

CARBON DIOXIDE EXCHANGE PATTERNS OF
A 15-YEAR-OLD LOBLOLLY PINE
(Pinus taeda L.) STAND.

By

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ABSTRACT

In the Spring of 1989, a study was initiated to determine the effects of seasonal moisture stress, crown positions, and foliage age and flush classes on carbon exchange rates (CER) of a 15-year-old, Southeast Oklahoma loblolly pine stand. This stand has been maintained near a basal area of 11.5 m²/ha for the past three years.

Diurnal trends in CER were measured at monthly intervals from April to November. These measurements were taken from the upper, middle, and lower one-third of the crowns of six trees. Within each crown position CER was measured on all age-flush classes of tissue. One plot, consisting of three pines, was equipped for irrigation during periods of summer moisture stress.

The pines were never irrigated due to an unusually wet summer; therefore, the effects of seasonal moisture stress on CER was not determined. However, both crown position and age-flush class of tissue had significant effects on the observed CER. Over the growing season, rates of net photosynthesis (P_n) across all age classes of foliage in the middle crown position and lower crown position were 82% and 52%, respectively of that measured for the upper canopy branches. Comparison of CER linear regression models developed for foliage in each of the crown positions and

age-flush classes by month indicate that the majority of the differences measured in CER among the crown positions could be explained by the variation in light within the canopy. These models took into account vapor pressure deficit, xylem pressure potential, crown air temperature, and chlorophyll content. Both light variations from the tip of the branch to the interior part of the branch and differences in photosynthetic capacity of the tissue accounted for most of the observed differences in CER between age classes while differences in CER between flushes could usually be explained by light variations alone. The ability of light to explain the variations in CER between foliage location and phenology possibly depends on foliage maturity and the effects of subfreezing temperatures.

INTRODUCTION

Loblolly pine (Pinus taeda L.) has a natural range that includes most of the southeast and the central Atlantic coastal states. This wide range, along with its occurrence in pure stands, its abundance, its high productivity, and its many uses, account for it being the principal commercial pine species in the southeastern United States (Fowells 1965), and therefore of prime economic importance to this region. In Oklahoma, the natural range includes the southeast corner of the state but the establishment of loblolly pine plantations has artificially expanded the range in Oklahoma.

To obtain maximum growth and health of these stands, it is important to understand the growth characteristics of loblolly pine. This growth is influenced by the relationship between photosynthesis and respiration as affected by environmental, physiological, and genetic factors. The environmental and physiological factors not only differ between trees, but they also differ within a tree. Troeng and Linder (1982b) found a greater variation in net photosynthetic rates within the crown of a 20 year-old Scots pine (Pinus sylvestris L.) than between the trees. Environmental factors which influence net primary production such as air temperature, light intensity, vapor pressure,

CO₂ concentration, and wind have been found to vary throughout the crown (Reifsnyder and Lull 1965, Woodwell and Botkin 1970, Satterlund 1972). The photosynthetic response in loblolly pine has been shown to vary with moisture stress levels (Brix 1962, Seiler and Johnson 1985, Teskey et. al. 1986, Seiler and Johnson 1988), temperature levels (Teskey et. al. 1986), humidity deficits (Teskey et. al. 1986, Fites and Teskey 1988), and light levels (Teskey et. al. 1986).

Besides differences in photosynthesis of needles in regard to their vertical position in the crown, there are possible physiological factors such as photosynthetic capacity that are associated with the different needle ages and flushes. Generally, loblolly pine retains its needles for two growing seasons. During all seasons except winter, leaves of two age classes are usually present. Foliage develops in distinct intervals or flushes during the spring and summer growing period; one to several flushes may develop during a single growing season depending on various environmental factors and position in the live crown. The leaves of different flushes differ not only in age, but are produced under different environmental conditions; hence, differences in photosynthetic capacity might be expected from different needle ages and flushes.

The reasons for studying net carbon exchange rates (CER) in loblolly pine include:

- 1) to obtain a better estimate of net carbon gain.

