

PHYSIOLOGICAL RESPONSES OF SUN AND SHADE FOLIAGE IN
THINNED AND UNTHINNED TEN-YEAR-OLD LOBLOLLY PINE STANDS

by

Jaroslav Nowak

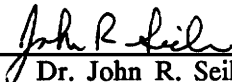
Thesis submitted to the Faculty of
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

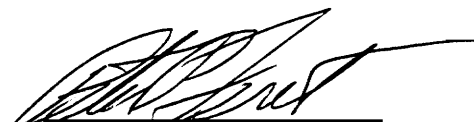
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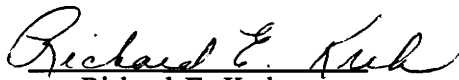
Dr. John R. Seiler
Chairman



Dr. Peter P. Feret
Committee member



Dr. Shepard M. Zedaker
Committee member



Richard E. Kreh
Committee member

November 1991

Blacksburg, Virginia

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(ABSTRACT)

During the third growing season after thinning, eight-year-old loblolly pine gas exchange parameters were measured. Full sunlight and stand light conditions for upper (sun) and lower (shade) crown foliage were examined. Xylem water potential, litterfall dynamics and tree growth were monitored. Nutrient availability, chlorophyll content and chlorophyll a/b ratio were assessed.

At the end of the third post-thinning growing season (eleventh season since planting),
→ thinned trees had larger stem and crown diameters, and live crown ratios. Thinned trees grew 11 cm more in height, and approximately 35% more in diameter, basal area and volume. Only crown diameter differences were statistically significant at $p=0.05$.

Upper crown foliage was found to have somewhat higher net photosynthesis, stomatal conductance and transpiration when measured under saturating light conditions. Lower crown needles displayed features usually associated with shade foliage: lower photosynthetic capacity, lower light compensation point and dark respiration rates. Observed physiological differences were not related to plant water status, chlorophyll content or chlorophyll a/b ratio. The higher light saturated gas exchange rates for upper crown foliage were paralleled by lower stomatal limitations to photosynthesis, possibly the effect of better potassium supply facilitating more efficient stomatal function.

Light conditions in thinned stands did not differ significantly between the upper and lower crowns, even though light levels in the lower crowns of unthinned stands were nearly a third of that in the upper crowns. This had an effect on in situ photosynthetic rates, which

were similar in the upper and lower crowns of thinned trees. In situ photosynthetic rates in thinned stands were also similar to those measured under saturating light. In the unthinned stands, because of light differences, gas exchange rates were significantly reduced in the lower crowns, with only upper crown foliage fully utilizing its potential for photosynthesis. The physiological activity in the upper crowns of unthinned trees tended to be even higher than in the upper crowns of thinned trees.

Litterfall timing did not differ between the thinned and unthinned stands. Litterfall per hectare was higher in unthinned stands, but when expressed on a per tree or unit basal area basis it averaged higher in thinned stands. A larger photosynthetic apparatus together with full utilization of photosynthetic potential in both crown positions are likely the major reasons for better growth of thinned trees.

ACKNOWLEDGEMENTS

I would like to express my thanks to Dr. John R. Seiler, my major professor, for his guidance and support throughout this project and my studies at VPI&SU. I appreciate very much all the time and advice he shared with me, and that he was always ready to do so. Thanks also go to Ben Cazell, who was a crew member on almost each measurement date. His assistance and experience made things much smoother in the field and on the computer.

I would like to thank members of my committee, Dr. Shepard M. Zedaker and Dr. Peter P. Feret for their critical reviews of my writings, and Richard E. Kreh for his help in the field. Without their advice my thesis would not be complete.

Thanks go also to Jack Bird from the Reynolds Homestead Experimental Station for his help in collecting data. My fellow students Piotrek Tyszko and Todd Fredericksen helped me a great deal to define my role in the University community. I would like to thank all other faculty and staff as well as all other students at VPI&SU, for creating friendly intellectual atmosphere during my studies.

Last but not least I would like to thank my wife Ana for her constant support and my family back in Poland for support and encouragement. Thank you all!

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INTRODUCTION AND JUSTIFICATION

Foresters recognized as early as the nineteenth century that thinning of forest stands allowed the remaining trees to maintain rapid growth rates. Since that time many different systems of thinning have been developed. The basic idea is, however, the same - to provide the residual trees with more space, so they have more light, nutrients and water. Allocation of resources to the remaining trees increases the quality and dimensions of these trees. This allows dimensional products to be obtained in a shorter time.

Although the advantages of thinning are well documented, the physiological mechanism responsible for the acceleration of growth is not well understood. Faster growth is commonly attributed to the increased photosynthetic capacity of the remaining trees due to larger crown dimensions and live crown ratios, as well as to increased photosynthesis of the lower parts of the crowns (Kramer and Kozlowski, 1979). It is not clear how foliage in thinned and unthinned stands differs physiologically, or whether differences have any biological significance. Some investigators have found that increased growth is related to improved water relations (Sucoff and Hong, 1974; Lilieholm and Hu, 1984; Donner and Running, 1986; Bassman, 1988).

Ginn (1989) tried to answer many of these questions by examining physiological and growth differences in eight-year-old stands of loblolly pine for two consecutive years after thinning. She investigated the physiological potential of needles by taking measurements in full light. This study is a continuation of that project, and a further attempt toward understanding physiological mechanisms of tree response to thinning of the stand. The main objective is to identify the reasons for increased growth in ten-year-old loblolly pine stands two years after thinning.

In contrast to Ginns' (1989) study, this study evaluates gas exchange rates of needles in situ, as well as under full sunlight. The relationship between the needle physiology and tree growth is given special attention.

OBJECTIVES

The specific objectives of this study are:

1. To determine: a. seasonal patterns of needle gas exchange under light saturated conditions, b. water status, c. nutrient and chlorophyll content of sun and shade foliage, and d. needle biomass production in relation to growth of trees.
2. To determine in situ seasonal needle gas exchange patterns under stand light conditions, for sun and shade foliage from thinned and unthinned stands and relate these variables to tree growth.
3. To compare photosynthetic responses to different light and CO₂ levels for sun and shade foliage from thinned and unthinned stands.

LITERATURE REVIEW

Thinning is one of the most common forestry management practice. Removing fraction of the growing stock, thinning alleviates competition and modifies environmental conditions within the stand. As a result remaining trees grow faster in diameter. This is caused by combination of reasons: improved water relations and nutrient status of the plants, better crown illumination, larger photosynthetic apparatus, increased gas exchange rates are among most commonly mentioned in the literature. There is substantial amount of writings on tree growth response, nutrient status and water relations after thinning. There is however, fewer examples on how thinning affects foliage gas exchange rates and none on foliage photosynthetic responses to different levels of light and CO₂.

Maximum size-density relationship

The number of trees planted in even-aged, single species plantations is up to ten times greater than the number harvested (Ford, 1984). As trees grow, competition develops between individuals because of limited space available. Some plants receive less solar radiation, nutrients, water and CO₂ than they can utilize for growth (Ford, 1984). Forest trees generally respond to crowding by reduced diameter growth. When the competition within the stand intensifies, the smaller, suppressed individuals die (Schmidting, 1988).

Reineke (1933), was among the first to quantify the relationship between the maximum number of trees per unit area (N) and their average diameter (D) in single species even-aged stands

$$\log N = - 1.605 \log D + k$$

where k is the constant depending on the species. He found the equation to be true for 12 out of 14 species including loblolly pine, regardless of the age of trees and site quality

(Reineke, 1933). Plotted on log-log scale the relationship assumes straight line with the slope of -1.605. Japanese researchers (Yoda et al., 1963), who related mean plant biomass to the number of live plants per unit area, found that the slope of the resulting line is equal to -1.5 for a variety of species. Drew and Flewelling (1979) proposed that in pure even-aged stands, the maximum mean tree volume (V) attainable for any density (N) can be described by the equation

$$\ln V = -1.5 \ln N + k$$

where -1.5 is the slope of the maximum size-density relationship.

Von Gadow (1986) found that the limiting relationship in the form of Reineke's equation varies among different pine species, and among growing sites within the same species. Variation in the slopes as well as in the intercepts was common. The slopes were also found to be steeper than those reported elsewhere (von Gadow, 1986). Working with nine provenances of loblolly pine Schmidting (1988) concluded that the slopes of volume/density curves did not differ significantly from each other by provenance and averaged -1.61. The same provenances differed significantly at the intercept (Schmidting, 1988). Although the universality of -1.5 slope is questionable, it seems that pure, even-aged stands of trees grow according to maximum size-density relationship proposed by Drew and Flewelling (1979). The mean tree volume increases until the zone of competition induced mortality is reached. Further growth in volume is accompanied by mortality unless thinning is applied. Thinning by reducing density of the stand sets higher limit for the maximum mean tree volume attainable (Drew and Flewelling, 1979).

Growth and yield after thinning

Increased diameter growth of the residual trees is an integrated thinning response to improved environmental conditions. Increased growth is due largely to greater water and

minerals availability as well as increased light availability. Released trees also increase their leaf area by expanding both crown width and live crown ratio (Kramer and Kozlowski, 1979). Litter collection may be a useful tool in assessing changes in the size of the assimilator apparatus (leaf biomass) due to thinning. In a study reported by Cousens (1988), needle production of Scots pine (*Pinus sylvestris* L.), peaked in the third growing season after thinning and remained more or less constant thereafter.

Leaf biomass increases are accompanied by higher photosynthetic rates and enhanced physiological activity of the crown. This in turn is followed by increased cambial growth leading to increased diameter growth (Kramer and Kozlowski, 1979). Height growth usually is not greatly affected regardless of thinning intensity (Kramer and Kozlowski, 1979).

Smith and Hafley (1986) evaluated eight long term thinning studies of loblolly pine plantations grown across the range of the species. Plantations early and heavy thinned yielded more than 15 Mbf per acre in a 30 year rotation. The 10 x 10 ft unthinned plantings would not yield equivalently until age 50. Selective thinning produced the largest stem diameters. The decrease in total yield associated with thinning intensity diminished as rotation length was increased. Row thinning with subsequent moderate to heavy selective thinning resulted in responses similar to selective thinning alone. Row thinning without subsequent selective thinning had only a small effect on average diameter but still significantly affected dominant trees diameters (Smith and Hafley, 1986).

Cregg et al. (1988) concluded that thinning a 10-year-old stand of loblolly pine in Oklahoma increased individual tree basal area growth without reducing wood density. Stands were selectively thinned from below and target basal areas were: 5.8 m²/ha, 11.5 m²/ha and 23 m²/ha (unthinned control). During two consecutive years after thinning, basal area growth per tree increased by about 70% and more than 100% (first and second year respectively), when compared with basal area growth on the control plots. Increases in diameter and basal area growth were greater on more intensively thinned plots (Cregg et al., 1988).

In the same stands being used in the current study, Ginn (1989) found that during the second growing season following a row thinning in 8-year-old loblolly pine, tree growth in diameter at breast height, basal area and volume in thinned stands was 50% higher than that in unthinned stands.

Physiological effects of thinning

Physiology of sun and shade foliage

Thinning treatments can influence the physiology of tree foliage by changing light conditions within the crown. It is generally accepted that sun and shade foliage differ morphologically, physiologically, and biochemically. Sun leaves are usually two or three times thicker, contain more palisade and spongy parenchyma (Bolhar-Nordenkamp, 1985) and have greater volume than shade leaves (Kramer and Kozlowski, 1979). The increased density of smaller stomata in sun leaves helps to avoid water stress since some CO₂ uptake remains possible even if the evaporative demand in the surrounding air is high (Bolhar-Nordenkamp, 1985). At the biochemical level, the thicker sun grown leaves contain more carboxylating enzyme (Rubisco) and more electron carrier per unit of leaf surface than shade leaves (Kramer and Kozlowski, 1979).

Shade foliage is often reported to have higher chlorophyll content (Koch, 1976 cited by Kull and Koppel, 1987). Schaffer and Gaye (1989) reported that the chlorophyll content of mango (*Mangifera indica* L.) leaves increased as percent of shading increased from 0 to 75%. Higginbotham (1974), however, working with mature loblolly pine found no crown position difference in chlorophyll concentrations.

It seems that the changes in the ratio of chlorophyll a/b proteins to cytochrome f are

more important for sun/shade character of foliage than changes in the chlorophyll concentration alone. Bolhar-Nordenkampf (1985) suggested that changes in the ratio of chlorophyll to cytochrome f in shade grown leaves indicated increased ratio of light harvesting complex to photosystems. This causes shade leaves to have a higher light use efficiency at low light intensities, but lower efficiency at high light intensities, because increases in light harvesting systems decreases the intensity at which light saturation occurs (Kramer and Kozłowski, 1979).

Ginn (1989) found light saturated net photosynthesis and stomatal conductance in lower crowns of thinned stands more similar to upper crown values than to lower crown values of unthinned stands. In addition, Ginn (1989) found that the specific leaf areas of lower crown needles in thinned stands were greater than those of the lower crown in unthinned stands, indicating that thinning caused morphological as well as physiological changes in needles due to increased light levels. Overall, needles in the lower crown of the thinned stands became more like sun foliage.

Foliage nutritional status

Nutrient supply is important for growth and other physiological processes. Thinning by reducing stand density increases nutrient availability. This does not always lead to increased foliar nutrient contents. After thinning pole-sized sugar maple Stone and Christenson (1975) observed small but consistent decreases in foliar concentrations of N, P, K, Ca, Mg, Fe, Mn and several other elements, along with significantly increased diameter growth. Researchers attributed the decreased foliar nutrient concentrations to dilution effects resulting from increased growth. In contrast, trees in thinned stands of 15 to 20-year-old Thuja plicata Donn ex D. Don, showed consistently higher foliar concentrations of N, K, and in some years S than the unthinned stands (Harrington and Wierman, 1990). Madgwick et al. (1983) showed that in

7-year-old Pinus radiata stands, nitrogen concentrations decreased with needle age, from the top to the bottom of the crown, and were unaffected by thinning.

