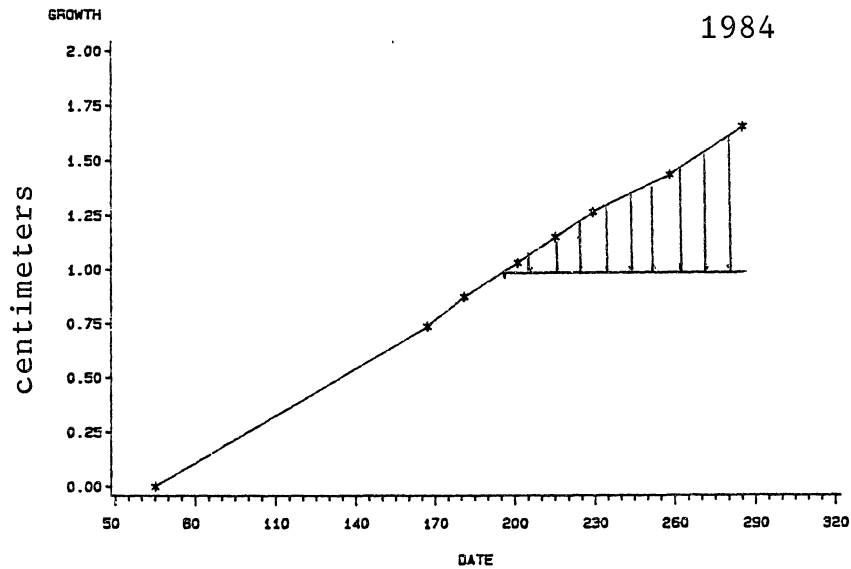
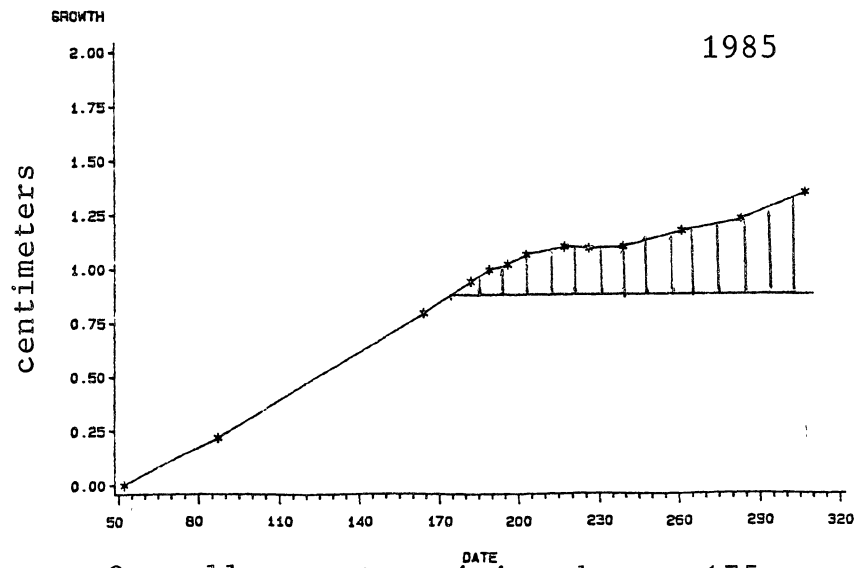


Figure 7. Cumulative Percentage of Trees Past Latewood Transition Date, 1984 and 1985. Percent represents percent of all trees past transition date.



Overall mean transition date = 197.



Overall mean transition date = 175.

Figure 8. Cumulative Diameter Growth Trend For All Treatments, 1984 and 1985. Hatched area represents growth after latewood transition.

VITA

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Candidate for the Degree of

Master of Science

Thesis: THE EFFECTS OF PRECOMMERCIAL THINNING ON WATER RELATIONS AND WOOD QUALITY OF LOBLOLLY PINE (Pinus taeda L.)

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