An equation developed by Teskey et. al. (1987) states that:

$$\text{Carbon gain} = \Sigma(L_i(A_i - R_i)) - B_x(R_x) \quad (1)$$

where: L_i = leaf area of age class i ,

A_i = photosynthetic rate of age class i ,

R_i = respiration rate of age class i ,

B_x = the surface area of non-photosynthetic tissue,

R_x = the respiration rate of non-photosynthetic tissue.

If the carbon exchange rate varies due to crown position, flush type, and/or season then it might be necessary to modify the equation to account for this variability.

- 2) to develop better net primary productivity (NPP) models (Reynolds et. al. 1980). If, as some have predicted, global warming is occurring (Mitchell 1989) then it is necessary to determine the impact of this environmental change on carbon exchange patterns as it affects the growth, health, and productivity of trees and stands. Therefore, there is a need to improve NPP models through a better understanding of the seasonal and within-tree variation of CO₂ exchange rates.
- 3) to provide a data base of seasonal and diurnal patterns of CO₂ exchange and its relationship to selected environmental variables, especially field

moisture stress. There is very little literature available on the relationship of CO₂ exchange rates and water stress in older trees and research has cast doubts on the reliability of applying information obtained from seedlings to older trees (Kull and Koppel 1987, Zelawski et. al. 1981).

The objectives of this research are:

- 1) to determine the effects of seasonal moisture stress on CER in a 15-year-old loblolly pine stand, and
- 2) to determine if variability in measured CER within the crowns of loblolly pines can be wholly or partially explained by differences in photosynthetic photon flux density (PPFD) after allowances have been made for any variations in needle xylem pressure potential (XPP), vapor pressure deficit (VPD), air temperature of the crown (T_C), and needle chlorophyll content.

MATERIALS AND METHODS

Site Description

The study site is a 15-year-old loblolly pine plantation located on Weyerhaeuser Company property in southeastern McCurtain County, approximately 8 km south of Eagletown, Oklahoma (legal description: Section 9, T7S, R26E, Indian Meridian). Summers are hot and humid while winters are usually mild. Average annual precipitation is 119 cm/year with the greatest amount occurring in spring. The soil is a Cohaba fine sandy loam of the Guyton-Ochlockonee association. It is characterized by deep, nearly level (0-1%) slopes. Maximum soil water holding capacity in the top 122 cm of soil is 23.17 cm (USDA SCS, 1974).

The site was prescribed burned and double-bedded following harvest of a pine-hardwood stand in 1975. The current stand was established from a seed source of local origin, and previous projects have divided the study area into 3 blocks with six 0.1 ha plots per block. Plots consist of thinned (approximately 11.5 m²/ha BA) or unthinned treatments (22.9 m²/ha BA). At the initiation of this study, the pine stands were approximately 14.5 m in height.

Treatment

Two of the thinned 0.1 ha plots were chosen, one of which was to be irrigated. At the beginning of the 1989 growing season, the irrigated and the unirrigated plot had a basal areas of 15.4 m²/ha and 16.6 m²/ha, respectively. In the irrigated plot, soil moisture at the 15 cm depth was measured with eight porous cup soil tensiometers located in a cross pattern. Up until October, the plot was watered through a sprinkler system network if average soil tensiometer readings fell below -0.05 MPa. In October, irrigation was halted regardless of soil tensiometer readings in order to allow the trees to set overwintering buds. Also, the end of September usually marks the end of the dry season in Oklahoma. Vegetation was also controlled in the irrigated plot to conserve soil moisture by limiting transpiration of the undergrowth.