Similar results were reported by Ginn (1989). Foliar analysis of N, P, K, Ca, Mg, Fe and S showed no differences between thinned and unthinned stands. Lower crown needles, however, contained significantly less N and K.

Changes in nutrient content may alter foliage gas exchange rates. Nitrogen status of needles can influence photosynthesis through chlorophyll and protein synthesis. A deficiency in nitrogen supply results in lower chlorophyll content, and consequently lower photosynthesis. The adverse effect of nitrogen deficiency on CO₂ uptake is thought to be stronger than phosphorus or potassium deficiency (Kramer and Kozlowski 1979). Shortages of potassium and phosphorus can impede energy transfer and increase respiration, therefore lowering net photosynthesis. Additionally, potassium ion flux is also important to stomatal closure and opening (Kramer and Kozlowski, 1979).

Plant water relations

Thinning has the potential to improve plant water relation. After treatment fewer individuals share available moisture. In a thinning and fertilization study by Brix and Mitchell (1986), thinning increased soil water potential during dry summer months (July through September) by 1 MPa throughout a 10-year period. Despite improved soil water potential, shoot water potentials were higher only during predawn and early morning measurements (Brix and Mitchell, 1986).

Cregg et al. (1988, 1990) also concluded that thinning increases soil moisture available for remaining trees by increasing throughfall and reducing losses due to transpiration. In their thinning study, pre-dawn xylem water potential did not vary consistently between the treatments (Cregg et. al, 1988). Also, seasonal noon xylem water potential showed no consistent

treatment effects associated with thinning (Cregg et al.,1990). These results support the findings of Sucoff and Hong (1974), who monitored soil and needle water potential in thinned and unthinned plots of red pine. They found that soil water potentials were always higher in the thinned plots. The pattern of needle water potential was inconsistent with that of soil water potential.

In situ foliage seasonal gas exchange patterns

Thinning may affect gas exchange characteristics of the whole crowns or their parts by changing environmental regime within the stand. Short term (instantaneous) measurements of photosynthesis and transpiration are often used to assess plant physiological status (Sasek and Richardson, 1989). Measurements are usually repeated at regular time intervals to follow seasonal changes in the measured parameters (Ginn, 1989; McLaughlin et al., 1990). Literature does not provide examples of in situ measurements of gas exchange parameters in relation to thinning with respect to upper and lower crowns or sun and shade foliage.

Using the Li-Cor 6200 portable photosynthesis system, McLaughlin with colleagues (1990) measured net photosynthesis and dark respiration rates of red spruce saplings on five dates during the 1987 growing season. They did not detach measured shoots from the trees, but were using supplemental artificial light to reduce variation in incident radiation levels. Only occasionally natural light levels were used during net photosynthesis measurements. On one of two sites growth in diameter at 25 cm above ground level was strongly correlated with net photosynthetic rates of current year foliage ($R^2=0.65$) (McLaughlin et al., 1990).

In a study conducted in southeastern Oklahoma (Cregg et al., 1990), stomatal conductance and transpiration of young loblolly pine trees increased during the first growing season after thinning. Increased transpiration was due to differences in light interception and crown exposure. Seasonal trends were established based on data collected during 4 to 5 dates

in each of three growing seasons. Researchers measured conductance and transpiration with a steady state porometer (Li-Cor 1600) working in the crowns of young loblolly pine trees. It is not clear however, if the needles were, or were not detached from the twig during the measurements (Cregg et al., 1990).

There is no evidence in the available literature how foliage respiration rates are related to the thinning of a stand. In a young loblolly pine stand needles respire about 30% of the total photosynthate produced (Kramer and Kozlowski, 1979).

Light and CO₂ foliage photosynthetic responses

Thinning may cause physiological changes in loblolly pine foliage which can not be assessed by short term gas exchange measurements. Short term measurements are useful for comparing major physiological differences between individual trees or treatments, but they do not provide good insight into the photosynthetic mechanism. In addition short term measurements can vary greatly during the day, during the season, even from branch to branch. Analysis of photosynthetic responses to light and internal CO₂ concentration provides clues to biochemical changes within the photosynthetic apparatus. Using those techniques one can estimate the relative importances of stomatal and biochemical limitations to photosynthesis (Sasek and Richardson, 1989; Long and Hallgren, 1985).

Photosynthesis as a function of light

Thinning may induce changes in sun/shade character of needles. Constructing light-photosynthesis curves facilitates analysis of changes in foliage photosynthetic capacity, efficiency of light utilization, location of light compensation points and magnitude of dark respiration rates.

The response of net photosynthesis rate (P_s) to photosynthetic photon flux density (PPFD) consists of two phases. An initial linear phase of increase in P_s with PPFD starts at the light compensation point. The slope of the initial linear phase is described as the apparent maximum quantum yield. When transmitted and reflected light are accounted for, the result is the true maximum quantum yield (Long and Hallgren, 1985). The quantum yield is the measure of the efficiency of light utilization by photosynthesis. It expresses the number of moles of CO_2 fixed per mole of photons absorbed by a leaf. The maximum quantum yield can only be measured at low PPFD, when photosynthesis is light limited and proportional to light level (Long and Hallgren, 1985). The steeper the slope of the linear portion, the higher the maximum quantum yield and therefore higher efficiency of light utilization.

Net photosynthesis responds hyperbolically to PPFD when light becomes less important as a limiting factor. At high irradiances, P_s is limited by the supply of the CO_2 and dark reactions of photosynthesis (Sasek and Richardson, 1989). Individual leaves of many C_3 plants are light saturated in approximately 25% of full sunlight, or roughly $500 \mu\text{E}\cdot\text{m}^2\cdot\text{s}$ (Long and Hallgren, 1985). The light saturated net photosynthetic rate ($P_{s_{\text{max}}}$) is considered a measure of the photosynthetic capacity of the leaf (Long and Hallgren, 1985; Sasek and Richardson, 1989). $P_{s_{\text{max}}}$ varies with almost all environmental factors which influence photosynthesis. It also depends on leaf age, ontogeny and preconditioning. Considerable variation in photosynthetic capacity of the leaves may be found even within the same plant (Long and Hallgren, 1985).

Light responses of photosynthesis are different for plants acclimated to low and high light habitats. Low light acclimated plants have a lower compensation point (in part because of lower respiration rates), and lower saturation points (Kozlowski et al., 1991). Their quantum yield is higher but the curvilinear portion of the function levels off quickly and often declines in very high light. The decline is caused by the photoinhibition of photosynthesis. In severe cases of light stress, photooxidation of the chlorophyll may occur (Kozlowski et al., 1991).

Plants acclimated to high light conditions have a lower quantum yield and the function line levels off at higher light intensities (higher saturation point). High light acclimated plants have a higher compensation point and the decline of photosynthesis in high PPFD is not observed. The latter because photoinhibition and/or photooxidation are seldom reported for those plants, they may occur however, in case of temperate and cool climate evergreens under high light and low temperature conditions (Kozłowski et al., 1991).

Photosynthesis as a function of CO₂

Examining foliage photosynthetic responses to different levels of CO₂ may provide evidence on how thinning of a stand changes parameters of carbon dioxide uptake and utilization. Carboxylation efficiency, CO₂ compensation point, stomatal and nonstomatal limitations to photosynthesis may be altered as foliage of the thinned stands adjust to operate in changed environmental regime.

The response of net photosynthetic rate (P_n) to intercellular CO₂ concentration (C_i) consists of two phases. At the beginning increases in the P_n rate (which starts at the CO₂ compensation point) is proportional to increases in C_i . This linear response is characteristic of CO₂ limited phase and is known as the demand function. A slope of the linear portion corresponds to the carboxylation efficiency (Sasek and Richardson, 1989), which is measured as a ratio of change in photosynthesis to change in CO₂ concentration at the mesophyll cell surface (C_i)(Long and Hallgren, 1985). The carboxylation efficiency depends on both mesophyll conductance to CO₂ (reverse of mesophyll resistance) and Rubisco efficiency. A steeper line indicates a higher mesophyll conductance (less resistance to CO₂ movement inside mesophyll cells), or higher Rubisco efficiency, or both.

A close agreement between the initial slope dP_n/dC_i with the amounts of extractable Rubisco suggests that when C_i approaches zero

$$dP_s/dC_i = v_{\text{Rubisco}}$$

where v_{Rubisco} = velocity of RuBP carboxylation ($\text{mol/m}^2\cdot\text{s}$) (Long and Hallgren, 1985). This means that at low C_i , net CO_2 fixation is determined by the kinetics of Rubisco since the substrate RuBP was shown to be present in saturating amounts (von Caemmerer and Farquhar, 1981). As a result the initial slope of the CO_2 response curve is proportional to CO_2 supply. If the maximum activity and the amount of the Rubisco are assumed to be proportional, then the initial slope of the P_s/C_i curve indicates the relative size of the Rubisco pool. The initial slope is affected by irradiance; in saturating light it is affected by the temperature and O_2 concentration (Sasek and Richardson, 1989).

When the function line reaches its asymptote, CO_2 becomes plentiful and the rate of net photosynthesis depends on RuBP regeneration, which in turn depends on ATP and NADPH regeneration and triphosphate utilization. The regeneration of ATP and NADPH may be dependent on the electron transport capacity and the rate of photophosphorylation (Sasek and Richardson, 1989).

Farquhar and Sharkey (1982) elaborated a method of calculating stomatal limitation to photosynthesis (l_s), which is most commonly used and referred to (Long and Hallgren, 1985; Assmann, 1988; Jones, 1985) using the following function

$$l_s = (P_{s0} - P_s) / P_{s0} = 1 - P_s / P_{s0}$$

where P_s = net photosynthesis rate in ambient CO_2 , P_{s0} = net photosynthesis rate which would occur if the resistance to CO_2 diffusion were zero (Farquhar and Sharkey, 1982).

Jones (1985) thoroughly discussed methods applicable to partitioning gas phase stomatal and nonstomatal limitations to photosynthesis resulting from resistances to diffusion of CO_2 across components of photosynthetic systems. He concluded that the differential method is the only one which does not rely on extrapolation and gives a good estimate of gas phase limitations (l_g) under the actual operating conditions. Generally the value of l_g computed using this method is within the range 0 and 1, and falls to zero as soon as the photosynthetic

system is CO₂ saturated. The calculation formula is given by

$$l_g = r_g / (r_g + r_*)$$

where r_g is inverse positive slope of the supply function and r_* is the inverse slope of the demand function, at the point of actual net photosynthesis. The method is particularly appropriate when small changes in component processes are investigated (Jones, 1985). The method may therefore prove useful in detecting physiological differences between sun and shade foliage from thinned and unthinned stands in our study.

MATERIALS AND METHODS

The Study Site

The study is conducted in three replicate loblolly pine stands 0.222 hectare each, planted in 1980 at the Reynolds Homestead Agricultural Experiment Station in Critz, Virginia. The stands were planted at an original spacing of 3.05 by 3.05 meter, on an old field site. A Wickham loam soil supports stand 1 and a Lloyd clay loam soil supports stands 2 and 3. Estimated site indices in these stands range from 23 to 25 meters (loblolly pine, base age 25). Original stands growth parameters at the age eight are given by Ginn (1989).

On March 2, 1988 one half of each stand was chosen randomly and thinned mechanically by removing alternate diagonal rows, so that a square spacing was maintained. The remaining trees averaged a residual basal area of 9.4 m²/ha in thinned plots and 16.8 m²/ha in the unthinned plots. A two row buffer of trees was maintained along borders of stands and between plots. On May and September of 1988 glyphosate herbicide was applied in both treatments to control understory vegetation: Rubus spp., Lonicera spp. and Rhus spp.

Two years after thinning (following the tenth growing season), average heights on thinned and unthinned plots were basically the same: 10.39 and 10.72 meters respectively. Average diameter at breast height (DBH) was 19.2 cm on thinned plots versus 17.4 cm on unthinned plots. Both live crown diameter and live crown ratio were larger on thinned plots, 4.84 m and 69.2% versus 3.88 m and 62.9% on unthinned plots (Ginn 1989).

Measurements

Experiment 1

Light saturated foliage gas exchange rates and growth of trees

Objective 1

To determine: a. seasonal patterns of needle gas exchange under light saturated conditions, b. water status, c. nutrient and chlorophyll content of sun and shade foliage, and d. needle biomass production in relation to growth of trees.

Gas exchange and water potential measurements.

Photosynthetic rate, transpiration rate, stomatal conductance, and twig water potential were measured monthly during the growing season, starting in May and ending in November 1990. Three permanent trees in each treatment/block combination (plot) were sampled on a measurement day, giving total of 18 trees. Two twigs, one from the upper (sun) and one from the lower (shade) third of the crown were clipped from each sampled tree. Measurements taken by Ginn et al. (1991) indicate that clipping does not lower the photosynthetic rate of loblolly pine twigs. The needles from clipped twigs were exposed to full ambient sunlight during gas exchange measurements. During cloudy weather a portable lamp was used to provide above saturation light levels (for loblolly pine approximately 700 $\mu\text{E}/\text{m}^2\cdot\text{sec}$).

A LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NB) was used for gas exchange measurements as well as for monitoring environmental factors (light level, relative humidity, temperature, and CO_2 concentration). Photosynthesis was monitored as the time required for a 10 ppm drop in CO_2 or the change in CO_2 over 30 seconds. A one quarter

liter cuvette was used for all gas exchange measurements. The water potential of each twig was determined using a pressure chamber (PMS Instrument Corp., Corvallis OR).

The needles used for gas exchange measurements were transported in sealed plastic bags in a cooler containing ice, back to the laboratory for determination of needle surface area and dry weight. Surface areas were determined using the formula:

$$SA = d l (3.142 + n)$$

where d = fascicle diameter, l = needle length, and n = number of needles in the fascicle. Computed surface areas were rounded to the nearest 0.01 cm^2 . After surface area determination, needles were oven dried at 60 C to a constant weight (at least 48 hours). Needles were then weighed to the nearest 1×10^{-4} gram.

Foliar nutrient and chlorophyll content.

Foliar nutrient content was analyzed on needles sampled from the sample trees on November 16th, 1990. The needles were dried and ground prior to analysis. Block digestion with hydrochloric acid and Pope Kjeldahl mixture were used to prepare the aliquot for nitrogen analysis. Samples were analyzed using the Technicon Auto Analyzer II according to the Technicon Industrial Method No. 329-74 W/B rev 11/78. Samples analyzed for potassium, phosphorus, calcium, magnesium, manganese and iron were ashed at 500 C for 16 hours then mixed with hydrochloric acid and deionized water. The resulting aliquot was analyzed by Inductively Coupled Plasma Spectrometry at the Soil Testing and Plant Analysis Laboratory of Virginia Tech.

In September multiple samples of first flush foliage were collected in the lower and upper crown of one tree per plot. Following extraction with N,N-Dimethyl-formamide (Moran, 1982) the samples were analyzed for chlorophyll content with a spectrophotometer.

Growth measurements

At the conclusion of the growing season (November), tree heights, diameters at breast height (DBH), live crown lengths, and two perpendicular live crown diameters were measured. Heights and live crown lengths were measured using a height pole. A diameter tape was used for measuring stem diameters at 1.37 meters above the ground (DBH). For each tree, two perpendicular live crown diameters were measured from the ground by vertical projection using a cloth measuring tape. To monitor diameter growth throughout the year, dendrometer bands placed at 1.37 meters above ground were used on three randomly chosen trees per plot.

To estimate needle biomass production, four wire screen litter traps (0.30 m² each) were placed randomly in each plot in the spring of 1988. As before (Ginn, 1989), the litterfall was harvested every month, dried at 60 C and weighed. The sum of the litterfall of two consecutive years is an estimate of the maximum amount of foliage present on the trees the previous year.

Experiment 2

In situ physiology of needles within stands

Objective 2

To determine in situ seasonal needle gas exchange patterns under stand light conditions, for sun and shade foliage from thinned and unthinned stands and relate these variables to tree growth.

One tree per treatment/block combination was sampled via scaffolding to estimate physiological variables of the needles under stand environmental conditions. Measurements started in May and were taken on a monthly basis until September. Two subsamples were

measured without detaching the needles in the upper (sun), as well as the lower (shade) third of the crown of each sampled tree. Care was taken to maintain the natural needle orientation. After taking the routine gas exchange measurements, the fascicles were detached and Li-Cor cuvette was wrapped in aluminium foil. Measurements of day-time dark respiration were taken after approximately 2 minutes of equilibration in the dark.

The LI-6200 portable photosynthesis system was used for gas exchange measurements. Rates of photosynthesis and respiration were determined as the CO₂ change over 30 seconds in a 1/4 liter cuvette. Needles used for the gas exchange measurements were taken back to the laboratory for surface area and dry weight determinations.

Experiment 3

Light and CO₂ foliage photosynthetic responses

Objective 3

To compare photosynthetic responses to different light and CO₂ levels for sun and shade foliage from thinned and unthinned stands.

After maturation of the first flush of foliage, light and CO₂ response curves on sun and shade needles were constructed. For both types of curves the same sampling procedure was used. One twig from the upper and one twig from the lower third of the crown of the scaffolded trees (one tree per plot) were clipped and delivered within 1 minute in the sealed plastic bag to the measurement station just outside the stand. The twig was then placed in a container and recut underwater. Three needle fascicles were inserted into 1/4 liter cuvette while taking measurements with a LI-6200 portable photosynthesis system, without removing the twig from the container with water.

To construct the Ps-light curves, an artificial light and shade cloth were used to provide a

wide range of light levels. The curves were constructed starting at the highest light level and working to below the compensation point. Measurements were taken roughly every 100-200 $\mu\text{E}/\text{m}^2\cdot\text{sec}$. Estimates of light saturated net photosynthetic rates (P_{max}), light compensation point (LCP) and dark respiration (R_d) were calculated as in Hanson et al. (1988), using the following equation and nonlinear regression

$$P_s = P_{\text{max}}\{1 - (1 - R_d/P_{\text{max}})[1 - (\text{PPFD}/\text{LCP})^z]\}$$

The parameter z is a constant that allows for a better fit to the whole shoot data. R_d is defined as a CO_2 exchange rate (P_s) at zero PPFD (Hanson et al., 1988). Regression was used to derive parameters of interests for each twig. The initial slope of each curve (apparent quantum yield) was obtained from the first derivative of the above function with respect to $\text{PPFD} = \text{LCP}$.

P_s - CO_2 curves started at a CO_2 concentration 650 ppm provided by breathing into the cuvette. CO_2 concentration was then dropped at roughly 100 ppm intervals to the compensation point. Because of strong linearity (R^2 close to 0.99), linear regression was run to determine the slope of the demand function (carboxylation efficiency) and C_i with respect to zero P_s (CO_2 compensation point) for each curve. The supply function was established for each P_s - CO_2 curve in an operating point corresponding to P_s at ambient CO_2 concentration (approx. 350 ppm) as shown in (Jones 1985). Stomatal limitations to photosynthesis at the operating points were computed as described in Farquhar and Sharkey (1982) and according to Jones' (1985) method V.

Experimental design and statistical analysis

Analysis of the gas exchange and water potential data was based on a split block experimental design with three blocks. The main treatments - thinned and unthinned plots are randomized across the blocks. The subunit treatments - upper and lower thirds of the crowns

can not be randomized by definition and are applied in strips across the blocks.

For full light measurements (Experiment 1), three trees were subsampled and the average used as the experimental unit. For in situ measurements (Experiment 2), two subsamples for each crown position per treatment/block combination were collected and the average used as the experimental unit. Data for each sampling date was analyzed separately and then pooled to compare seasonal means of physiological variables for treatments. The following general analysis of variance table was used:

<u>Factor</u>	<u>Degrees of Freedom</u>
Thinning treatment (T)	1
Block (B)	2
Main plot error (T*B)	2
Crown position (P)	1
Sub-plot error (P*B)	2
Interaction (P*T)	1
Error (P*B*T)	2

Physiological variables derived from light and CO₂ curves (Experiment 3) were compared using the same procedure.

Tree growth and litterfall data were analyzed as a randomized complete block design with three blocks.

Monthly diameter growth of three trees per treatment/block combination was correlated with full light gas exchange measurements taken for those trees at the same date as DBH growth readings (Experiment 1). Diameter growth data of one tree per plot were correlated with in situ gas exchange measurements taken for those trees in the middle of the DBH growth reading period (Experiment 2). Pearson correlation coefficients were computed across thinning treatments, crown positions and for all measurement dates within each of the two experiments.

RESULTS

Growth and biomass production

Growth and yield

After the third growing season following thinning average height of the trees did not differ due to thinning (Table 1). Basal area (per hectare) and height to live crown were higher in the unthinned stands. Diameter at breast height (DBH), crown diameter and live crown ratio averaged higher in the thinned stands. Only basal area and crown diameter differences were statistically significant at $p=0.05$ (Table 1).

Crown diameter growth was higher ($p=0.06$) in thinned stands. No other growth parameters differed significantly; however DBH, basal area and volume growth were all higher in thinned stands (Table 2). Throughout 1990, DBH growth was always higher in the thinned stands, but significantly higher (at $p=0.05$) only in April (Figure 1). The differences were of course greater during the growing season, when the DBH growth was on an average up to 10 times higher than during the winter months. During the third growing season after thinning, DBH growth peaked in April and May and was always lower thereafter.

Needle biomass production

On a yearly basis, the unthinned stands dropped 1.33 times more needle mass per hectare than the thinned stands ($p=0.08$) (Table 3). Litterfall was higher in the unthinned stands for almost every month (Figure 2). The differences were statistically significant on 6 out of 17 collection dates. When expressed per unit tree basal area yearly litterfall was higher ($p=0.09$), and expressed on a tree basis significantly higher in the thinned stands (Table 3).

Table 1 - Average height, diameter, live crown dimensions and basal area of loblolly pine trees in thinned and unthinned stands after third growing season following thinning

	<u>Thinned</u>	<u>Unthinned</u>	<u>p-value</u> *
Height (m)	11.12	11.34	0.70
DBH (cm)	21.09	18.83	0.11
Crown Diameter (m)	5.30	3.94	0.04
Live Crown Ratio (%)	67.4	60.5	0.18
Height to Live Crown (m)	3.61	4.50	0.19
Basal Area (m ² /ha)	21.2	34.0	0.05

* p-value indicates probability level for statistical significance between treatments.

Table 2-Average growth of loblolly pine trees in thinned and unthinned stands during the third growing season after thinning

<u>Growth Parameter</u>	<u>Thinned</u>	<u>Unthinned</u>	<u>p-value</u> *
Height (cm)	72.5	61.7	0.67
DBH (cm)	1.90	1.44	0.25
Crown Diameter (cm)	45.4	5.76	0.06
Live Crown Ratio (% change)	-1.74	-2.35	0.81
Basal Area (cm ²)	61.3	44.6	0.27
Volume (m ³)	0.039	0.029	0.29

* p-value indicates probability level for statistical significance between treatments.

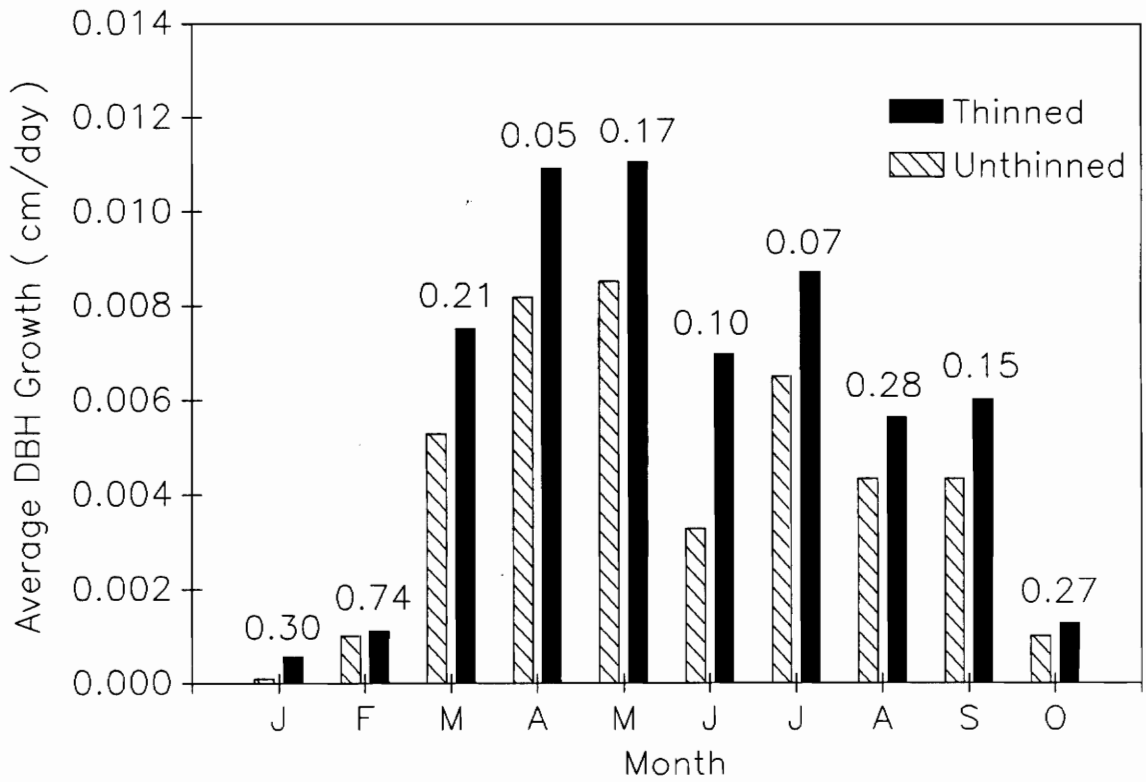


Fig. 1 Average monthly diameter growth at breast height (DBH) in thinned and unthinned stands of loblolly pine during 1990. Numbers above dates are probability levels for statistical significance between thinning treatments.

Table 3-Total yearly litterfall in thinned and unthinned loblolly pine stands from November 2, 1989 until November 5, 1990

<u>Litterfall</u>	<u>Thinned</u>	<u>Unthinned</u>	<u>p-value</u> *
kg/ha	4564.2	6064.2	0.08
kg/m ² basal area	215.8	178.2	0.09
kg/tree	8.5	5.6	0.02

* p-value indicates probability level for statistical significance between treatments.