Net Carbon Exchange Rates

Net photosynthesis (P_N) and dark respiration (R_d) measured on three selected pines per plot using a closed-flow CO₂ exchange system (LI-6200 Portable Photosynthesis System, Li-Cor, Inc.). This system consists of an infra-red gas analyzer (IRGA) to determine the CO₂ content of the air being sampled, a computer control console, a quarter liter leaf chamber, and battery packs. The theory of operation for the IRGA is based on the principal that CO₂ absorbs

infra-red radiation. A quantity of CO₂ in the sample is determined by comparing the amount of infra-red radiation that passes through the sample with the amount of infra-red radiation that passes through a reference tube of known CO₂ concentration. The pump in the IRGA circulates air from the leaf chamber to the analyzer and back. The flow valve is used to divert a portion of the flow through the desiccant tube which dries the air in order to maintain a steady water vapor pressure in the leaf chamber during measurement. Air temperature and relative humidity are measured in the leaf chamber. A light sensor located on the outside of the chamber records photosynthetically active radiation.

When a leaf is enclosed in the chamber, the average rate of change in CO₂ concentration in the air is determined for a short period of time (measured at about 3 s intervals for 30 s or 45 s for this study). The P_n and R_d rate is then calculated using this rate of change plus the amount of leaf area enclosed in the chamber, the temperature, atmospheric and water vapor pressure, and other factors. An artificial transpiration rate is calculated since the boundary layer conductance of the leaf is usually different from that of the leaf in the chamber. Since the boundary layer conductance value of the foliage in the chamber is experimentally determined, values of stomatal conductance can be calculated.

The study ran from late March to early November of 1989. CO₂ exchange, phenology, and growth measurements were

taken near the beginning of each month. Until August the CER measurements consisted of three consecutive days or as close to consecutive as weather permitted. Each day, the CERs were obtained from two trees, one from each plot, until all six trees had been sampled. After July, the availability of a second LI-6200 enabled simultaneous CER measurements from the two plots. This allowed for CER measurements to be completed within a twenty-four hour period.

Personnel requirements for the CO₂ exchange measurements consisted of two crews of three people. A crew consisted of one person operating the LI-6200, one placing the needles in the cuvette, and one notekeeper whose responsibilities also included operating the pressure bomb.

Pines selected were codominants of similar diameter, height, form, and crown shape at least one crown width away from the 0.1 ha plot border to minimize any edge effect (Table I). Each crown was divided into thirds -- upper, middle, and lower. In each crown level the foliage was divided into age-flush classes. The age was determined by the year the needles were initiated, usually in 1988 ('88) or 1989 ('89), and the flushes within an age are distinguished by their order of emergence, first flush (1) and second flush (2). Access into each tree's crown is provided by a 15.24 m high, 0.32 m wide, tripod base T.V. tower (Rohn 25g) with three 1.83 m long swingable platforms attached at the appropriate measurement levels.

TABLE I
 CHARACTERISTICS OF RESEARCH TREES, CROWN DIVISIONS,
 AND SAMPLE BRANCHES AS OF MARCH 1989.

Treatment	Tree Number	DBH	Total Height	Height From Base to Measurement Area of Sample Branch by Crown Position		
				Upper	Middle	Lower
		-cm-		-----m-----		
irrigated	19	29.2	14.32	11.70	9.70	5.90
	725	32.2	14.97	11.78	9.42	7.15
	728	25.6	13.40	11.64	10.00	7.72
unirrigated	563	29.8	15.25	13.80	10.00	7.60
	572	24.6	14.10	12.80	9.80	7.40
	575	21.0	14.17	12.80	10.00	7.70

Each gas exchange measurement was obtained with a horizontally held 0.25 liter chamber clamped across nine to sixteen needles laid parallel to the width of the chamber. Care was taken to prevent overlapping of needles inside the chamber. Ideally, 5 three-needle fascicles of the same flush and age were used for each measurement but availability required the occasional use of less than five fascicles and/or the use of four-needle fascicles. The natural orientation of the fascicles were generally maintained.

Once a month, CER were measured and analyzed from one set of healthy needles near the outer edge of the crown on a major southerly-facing branch for each crown position of each tree. A set consisted of one CER measurement from each combination of age class and flush that were present at that crown position and with a needle length of at least 6.5 cm. This minimum length allowed the flush to be placed completely across the chamber and the total needle surface area inside the chamber to be determined without destructive sampling. Throughout the study CER measurements were obtained from the same flushes on the same branch. If CER measurements and analysis from previous months consistently showed no significant difference between older flushes of the same age class, then the second flush from the older age class was not measured.