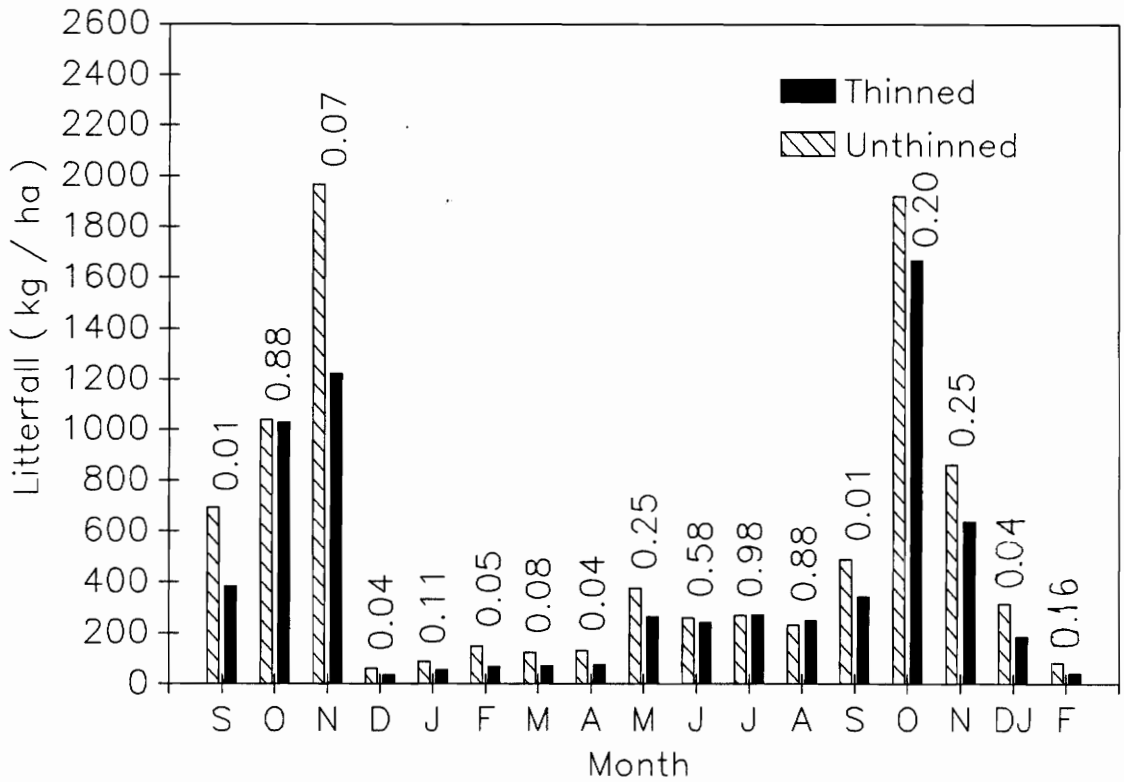


Fig. 2 Monthly litterfall collected in thinned and unthinned loblolly pine stands from October 2, 1989 until March 9, 1991. Numbers above dates are probability levels for statistical significance between thinning treatments.

Physiological effects of thinning

Light saturated foliage gas exchange rates

During the third growing season after thinning there was no statistically significant interactions between the thinning treatments and crown positions with respect to light saturated gas exchange rates. Average seasonal net photosynthetic, transpiration, and needle conductance rates measured under saturating light conditions for thinned and unthinned stands, and for upper and lower crown positions, were not significantly different when expressed on an area or dry weight basis (Table 4). When expressed on the area basis however, gas exchange parameters were always higher in upper crowns, with net photosynthetic rates being statistically higher ($p=0.06$).

The difference in net photosynthetic rates between the thinned and unthinned stands was not significant on any of the measurement dates (Figure 3a). The highest light saturated net photosynthetic rates occurred early in the year during the May and June measurement dates. From July on, when measurements were switched to fully expanded, current year needles, rates measured under saturating light were approx. 30% lower for both thinned and unthinned stands (Figure 3a). The same kind of pattern was observed for upper and lower crown positions (Figure 4a), with the upper crown values being higher on every date except for the beginning of May. The differences were statistically significant on August 8th and October 5th, 1990.

Needle stomatal conductance measured under saturating light peaked in the beginning of June for both thinned and unthinned stands (Figure 3b) as well as for upper and lower crowns (Figure 4b). From then on the stomatal conductance exhibited a declining pattern as the growing season progressed. The thinned and the unthinned stands had very similar needle conductances with the thinned stands values being slightly higher on each date except May 8th,

Table 4-Average net photosynthesis, transpiration and needle conductance in loblolly pine foliage from thinned and unthinned stands and from upper and lower crown positions measured under full light conditions¹

Treatment or Crown Position	Net Photosynthesis (uMol/m ² sec)	Transpiration (mMol/m ² sec)	Needle Conductance (mMol/m ² sec)
Thinned	2.62 (0.31)	2.21 (0.78)	55.1 (0.41)
Unthinned	2.52	2.23	53.1
Upper Crown	2.81 (0.06)	2.32 (0.26)	58.9 (0.15)
Lower Crown	2.33	2.12	49.3

Treatment or Crown Position	Net Photosynthesis (nMol/g sec)	Transpiration (uMol/g sec)	Needle Conductance (uMol/g sec)
Thinned	36.2 (0.39)	31.6 (0.16)	782 (0.58)
Unthinned	37.3	34.5	804
Upper Crowns	36.6 (0.89)	31.3 (0.31)	787 (0.86)
Lower Crowns	36.9	34.8	799

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively

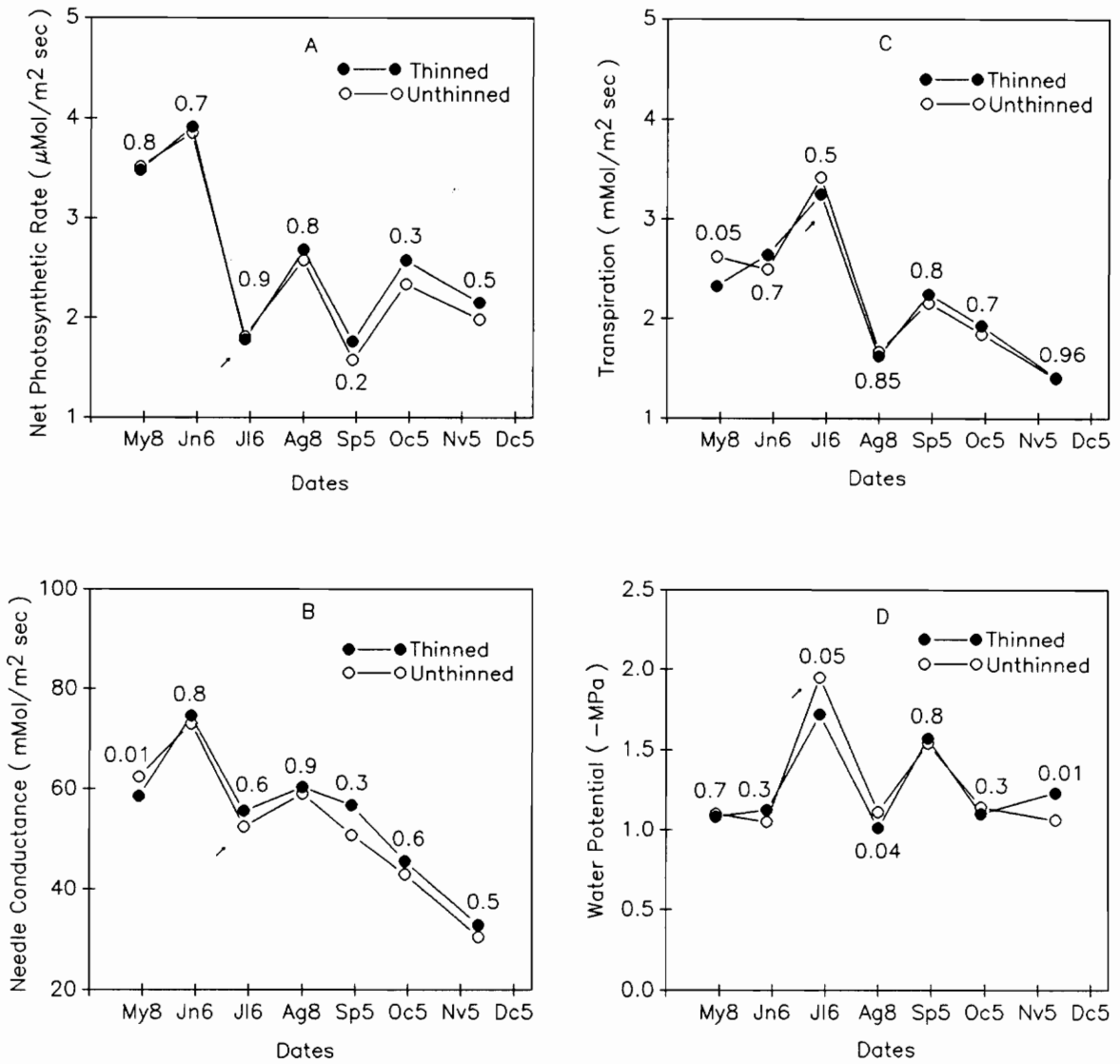


Fig. 3 Average net photosynthetic rates, needle conductance, transpiration and water potential for thinned and unthinned loblolly pine stands measured under saturating light from May 8, 1990 through November 16, 1990.

† Indicates switching date to current year foliage in gas exchange measurements.

Numbers above dates are probability levels for statistical significance between thinning treatments.

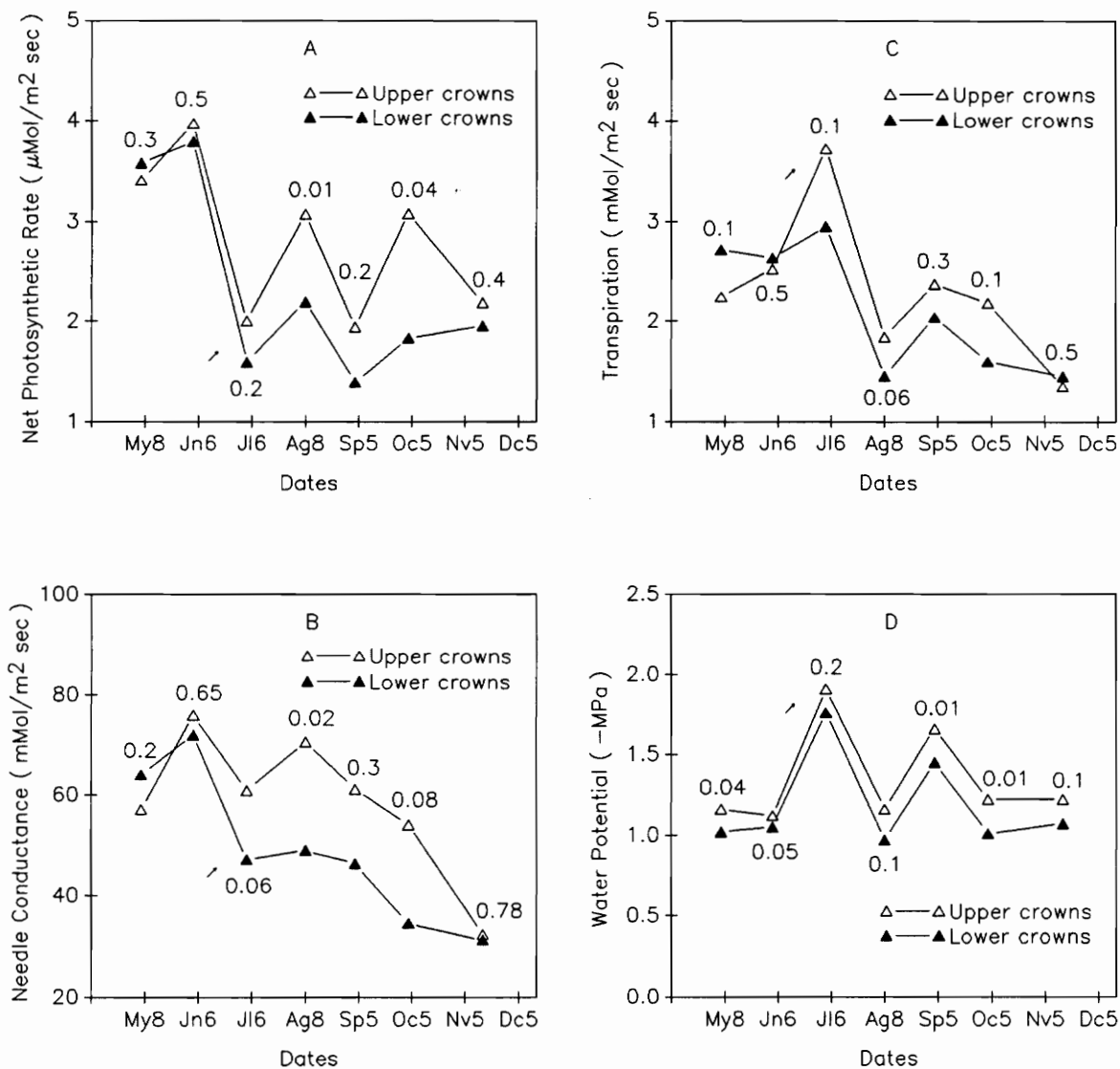


Fig. 4 Average net photosynthetic rates, needle conductance, transpiration, and water potential for upper and lower crowns of loblolly pine stands measured under saturating light from May 8, 1990 through November 16, 1990. / Indicates switching date to current year foliage in gas exchange measurements. Numbers above dates are probability levels for statistical significance between crown positions.

1990. Similarly upper crown values were always higher with the exception of the first measurement date. Differences between upper and lower crowns were more pronounced (Figure 4b) than differences between the thinned and unthinned stands (Figure 3b).

Transpiration rates for thinned and unthinned stands were very similar on each measurement date except for May 8th when the trees in unthinned stands had significantly higher transpiration than the trees in thinned stands. The seasonal pattern of the transpiration for the thinned and unthinned stands (Figure 3c) paralleled that of the seasonal water potentials (Figure 3d). Higher transpiration rates were coupled with more negative water potentials except for the end of the growing season. Similar was true for upper and lower crowns (Figures 4c, 4d) except for the beginning and the end of the growing season. The differences in transpiration rates between upper and lower crowns were generally greater (although not always statistically significant) than those between the thinned and unthinned stands.

Plant water relations

Average seasonal midday xylem water potentials did not differ significantly between the thinned and unthinned stands (Table 5). The average water potential of the upper crowns was significantly less than that of the lower crowns. The seasonal patterns of the water potential for the thinned and unthinned stands were similar, with the unthinned stands being significantly lower in the beginning of July and August, and the thinned being significantly less on the November measurement date (Figure 3d). Upper crowns had consistently more negative water potentials when compared with lower crowns, with the differences being statistically significant on 4 out of 7 measurement dates (Figure 4d).

Table 5-Average seasonal loblolly pine xylem water potential as influenced by thinning and crown position during the third growing season after thinning¹

	Water Potential (MPa)		
Thinned Stands	-1.26 (0.45)	Upper Crowns	-1.35 (0.02)
Unthinned Stands	-1.28	Lower Crowns	-1.19

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively.

Foliar nutrient and chlorophyll contents

After the second (1989) and the third (1990) growing seasons following thinning, few statistically significant differences existed for foliar nutrient contents between thinned and unthinned stands (Table 6). There were more statistically significant difference in nutrient content between crown positions. The upper crowns contained more nitrogen, phosphorus and potassium, while the lower crowns contained more calcium, magnesium and manganese (Table 6). With the exception of nitrogen and phosphorus in 1989, all these differences were statistically significant. Iron concentrations did not differ in either year.

Although not compared statistically, it is interesting that the 1990 nutrient contents were generally lower than in 1989.

During the third growing season following thinning there were no statistically significant differences between the thinning treatments or crown positions in chlorophyll concentrations (Table 7). The chlorophyll a/b ratio was significantly higher in the lower crown position ($p=0.06$).

Physiology of needles in situ under stand light conditions

During the third growing season following thinning there were significant thinning treatment x crown position interactions with respect to physiological variables measured under stand light conditions. Therefore the differences were examined separately for the two crown positions for each thinning treatment (Table 8).

Table 6-Foliar nutrient contents in thinned and unthinned loblolly pine stands in upper and lower crowns during the second and third growing season following thinning¹

Nutrient	1989			1990		
	Thinned (ppm)	Unthinned (ppm)	p-value	Thinned (ppm)	Unthinned (ppm)	p-value
N	12361	13144	0.13	12128	12550	0.57
P	1329	1448	0.09	1246	1277	0.73
K	4729	5504	0.33	4590	5113	0.13
Ca	1678	2300	0.53	1677	1961	0.26
Mg	810	1041	0.09	1001	1087	0.57
Mn	205	204	0.99	239	188	0.17
Fe	43	57	0.32	35	41	0.51

Nutrient	1989			1990		
	Upper Crown (ppm)	Lower Crown (ppm)	p-value	Upper Crown (ppm)	Lower Crown (ppm)	p-value
N	13128	12378	0.28	13089	11589	0.04
P	1459	1318	0.20	1344	1179	0.01
K	5783	4451	0.01	5390	4313	0.01
Ca	1539	2440	0.06	1522	2115	0.05
Mg	804	1046	0.04	905	1183	0.04
Mn	170	240	0.07	186	241	0.02
Fe	47	54	0.73	41	35	0.55

¹p-value indicates probability level for statistical significance between the treatments or crown positions respectively.

Table 7-Fresh needle chlorophyll a and b contents and chlorophyll a/b ratios in thinned and unthinned loblolly pine stands for two crown positions, during the third growing season following thinning¹

Treatment or Crown Position	Chlorophyll a (mg/g)	Chlorophyll b (mg/g)	Total Chlorophyll (mg/g)	Chlorophyll a/b Ratio
Thinned	0.599 (0.80)	0.510 (0.87)	1.108 (0.83)	1.172 (0.39)
Unthinned	0.626	0.523	1.149	1.195
Upper Crowns	0.618 (0.58)	0.527 (0.36)	1.145 (0.46)	1.171 (0.06)
Lower Crowns	0.606	0.506	1.112	1.196

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively.

Table 8-Average net photosynthesis, transpiration, needle conductance, dark respiration, net photosynthesis to dark respiration ratio and photosynthetic photon flux density (PPFD) under stand light conditions in thinned and unthinned stands of loblolly pine for two crown positions¹

	Net Photosynthesis ($\mu\text{Mol}/\text{m}^2\text{sec}$)		Net Photosynthesis ($\text{nMol}/\text{g sec}$)	
	Thinned	Unthinned	Thinned	Unthinned
Upper Crown	2.79 aA	2.92 aA	35.7 aA	46.3 aA
Lower Crown	2.34 aA	1.40 bB	35.0 aA	23.9 aB

	Transpiration ($\text{mMol}/\text{m}^2\text{sec}$)		Transpiration ($\mu\text{Mol}/\text{g sec}$)	
	Thinned	Unthinned	Thinned	Unthinned
Upper Crown	1.59 aA	1.78 aA	20.4 aA	28.2 aA
Lower Crown	1.51 aA	1.34 aB	22.3 aA	22.7 aB

	Needle Conductance ($\text{mMol}/\text{m}^2\text{sec}$)		Needle Conductance ($\mu\text{Mol}/\text{g sec}$)	
	Thinned	Unthinned	Thinned	Unthinned
Upper Crown	59.5 aA	68.9 aA	768 aA	1044 aA
Lower Crown	52.8 aA	51.8 aB	785 aA	863 aB

	Dark Respiration ($\mu\text{Mol}/\text{m}^2\text{sec}$)		Dark Respiration ($\text{nMol}/\text{g sec}$)	
	Thinned	Unthinned	Thinned	Unthinned
Upper Crown	0.597 aA	0.541 aA	7.94 aA	9.03 aA
Lower Crown	0.524 aA	0.441 aB	8.38 aA	7.75 aA

	Net Photosynthesis to Dark Respiration Ratio		Photosynthetic Photon Flux Density (PPFD) ($\mu\text{E}/\text{m}^2\text{sec}$)	
	Thinned	Unthinned	Thinned	Unthinned
Upper Crown	5.02 aA	7.19 aA	588 aA	592 aA
Lower Crown	5.21 aA	4.24 aA	465 aA	203 bB

¹Values for thinned and unthinned stands in each row followed by the same lower-case letter are not significantly different; values for upper and lower crowns in each column followed by the same upper-case letter are not significantly different ($p=0.05$).

Photosynthesis

Seasonal averages

Seasonal average net photosynthesis rate expressed on an area basis did not differ significantly between crown positions for thinned stands. In the unthinned stands however, upper crowns had significantly higher photosynthesis (Table 8). In the lower crowns average net photosynthetic rate for the season was significantly higher in the thinned stands.

When expressed on a dry weight basis, the pattern for net photosynthesis was generally the same. Rates differed significantly only for upper and lower crowns in the unthinned stands. Upper crowns of the unthinned stands had the highest rates, and the thinned stands had similar net photosynthesis rates regardless of the crown position (Table 8).

Seasonal patterns

The highest net photosynthesis rates occurred at the first measurement date on May 24, 1990, after which the net photosynthetic rates showed a declining pattern as the growing season progressed, regardless of the thinning treatment or crown position (Figures 5a, 5b). In the unthinned stands upper crown photosynthesis was always significantly higher than that in the lower crowns ($p < 0.1$).

Photosynthetic photon flux density (PPFD)

Three growing seasons following thinning, average PPFD did not differ significantly between the crown positions in the thinned stands (Table 8). In the unthinned stands, the light levels for upper crowns averaged almost three times higher than for the lower crowns.

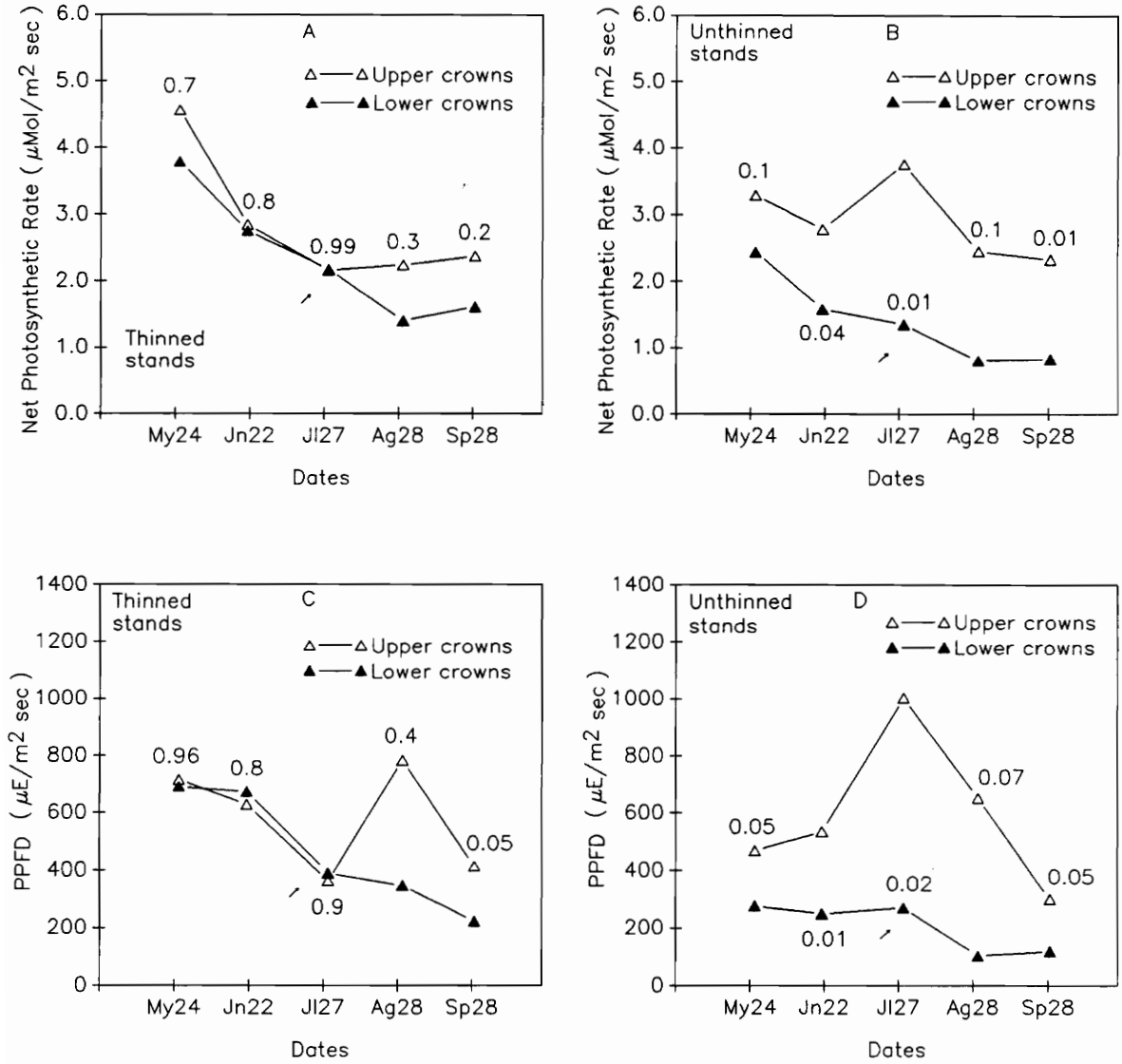


Fig. 5 Average net photosynthetic rates and photosynthetic photon flux density (PPFD) in thinned and unthinned stands of loblolly pine for upper and lower crowns measured under stand light conditions from May 24, 1990 through September 28, 1990.

† Indicates switching date to current year foliage in gas exchange measurements.

Numbers above dates are probability levels for statistical significance between crown positions.

Lower crowns in the thinned stands were receiving on an average more than twice as much light as the lower crowns of the unthinned stands. The average amount of light received by the upper crowns in both thinning treatments was almost identical (Table 8).

At the start of the third growing season following thinning, the levels of PPFD in the thinned stands were similar in both crown positions (Figure 5c). On the August and September measurement dates large differences were apparent between crown positions in the thinned stands. In the unthinned stands, upper crowns were consistently receiving more light than the lower crowns throughout the entire season (Figure 5d).

Needle conductance and transpiration

In general needle stomatal conductance and transpiration rates followed patterns similar to that of net photosynthesis. Average seasonal needle conductance and transpiration rates differed significantly only for upper and lower crowns in the unthinned stands, with the upper crowns having the highest rates of all compared (Table 8). The above was true both on an area and dry weight basis.

Over the growing season needle conductance was always higher in the upper crowns regardless of the thinning treatment (Figures 6a, 6b). However, differences tended to be larger and statistically significant in the unthinned stands (Figure 6b). As with needle conductance, in both thinned and unthinned stands upper crowns tended to transpire more. This was particularly true for the unthinned stands where differences were much larger (Figure 6c).