Gas exchange measurements began approximately two hours before sunrise, were repeated about every 3.0 hours, and

ended about two hours after sunset. This allowed the day to be divided up into distinct time or measurement periods consisting of a set of full gas exchange measurements for both plots. For July, CER measurements were made approximately every 3 hours for a complete 24 hour period starting at one hour after sunset and continuing until sunset of the next day.

Environmental Variables

With each CER measurement, the CO₂ exchange system measured the corresponding photosynthetically active radiation (PAR), air temperature, relative humidity, and stomatal conductance for that particular set of needles. A Scholander pressure bomb was used to measure needle XPP for each set of CO₂ exchange readings taken.

Precipitation was collected and measured about every week with two standard rain gauges stationed at two different open areas adjacent to the plots. Daily temperature and relative humidity extremes for the region were obtained from National Oceanic and Atmospheric Administration records measured at the Oklahoma Forestry Division weather station at Broken Bow, OK, approximately 16 km northwest of the study site. Using these air temperatures and relative humidities, daily minimum and maximum VPD values were calculated (Lowe 1976).

Needle Surface Area and Growth

Growth characteristics that were recorded monthly included flush length, needle length, dates of needle drop, and date of bud break.

Estimation of needle surface area is based on the principle that pine needle fascicle shapes are extremely regular and can be considered to be cylindrical except for about the last 0.5 cm that tapers which can be approximated as a conical structure (Bingham 1983). For calculation of CO₂ exchange rates, the tapered end was ignored since the needles were spread across the chamber with the tapered end outside the chamber, and therefore the following equation was used for the determination of needle surface area:

$$\text{AREA (cm}^2\text{)} = 2RFL(N + \pi) \quad (2)$$

where R is the average radius of the fascicle or fascicles, F is the number of fascicles, L is the total fascicle or average fascicle length, and N is the number of needles per fascicle. R was measured with a measuring magnifying glass.

Chlorophyll Determination

At the end of each measurement day, one fascicle was taken from each flush, age, and crown position that was measured for gas exchange. The samples were stored up to three days in a dark, cold container before the chlorophyll was extracted with N,N-dimethylformamide (DMF) (Moran and Porath 1980). A 4.5 cm segment from the mid-section from

each of two needles of a fascicle was sampled and the leaf area was determined. The needle sections were then cut into 1 cm segments and placed in a vial with 5.0 ml of DMF. After at least 48 hr in DMF the absorbance of the solutions was read with a spectrophotometer (Spectronic 1201, Milton Roy Co.). The quantity of chlorophyll a (chl a), chlorophyll b (chl b), and chlorophyll a+b (total chl) in DMF was then determined using the extinction coefficients developed by Inskeep and Bloom (1985).

Analysis

Due to the timing of needle initiation and senescence certain age-flush classes are not present during various times through the study. Therefore, it was necessary to perform most of the comparisons using SAS General Linear Models (GLM) procedure (SAS 1985) to avoid the problems with missing cells. In all comparisons, differences were considered to be significant at the 0.05 level or lower.

To check for plot differences, an initial comparison of CER between plots was run using the GLM procedure. Within a month, comparisons of average P_n and XPP were divided into two groups: 1) within a crown position but between age-flush classes, and 2) within an age-flush class but between crown positions. This was necessary to remove problems associated with the mixing of comparisons between and within branches. Age-flush classes on a tree within a crown position were from the same branch while crown positions

within an age-flush class were from different branches. Within a month and age-flush, if there was no significant interaction between the variable of interest and the measurement period, then P_n and XPP were compared by crown position using the tree*crown position interaction as the error term. The error term for within a month and crown position consisted of the sum of all interaction terms with tree (branch) as a factor (age-flush*tree + period*tree + age-flush*period*tree). CER values from measurement periods in which there was total darkness were not used in the calculation of the average for that month.