Dark respiration

Seasonal average dark respiration rates expressed on an area basis differed significantly only for upper and lower crowns in the unthinned stands, with the upper crowns being higher

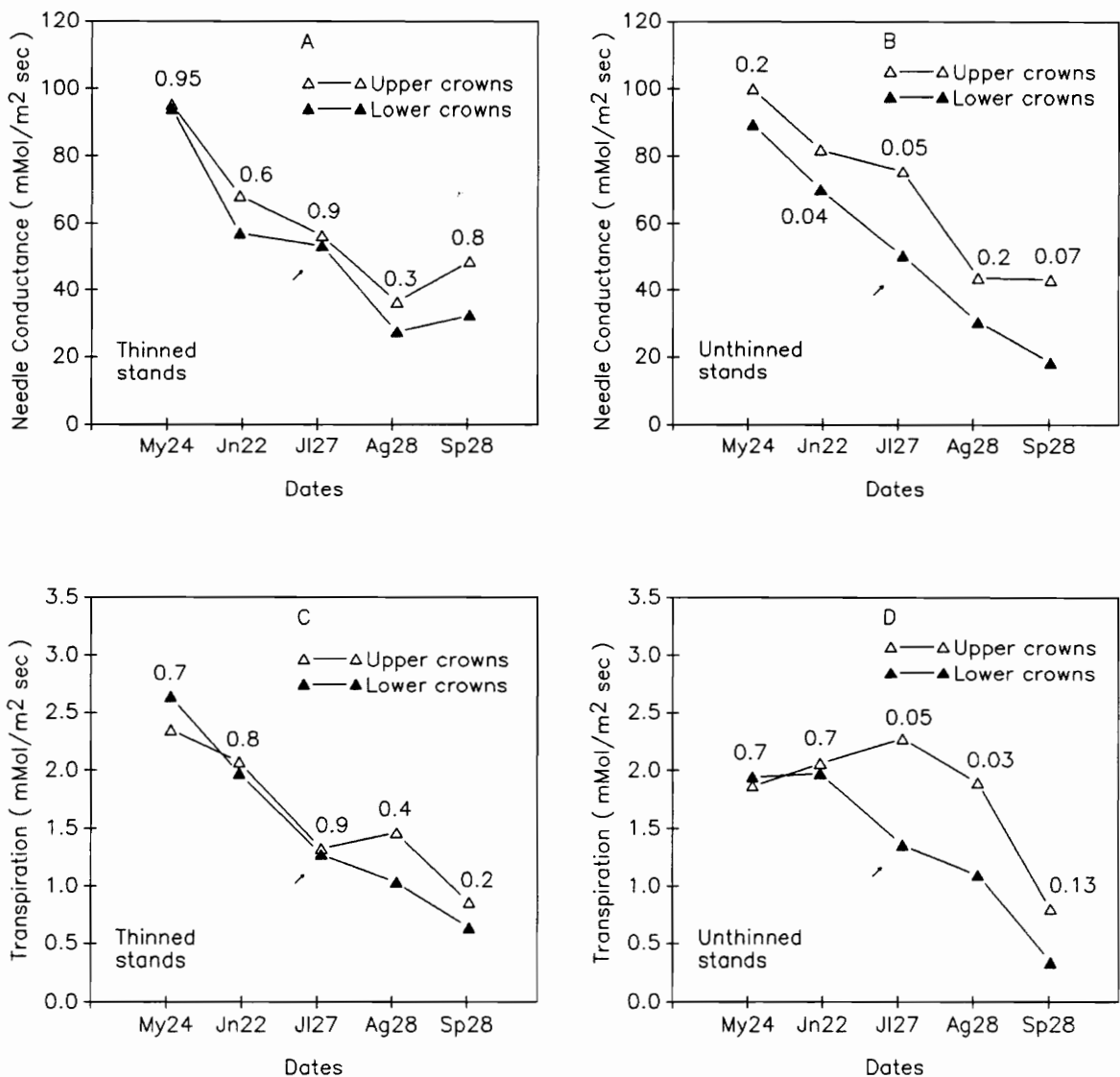


Fig. 6 Average needle conductance and transpiration rates in thinned and unthinned stands of loblolly pine for upper and lower crowns measured under stand light conditions from May 24, 1990 through September 28, 1990.

† Indicates switching date to current year foliage in gas exchange measurements.

Numbers above dates are probability levels for statistical significance between crown positions.

(Table 8). The difference between the thinned (higher rates) and the unthinned stands in the lower crowns was significant at $p=0.06$ (p level not shown in the table). When expressed on a dry weight basis, dark respiration rates did not differ significantly between the thinning treatments or between the crown positions (Table 8).

Over the growing season, the upper crown respiration rates were showing much more fluctuations than the same rates in the lower crowns in both thinning treatments (Figure 7a, 7b). Generally upper crown respiration rates were higher than those of the lower crowns. No differences between the crown positions in the thinned or in the unthinned stands were statistically significant.

Net photosynthesis to dark respiration ratio

Average seasonal net photosynthesis to dark respiration ratio was very similar for upper and lower crowns in the thinned stands, and almost two times higher in the upper crowns when compared with lower crowns in the unthinned stands (Table 8). The difference between the crown positions in the unthinned stands was significant at a $p=0.07$ level (value not shown in the table).

Over the growing season the thinned stands ratios were similar for upper and lower crowns (Figure 7c). The ratio was the highest in the beginning of the growing season and then declining in later months. In the unthinned stands, the ratio was always higher in the upper crowns, although the difference was statistically significant only on July 27th (Figure 7d). For unthinned stands the ratio was the highest in the beginning and the end of the growing season, being lower in the middle of the summer.

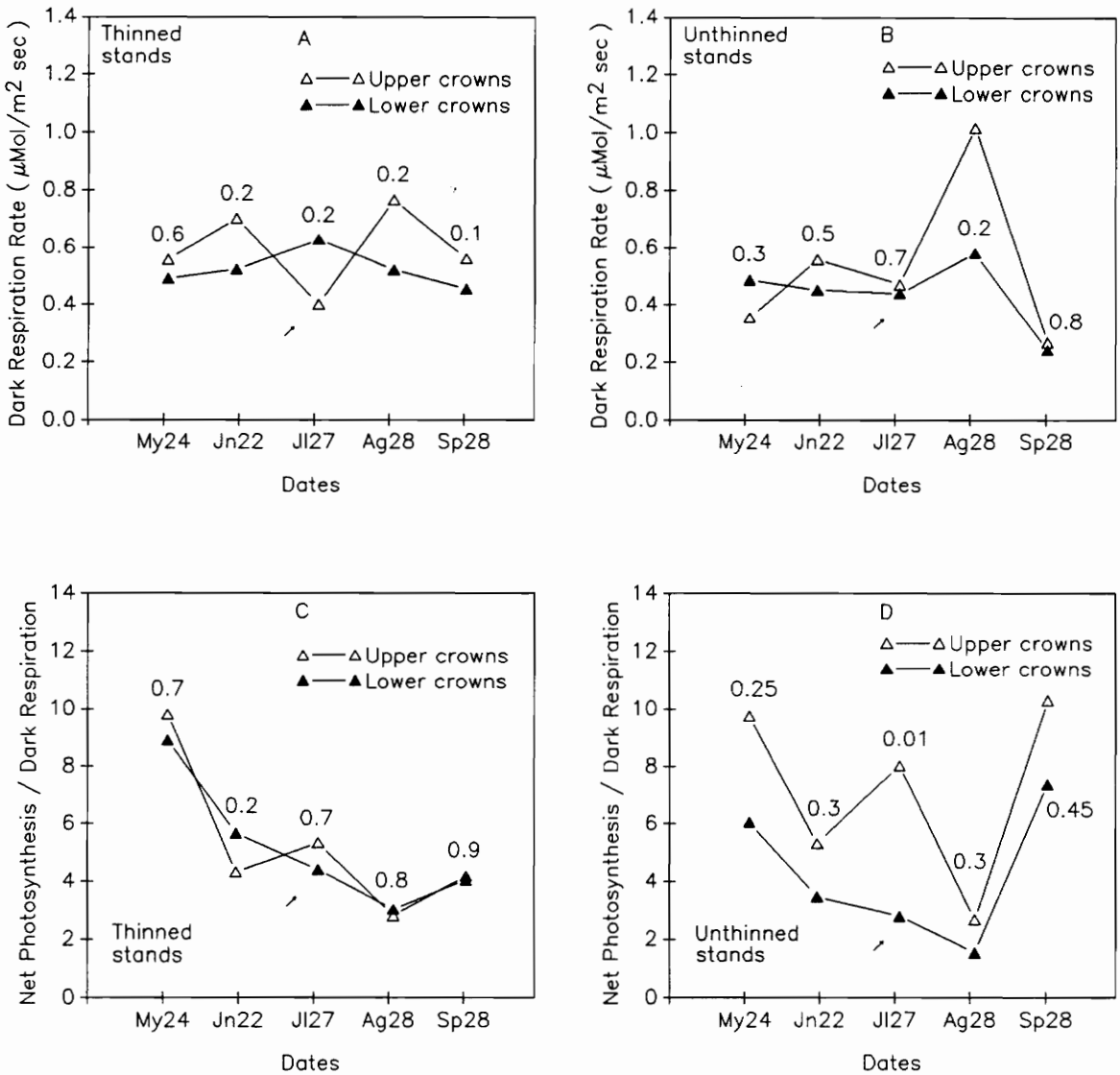


Fig. 7 Average dark respiration rates and net photosynthesis to dark respiration ratios in thinned and unthinned stands of loblolly pine for upper and lower crowns measured within the crowns of the trees from May 24, 1990 through September 28, 1990. † Indicates switching date to current year foliage in gas exchange measurements. Numbers above dates are probability levels for statistical significance between crown positions.

Correlation of gas exchange parameters and water potentials
with DBH growth

During the third growing season, following thinning, monthly DBH growth was positively and significantly correlated with water potential and all light dependent gas exchange parameters except for transpiration expressed on the dry weight basis. Negative correlation existed only between diameter growth and the net photosynthesis to dark respiration ratio (Tables 9, 10). DBH growth was better correlated with gas exchange parameters expressed on a leaf area basis, except for the dark respiration rate which was higher and significantly correlated only when expressed on dry weight basis (Table 10).

DBH growth was best correlated with the net photosynthesis rate measured under saturating light conditions (Table 9). Under those conditions, stomatal conductance had the next best relationship with DBH growth. Under stand light conditions stomatal conductance was more strongly correlated with DBH growth than net photosynthesis (Table 10).

Light and CO₂ foliage photosynthetic responses

Several physiological parameters were derived from light and CO₂ curves constructed for the upper and lower crown foliage of thinned and unthinned trees. Although the interactions between the crown positions and the thinning treatments were expected neither of the parameters described below showed statistically significant interactions.

Quantum yield, light compensation and dark respiration

Average apparent quantum yield did not differ significantly when expressed on either an area or dry weight basis for either thinning treatments or crown positions (Table 11).

Table 9-Pearson correlation coefficients (R) between monthly DBH growth and net photosynthesis (Ps), transpiration (Ts), needle conductance (Cd), water potential (WP). Gas exchange rates were measured under full light conditions. R was computed across thinning treatments and crown positions¹

Gas Exchange Parameters Computed on an Area Basis				
	Ps	Ts	Cd	WP
R	0.53	0.13	0.42	0.24
Prob.> R	0.0001	0.04	0.0001	0.0001
N	247	247	247	248

Gas Exchange Parameters Computed on a Weight Basis			
	Ps	Ts	Cd
R	0.36	-0.08	0.20
Prob.> R	0.0001	0.24	0.002
N	247	247	247

¹N=Number of observations

Table 10-Pearson correlation coefficients (R) between monthly DBH growth and net photosynthesis (Ps), transpiration (Ts), needle conductance (Cd), dark respiration (Rs), net photosynthesis to dark respiration ratio (RAT) measured under stand light conditions. R was computed across thinning treatments and crown positions¹

Gas Exchange Parameters Computed on an Area Basis					
	Ps	Ts	Cd	Rs	RAT
R	0.46	0.37	0.50	0.12	-0.41
Prob.> R	0.0001	0.0001	0.0001	0.21	0.0001
N	119	119	119	119	118

Gas Exchange Parameters Computed on a Weight Basis				
	Ps	Ts	Cd	Rs
R	0.35	0.23	0.42	0.22
Prob.> R	0.0001	0.01	0.0001	0.02
N	119	119	119	119

¹N=Number of observations

Table 11-Apparent quantum yields, light compensation points and dark respiration rates, derived from photosynthesis light response curves, constructed for thinned and unthinned loblolly pine stands for two crown positions, during the third growing season following thinning¹

Photosynthesis Computed on an Area Basis			
Treatment or Crown Position	Apparent Quantum Yield (uMol CO ₂ /uE)	Light Compensation Point (uE/m ² sec)	Dark Respiration Rate (uMol/m ² sec)
Thinned	0.00263 (0.36)	188 (0.20)	0.431 (0.32)
Unthinned	0.00840	119	0.686
Upper Crown	0.00602 (0.65)	203 (0.15)	0.692 (0.03)
Lower Crown	0.00500	104	0.424
Photosynthesis Computed on a Weight Basis			
Treatment or Crown Position	Apparent Quantum Yield (nMol CO ₂ g ⁻¹ sec ⁻¹ /uE m ⁻² sec ⁻¹)	Light Compensation Point (uE/m ² sec)	Dark Respiration Rate (nMol/g sec)
Thinned	0.0397 (0.34)	179 (0.31)	6.24 (0.19)
Unthinned	0.1432	120	12.15
Upper Crown	0.0859 (0.57)	194 (0.12)	11.08 (0.03)
Lower Crown	0.0970	105	7.32

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively.

Apparently, large amounts of variation exist since apparent quantum yields on average were three times higher in the unthinned stands when compared with the thinned stands regardless of the computational method. Although not significantly different, average light compensation point was almost twice as high for the upper crowns when compared with the lower crowns and much higher in the thinned stands than in the unthinned. Both methods of computation (based on the leaf area and on the dry weight) yielded virtually the same values for light compensation points (Table 11).

Dark respiration rates (estimated photosynthesis at zero light) derived from the light photosynthetic response curves were significantly higher in the upper crown foliage (Table 11). Unthinned stands also had much higher respiration rates although not significantly so. The rates for the unthinned stands and the upper crowns were very similar, as were the rates for the thinned stands and the lower crowns, regardless of the computational method (Table 11).

Carboxylation efficiency and CO₂ compensation points

The carboxylation efficiency was significantly higher in the unthinned stands when computed on a dry weight basis (Table 12). No other differences were statistically significant. The lower crowns and the unthinned stands had significantly higher CO₂ compensation points than the upper crowns and the thinned stands respectively (Table 12).

Stomatal limitations

Stomatal limitations of photosynthesis calculated using two different methods produced very similar results (Table 13). The lower crowns and the unthinned stands had approximately 10% higher (and similar) stomatal limitations in comparison with the upper crowns and the thinned stands respectively (Table 13).

Table 12-Carboxylation efficiencies and CO₂ compensation points derived from photosynthesis CO₂ response curves, constructed for thinned and unthinned loblolly pine stands for two crown positions during third growing season following thinning¹.

Photosynthesis Computed on an Area Basis		
Treatment or Crown Position	Carboxylation Efficiency (uMol CO ₂ /m ² sec ppm CO ₂)	CO ₂ Compensation Point (ppm CO ₂)
Thinned	0.0218 (0.21)	67.3 (0.10)
Unthinned	0.0250	93.5
Upper Crown	0.0225 (0.60)	58.8 (0.01)
Lower Crown	0.0244	102.0
Photosynthesis Computed on a Weight Basis		
Treatment or Crown Position	Carboxylation Efficiency (nMol CO ₂ /g sec ppm CO ₂)	CO ₂ Compensation Point (ppm CO ₂)
Thinned	0.360 (0.01)	65.4 (0.09)
Unthinned	0.464	91.0
Upper Crown	0.370 (0.37)	57.2 (0.01)
Lower Crown	0.454	99.2

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively.

Table 13-Stomatal limitations of photosynthesis (I_s , I_g) calculated according to two different methods based on the photosynthesis CO_2 response curves, computed for thinned and unthinned loblolly pine stands for two crown positions during third growing season following thinning¹

Treatment or Crown Position	I_s^* (%)	I_g^{**} (%)
Thinned	36.4 (0.09)	38.0 (0.07)
Unthinned	46.3	47.7
Upper Crown	35.4 (0.01)	37.6 (0.01)
Lower Crown	47.3	48.0

¹Numbers in parenthesis are probability levels for statistical significance between the treatments or crown positions respectively.

* Farquhar and Sharkey 1982

** Jones 1985, method V

DISCUSSION

Effects of thinning on loblolly pine growth and foliage physiology

Three years after thinning growth of individual trees was greater in the thinned than in the unthinned stands (Tables 1, 2; Figure, 1). The effects of thinning on growth however appear to be diminishing. During 1989, diameter at breast height, basal area and volume growth per tree in thinned stands were 1.5 times higher than those in the unthinned stands and significant at $p=0.08$ (Ginn, 1989). In 1990, the same parameters were approximately 1.35 times higher in the thinned stands and the differences were only significant at $p=0.29$.

In the 1990 growing season, trees in the thinned stands continued to have larger foliage surface area than unthinned trees. At the same average height, trees in the thinned stands had larger live crown ratios and their crown diameters expanded on an average 8 times more than those in the unthinned stands (Tables 1, 2). Litterfall collected between the September 1989 and February 1991 indicates that the unthinned stands produced substantially more foliage per hectare during the first and second growing season following thinning (dropped needles were two years old) (Figure 2). Litterfall per unit basal area was higher and on a tree basis significantly higher in the thinned stands indicating that thinning did increase individual tree foliar mass Table 3). In fact larger foliage surface area of the thinned trees is likely a major factor contributing to the increased growth of those trees. Larger photosynthetic leaf area was not off set by higher carboxylation efficiency (only when expressed on a dry weight basis) of the needles from the unthinned trees, since their growth was shown to be lower than that of the thinned trees.

In 1990 as compared with 1989 major litterfall occurred one month earlier (October). This was probably due to the atmospheric conditions, heavy rain in October 1990 (Figure 8)

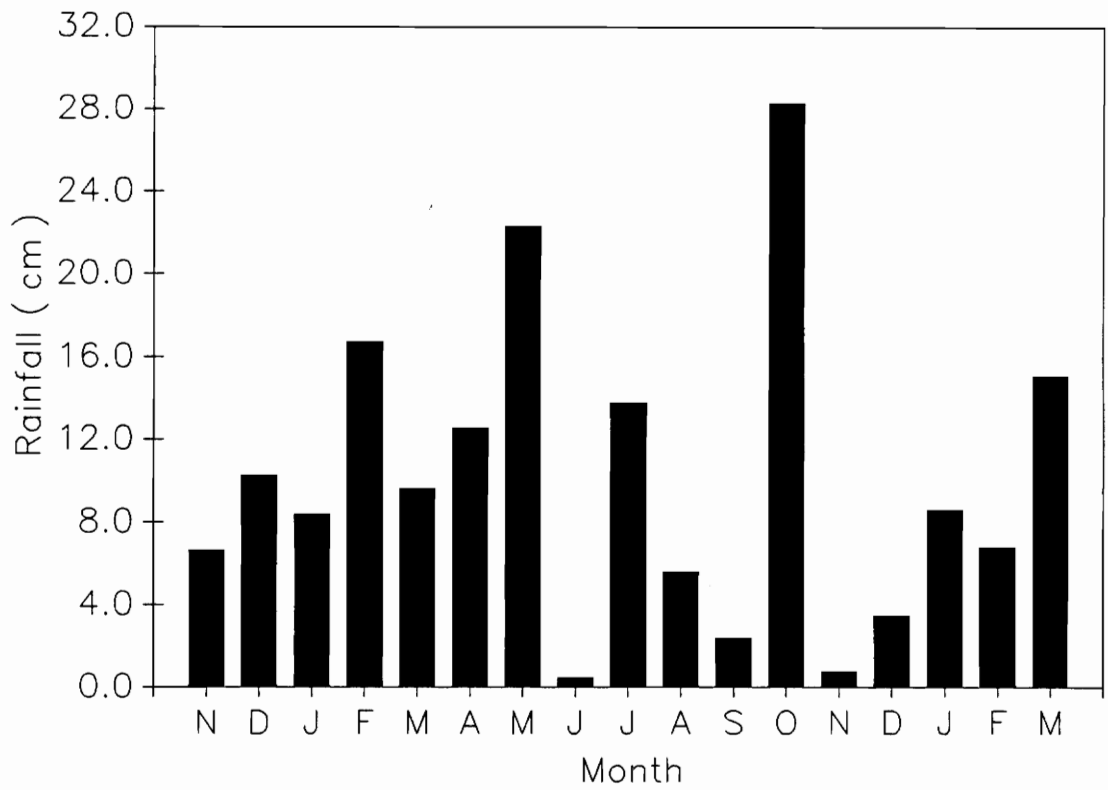


Fig. 8 Monthly rainfall in Critz, VA from November 1989 until March 1991.

and possibly strong winds. In 1990, there were three distinct phases of litterfall, very small from January until May, moderate during the actual growing season and heavy from the beginning of October until December with the peak in October. Amount of foliage produced per hectare during the second growing season following thinning (collected throughout 1990), became more uniform between the thinning treatments when compared with the first growing season (litterfall collected in 1989). This suggests crown closure is occurring in the thinned stands as the result of their crown diameter expansion.

Some investigators suggested that the most important factor contributing to the increased growth of the remaining trees in thinned stands is better water supply. Donner and Running (1986) found that with increasing stand density, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) had more negative pre-dawn leaf water potentials. Lower water potentials corresponded with higher seasonal soil moisture depletion. Reduction of overall transpiring leaf surface area, reduction of live root density, and reduction of canopy interception of precipitation were concluded as factors improving the water relations of thinned stands. Similar results were reported by Lilieholm and Hu (1984). In their study, the most intensively thinned stands, had significantly more water in the upper eight feet of the soil profile than control stands. Loblolly pine diameter growth was also the greatest on the most intensively thinned plots. Cregg et al. (1990), also found soil water potential to increase significantly in response to thinning of loblolly pine. Despite higher soil water potential they found no differences in xylem water potentials in 48 out of 55 sampling periods.

In our study, although soil water potentials were not monitored, the observed growth differences between the thinning treatments were not consistently related to differences in plant water relations. At times growth changes (Figure 1) paralleled changes in plant water status (Figures 3d, 4d). Early peak diameter growth in May/April of 1990 was followed by a steady decline disturbed by the temporarily bigger drop in June which can be associated with very low precipitation during that month. There was only 0.46 cm of rainfall during June of 1990, while

average monthly rainfall for the whole year was 10.36 cm (Figure 8). Diameter growth can be interrupted by drought due to sensitivity of cambial activity to the environmental stress (Kozlowski et al., 1991). In fact in the beginning of July 1990, water potentials were the lowest for the whole growing season, and significantly lower for the unthinned trees when compared with the thinned (Figure 3d). As a result monthly diameter growth of the unthinned trees averaged only 47% of that for the thinned trees, however the difference was only significant at $p=0.1$ (Figure 1). Although overall growth patterns were related to tree water potentials, DBH growth was reduced in the unthinned stands throughout the entire season, even when the xylem water potentials did not differ or water was plentiful in both treatments (water potentials were around -1.0 MPa). In fact, average water potential for the season was the same in both thinning treatments (Table 5).

Based on foliar nutrient contents, the observed differences in growth between the thinned and unthinned stands do not appear to be caused by differences in the nutrient availability (Table 6). The foliage of the unthinned stands contained (insignificantly) higher levels of almost all examined nutrients (N, P, K, Ca, Mg, Fe), with only Mn being slightly higher in the thinned stands. Such results agree with those reported by Stone and Christenson (1975), who found that thinning of pole-sized sugar maple resulted in small but consistent decreases in foliar concentrations of nutrients including Mn and several others. Those authors attributed the decreased foliar nutrient concentrations to dilution effects due to increased growth. A similar effect is likely in our study.

In 1990, concentrations of N, P, K, and Fe were lower in both thinned and unthinned stands than in 1989. This may indicate that those nutrients are becoming increasingly limiting on the site. Calcium and manganese may be becoming limited in the unthinned stands (their foliage concentrations decreased), but not in the thinned stands where the Ca concentration stayed the same, and that of Mn increased. Three years after thinning, only magnesium seemed to be fully available regardless of the thinning treatment, since the concentration of

this macronutrient increased in both thinned and unthinned trees foliage.

Needles in thinned and unthinned stands seemed to have very similar physiological capacity as indicated by the seasonal patterns (Figure 3) and averages (Table 4) of the gas exchange parameters measured under saturating light conditions. Needles in the upper crowns however, had the capacity to outperform those from the lower crowns, although the differences between the seasonal averages (Table 4) and on particular dates (Figure 4) were, most of the time, statistically insignificant. The observed differences did not seem to result from differences in water status, since higher gas exchange rates were accompanied by more negative water potentials throughout the growing season (Figure 4d). Light saturated gas exchange parameters in the lower crowns generally were similar or higher for the season when compared with those measured under stand light conditions. Therefore light saturated rates in the lower crown needles were not reduced as a result of a photooxidation of chlorophyll caused by sudden exposure of more shade accustomed needles to full sunlight during the measurements.

Light saturated gas exchange rates for lower and upper crowns could have been different in part because of differences in foliar nutrient content (Table 6). Madgwick et al., (1983), working with 7-year-old *Pinus radiata* stands showed that nitrogen concentration were unaffected by thinning but decreased with needle age and from the top to the bottom of the crown. Likewise, in our study, no significant differences were found between the thinning treatments, but the upper crowns contained more N, P, and K. These results are consistent with the previous findings in those stands (Ginn, 1989).

Nitrogen is thought to be critical in achieving high photosynthetic rates mainly because of its role in chlorophyll synthesis. In the current study however, decreased N concentration in the lower crowns were not reflected in significantly lower chlorophyll contents (Table 7). Nitrogen also plays an important role in protein synthesis and if insufficient for synthesis and replacement of enzymes taking part in photosynthesis could be a limiting factor for that

process. In our study, at least amounts of Rubisco (a key enzyme for Ps) could be assumed similar in foliage from both crown positions, since we did not detect significant differences in carboxylation efficiencies (Table 12), thought to be proportional to quantities of the enzyme. Therefore it is unlikely that the nitrogen was truly deficient for photosynthesis in the lower crown foliage three years after thinning. Shortages of potassium and phosphorus could lower net photosynthesis through increased respiration because of impeded energy transfer. In our study however, dark respiration estimates were never significantly higher for lower crowns, in fact they were often decreased when compared with the upper crown foliage (Tables 8, 11). Decreased potassium concentration could also impede stomatal function, limiting CO₂ access into the carboxylating sites. That may explain in part the significantly higher estimates of stomatal limitations to photosynthesis found in this study for the lower crown foliage (Table 13). Needles of the unthinned trees also had higher stomatal limitations of photosynthesis when compared with those from the thinned trees, although these differences could not be attributed to decreased potassium concentrations.

Higher stomatal limitations to photosynthesis were coupled with higher CO₂ compensation points. Possibly the increased stomatal limitations resulted in lower intercellular CO₂ concentrations, this in turn favored oxygenase activity of Rubisco in the mesophyll cells and subsequently photorespiration. As a result the CO₂ compensation point would be increased. This is similar to C₃ plants which have much higher CO₂ compensation points than C₄ plants (Larcher, 1980), largely because of their greater photorespiration. The increased stomatal limitations to photosynthesis and the higher CO₂ compensation point could be contributing to the lower potential photosynthesis in lower crown foliage.

Lower crown needles, when compared with those from upper crowns, tended to show some characteristics associated with shade foliage. Their photosynthetic capacity was somewhat lower as shown by seasonal patterns (Figure 4a) and averages (Table 4) of light saturated photosynthesis. Light compensation points for those needles were almost 2 times lower

($p=0.15$), although there was a large variation in this parameter. This concurs with Loach (1967), who found that the light compensation point decreased by 50 to 75% for five broadleaved species as the light conditions during growth decreased from full to 3% of sunlight. Light compensation points for sun leaves are typically higher than those of shade grown leaves because of higher respiration rates which are associated with increased costs of synthesis and maintenance of expanded photosynthetic machinery (Kozłowski et al., 1991). This is in agreement with the current study where significantly higher dark respiration rates for the upper crowns were accompanied by higher light compensation points (both parameters derived from light curves) (Table 11). Also dark respiration rates measured with Li-Cor 6200 were generally higher in the upper crowns (Table 8).

Needles from the lower crowns, however, were lacking some of the features of typical shade foliage. The quantum yield of shade grown leaves was reported to be higher than that of the sun leaves for a number of tree species (Kozłowski et al., 1991). This was not observed in our study. Higher quantum yield along with lower light compensation point and respiration rates would help to compensate for typically light limited conditions. Shade foliage is often found to have higher total chlorophyll content (Koch, 1976 cited in Kull and Koppel, 1987), but lower chlorophyll a/b ratio (Lewandowska et al., 1976; Lichtenthaler et al. 1981). Such changes are interpreted as acclimations towards a more efficient harvesting of light in low light conditions (Lewandowska et al., 1976). The decrease in chlorophyll a/b ratio in shade foliage reflects an increase in relative and/or absolute amount of chlorophyll b, which forms a large part of the light-harvesting pigment in Photosystem II. Such changes were not observed in this study. An ability to harvest a larger percentage of the available energy would probably lead to a larger reduction in light saturated photosynthetic rates than that observed for lower crown foliage in our study.

Needles of the thinned stands (regardless of crown position) displayed some of the features of sun foliage when compared with the needles of the unthinned trees. That was

especially true in case of the quantum yield and light compensation point comparisons, although large variation made the existing differences statistically insignificant (Table 11).

During the 1990 growing season net photosynthetic rates both for the thinning treatments and crown positions tended to decrease from July 6th on (Figure 3a, 4a), the date gas exchange measurements were started on the fully expanded current year foliage. High photosynthetic rates in previous year foliage in the beginning of the growing season could be due to the necessity of supplying carbohydrates to the newly expanding foliage and the large stem diameter increment which occurred during that time of the year (Figure 1).

Photosynthetic compensation due to changes in source or sink strength has been reported for several species (Kramer and Kozlowski, 1979). Possibly, gas exchange rates drop in the old foliage after stem diameter growth slows and the new foliage is elongated (we did not continue to measure 2-year-old foliage once new foliage was fully elongated). This is supported by Ginn (1989), who found that the light saturated net photosynthetic rate of 2-year-old foliage was lower than the new foliage on every measurement date from June 30 through October 5, 1989. In her study average photosynthesis rate for old and new foliage declined in late summer repeatedly for two consecutive years (Ginn, 1989). It was shown for several conifer species that the rate of photosynthesis of needles living more than one year usually decreases after the first year (Kozlowski et al., 1991). Tyszko (1991) also found current year needles of red spruce to photosynthesize at higher rates than older foliage.

In the 1990 stomatal conductance also peaked in the beginning of the growing season regardless of the thinning treatment or crown position (Figure 3b, 4b). Steady decline of stomatal conductance on consecutive measurement dates can not be attributed to the change in sampling to the new foliage, because it was shown by Ginn (1989) that new foliage tends to have slightly higher stomatal conductance than the previous year foliage. Transpiration rates measured under saturating light also showed a somewhat declining pattern regardless of the thinning treatment or crown position as the growing season was progressed (Figures 3c, 4c).

This parameter appears to be more tightly coupled with the xylem water potential than the other gas exchange parameters (Figures 3, 4). It is hypothesized here that loblolly pine foliage reaches its maximum physiological capacity during the next spring, before the new foliage is fully elongated.

Under stand light conditions there were no significant differences in physiological activity of needles from the upper and lower crowns of thinned stands. On the contrary, in unthinned stands, lower crown needles had lower net photosynthesis, stomatal conductance and transpiration rates than those from upper crowns (Figures 5, 6). Seasonal averages for upper crown foliage photosynthetic rates did not differ significantly regardless of the thinning treatment, those in the lower crowns were significantly decreased in the unthinned stands when compared with the thinned (Table 8). Additionally, *in situ* rates in both crown positions for thinned trees were similar to rates measured under full light (Table 4). Therefore, under stand environmental conditions the thinned trees were fully utilizing their capacity for photosynthesis in both crown positions, while the unthinned trees only in the upper crown sun foliage.

It was shown in the course of this discussion that the physiology of needles from the upper and lower crowns differed to some extent, and that lower crown needles had some of the features of shade foliage. The decrease in physiological activity in the lower crowns of the unthinned stands measured under stand conditions was however, greater than that observed for lower crown needles measured under saturating light. That means that lower crown needles of the unthinned stands were not fully utilizing their physiological capacity under stand environmental regime. As opposed to Ginn (1989), in the current study lower crown needles from the thinned stands were not more sun-like than those from lower crowns of unthinned stands. This conclusion is supported by no significant interactions between the thinning treatments and crown positions when the measurements were taken under saturating light as in Ginn (1989) study. Additionally, in full light lower crown needles from both treatments had

similar average net photosynthetic rates, 2.48 and 2.18 $\mu\text{Mol}/\text{m}^2\text{sec}$ (expressed per unit leaf surface area), and 37.4 and 36.4 $\text{nMol}/\text{g sec}$ (expressed per unit dry weight) for thinned and unthinned trees respectively (data not shown). The decreased physiological activity of the shade leaves below that of potential capacity together with smaller foliage surface area (biomass) were probably the major reasons for decreased growth of the unthinned trees.

Reduced physiological activity in the lower crowns of unthinned trees was probably caused by one or more limiting factors present under stand environmental regime. Water status, foliar chlorophyll and nutrient contents of the lower crown needles did not depend on the thinning treatment, since no significant interactions between the crown positions and thinning treatments with respect to those parameters were observed. Lower crown foliage in the unthinned stands, however was receiving on an average less than half of the light measured in the lower crowns of the thinned stands. In fact the lower crowns of unthinned trees were receiving an average light level equivalent to that of the compensation point for the upper crown foliage (Tables 8, 11). Only the decreased light compensation point (the same for lower crown needles regardless of the treatment), allowed those crowns to contribute to carbon gain. Also the in situ gas exchange rates were higher whenever light levels were increased. Therefore the different characteristics of gas exchange parameters were likely due to light availability. In fact, the correlation coefficient between in situ light levels and net photosynthetic rates was 0.78. Additionally, when the photosynthetic photon flux density (PPFD) was used as a covariate in the statistical analysis of in crown measurements, no significant differences were detected between the crown positions. Also Cregg et al. (1990), who found higher needle conductance in loblolly pine the first year after thinning, concluded that it was the differences in light interception and crown exposure that was responsible for the observed changes.

According to Baker and McKiernan (1988) many higher plants can modify their photosynthetic apparatus not only in response to changes in light intensity, but also to changes

in spectral composition. In this way plants can optimize their photosynthetic rates depending on light conditions. It is important that in the natural environment, mature leaves are capable of changing their physiology from "sun" to "shade" or the other way round, over a relatively short time (Baker and McKiernan, 1988). In the first years of this study, thinning probably induced this kind of change in the lower crown foliage, increasing its potential gas exchange rate (Ginn, 1989; Ginn et al., 1991). During the third growing season after thinning we may be observing the start of a reversal of that process due to changes in light conditions. Light levels were still much higher in the lower crowns of thinned stands, but they were starting to decrease (Table 8 and Figure 5c). The decreasing light may have been enough to increase the "shade" character of the needles in lower crowns of thinned stands. This stand closure (decreasing light) could also be the reason for less pronounced growth differences between thinning treatments in comparison with Ginn's (1989) results.

In the current study the physiological activity of upper crowns in unthinned stands measured under stand light conditions, seemed to be even higher than that of upper crowns of thinned stands. Probably, needles in the upper crowns of unthinned stands are trying to compensate for the lower production in the shaded needles. This could be explained in terms of photosynthetic compensation due to changes in source or sink strengths, phenomenon observed also for other species (Kramer and Kozlowski, 1979). That idea is further supported by the photosynthesis to respiration ratio, which is an indicator of the efficacy of the tree assimilation-respiratory apparatus. The highest efficiency was observed for the upper crowns of the unthinned stands, lower and almost even for the both crown positions in the thinned stands, and the lowest in the lower crowns of the unthinned stands (Table 8 and Figures 7c, 7d).

Correlation between physiological measurements and DBH growth

Difficulties in relating yield to gas exchange rates arise mainly from the fact that not all photosynthate is directed for growth and some is used to increase biomass but not merchantable yield. In fact even a lack of a positive relationship between leaf photosynthesis and crop yield has been reported for some species (Nelson, 1988). Additionally, instantaneous measures in crown are usually a very small sample of an entire crown rates.

In our study the generally declining pattern of gas exchange rates on consecutive measurement dates was in agreement with the diminishing DBH growth as the growing season progressed. That was also reflected in the relatively strong correlations between the gas exchange measurements and diameter growth (Table 9, 10). The correlation coefficients were slightly higher when DBH growth was correlated with the *in situ* gas exchange rates. As expected, within the crown gas exchange measurements appeared to be more representative of actual tree carbon uptake than the measurements taken under the saturating light.

Variation in photosynthetic rates resulting from diurnal and seasonal patterns and differences in leaf exposure to light are often reasons for poor correlation between short term measurements of photosynthesis and dry matter production (Kozłowski et al., 1991). In our study the employed sampling procedure: measurements taken generally between 10 a.m. and 2 p.m. on several dates over the growing season using twigs from upper and lower crowns, probably helped to account for some of the variability.

In studies dealing with plant productivity, respiration is usually considered in two parts; maintenance respiration is that associated with the sustaining of the plant structure, and growth respiration is associated with the synthesis of new tissues (Jarvis and Leverenz, 1983). Lower correlation coefficients between diameter growth and leaf dark respiration in our study, could have resulted from only indirect importance of that process for wood increment. Most of measured dark respiration was probably maintenance respiration associated with leaf internal

energy requirements. This is supported by the fact that, in general, higher rates of respiration were associated with physiologically more active foliage. If growth respiration was occurring after needles were fully elongated, the products were probably used for synthesis of needle supplies for cell wall thickening, cuticular wax production, etc. Dark respiration was the only gas exchange parameter better correlated with the DBH growth when expressed per unit leaf dry weight. Probably, the higher mass of respiring tissue could provide more maintenance supplies for the foliage, which in turn produced more photosynthate for growth and other uses.

As indicated earlier, high net photosynthesis to dark respiration ratio observed in the upper crowns of the unthinned trees might be a sign of a compensation effort for the lower production of the shaded foliage of those trees. That increased physiological activity apparently did not fully compensate since the unthinned trees had lower monthly diameter growth than the thinned trees. Likely the higher ratio and therefore higher photosynthate output was limited to only a fraction of the crowns. This coincidence of high net photosynthesis to dark respiration ratio and small DBH growth (which could have occurred for as much as a quarter of all our observations) was probably the main reason for the negative correlation between the two.

Relatively low correlation coefficient between the DBH growth and water potential was probably the reflection of the fact that water was not a limiting factor for diameter growth during the third growing season following thinning.

CONCLUSIONS

During the third growing season following treatment the thinned trees grew 11 cm more in height, 35% more in diameter, basal area and volume in comparison with the unthinned trees but the differences were not statistically significant at $p=0.05$. Three years after treatment crown diameter grew more and was still significantly higher for thinned trees.

Upper crowns of the thinned and unthinned stands had the physiological potential to somewhat outperform lower crowns in terms of net photosynthesis, stomatal conductance and transpiration. Increased physiological activity of upper crowns was paralleled by lower stomatal limitations to photosynthesis, possibly the result of better potassium supply facilitating more efficient stomatal response to environmental conditions.

Lower crown needles displayed some of the features of the shade foliage (lower photosynthetic capacity, light compensation point and dark respiration rates), but did not have higher quantum yield, and their light harvesting abilities seemed not to be increased in comparison with the upper crown sun needles.

Light conditions in the lower crowns of thinned stands were similar to those in the upper crowns. This had an effect on *in situ* gas exchange rates, which were similar in the upper and lower crowns of thinned stands. Seasonal averages of photosynthetic rates and stomatal conductances were like those taken under saturating light, indicating that thinned trees were fully utilizing their potential for CO₂ uptake. This together with the larger foliage surface area are likely the major reasons for better growth of those trees.

In the unthinned stands because of light differences, gas exchange rates were significantly reduced in the lower crowns, with only upper crown foliage fully utilizing its photosynthetic capacity. The physiological activity in the upper crowns of unthinned trees tended to be even higher (highest net photosynthesis to dark respiration ratio) than that in the upper crowns thinned trees in an effort to compensate for the lower production in the shaded foliage.

As a whole, foliage of the thinned trees resembled in many aspects sun foliage of the upper crowns, and that of the unthinned trees was similar to more shade like foliage of the lower crowns. The sun and shade character of the foliage however, was better pronounced for upper and lower crown positions than for the thinning treatments.

Diameter growth was strongly correlated with gas exchange rates, particularly with net photosynthesis and stomatal conductance. Higher stomatal conductance was especially important for better CO₂ assimilation and increased growth under stand environmental conditions.

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VITA

Jaroslav Nowak, son of Franciszek R. Nowak and Teresa H. Nowak, was born in Pruszkow, Poland on March 8, 1961. He attended elementary and secondary schools in his home town. In October 1980 he began studies at the Forestry Department in Warsaw Agricultural University, Poland. He received his Master of Science Degree in Silviculture in October of 1986. After three years of professional work as a Research Assistant in the Forestry Research Institute (Sudety Mountains Experimental Station) in Poland, he entered the Graduate School at VPI&SU in August 1989. He received his Master of Science degree in Forestry (Tree Ecophysiology) in November 1991.

Jaroslav Nowak