GLM was also used in the analysis of total chl and chlorophyll a:b (chl a:b). Initial analysis found that within a month the interaction of crown position with age-flush is not significant. Therefore, further monthly chlorophyll analysis disregarded crown positions while comparing chlorophyll between age-flush classes. Significant differences in chlorophyll content by crown positions were determined by averaging the means of the chlorophyll values of the age-flush classes for each crown position. The error term consisted of crown position*tree + age-flush*tree(crown position). This was also the same error term used in the comparison of chlorophyll between age-flush classes.

The chlorophyll means by age-flush classes were also compared among months. Due to the variability between trees in the time of needle emergence and senescence interactions

were combined with the initial error term of tree*month*crown position if they were not found to be significantly different. This allowed the analysis of means for every month including those that could not be previously analyzed when using just the initial error term.

The CER regression models were formulated with PPF_D, the square root of PPF_D (PPFD^{0.5}), XPP, VPD, "stress", T_C, total chl, chl a, and chl b as independent variables. Changes in PPF_D at low light levels have been shown to have a greater effect on CER than changes at high irradiance levels (Larcher 1969); therefore, PPF_D^{0.5} was used to simulate the non-linear relationship between irradiance and CER. Due to morning and late evening dew on the needles, stomatal conductance was measured but was not used in the models because of the number of missing values. As a possible better indication of stomatal conductance than VPD or XPP alone, the variable "stress" was developed by multiplying VPD by XPP.

To determine the response of CER by light, two types of models, full and reduced, were developed and compared. The full regression models of CER were developed for each month from all of the independent variables along with the appropriate dummy variables to represent the different crown positions, age-flush classes and the interaction of these dummy variables with PPF_D. The reduced models were developed from the same variables used in the full models minus the appropriate dummy variables from the crown

position and/or age-flush class being compared and the interaction of these dummy variables with PPF. The dummy variables and interactions present in either model depends on what is to be compared, such as age, flush, and/or crown position. Using an F-test, the model of a given crown position, age-flush class, or combination of the two categories was then compared with the model developed for all crown positions and age-flush classes that were not previously determined to be significantly different. This determined if differences in P_n could likely be explained by the various values of PPF encountered at the various crown positions and age-flush classes. This method of comparison uses the sums of squares error (SS_{er}) of the reduced model, the sums of squares error (SS_{ef}) of the full model, and the mean square error (MS_{ef}) of the full model to make the following F-test (Neter and Wasserman 1974):

$$F(df_r - df_f, df_f) = (SS_{er} - SS_{ef}) / (df_r - df_f) / MS_{ef} \quad (3)$$

The terms df_r and df_f are the degrees of freedom for SS_{er} and SS_{ef} , respectively. The models were considered to be different, and hence the relationship between CER and PPF and the models' intercepts was considered different when the F-test was significant.

RESULTS AND DISCUSSION

Plant and Soil Water Potential

The summer of 1989 was unusually wet (fig. 1) when compared with the monthly average (based on 1951 to 1980) of Broken Bow, OK (NOAA National Climatic Data Center 1987). While summer precipitation was greater than normal, drought conditions were experienced in the fall. During the study, precipitation exceeded pan evaporation (evaporation from a free water surface) only in March, May, and June (fig. 2).

Figure 3 illustrates the ambient temperature and VPD that occurred during the study period. Figure 3 also depicts the initiation and termination of needle elongation for '89-1 and '89-2 foliage and the occurrence of senescence for the combination of '88-1 and '88-2 foliage. The abundant precipitation during the growing season resulted in a second flush at most of the crown positions. The lower crown of tree 572 developed only one flush in 1988 but still retained a considerable amount of '87-1 needles until June 1989. These were measured and are included in graphs and tables but are not discussed or analyzed since the information consists of a sample of one. Since initial analysis from previous months had shown little differences between '88-1 and '88-2 foliage, measurement of '88-2 foliage stopped after July. Not measuring the '88-2 foliage

in the later half of the growing season also provided the extra time needed to measure the '89-2 foliage in October and November.

Through September, the soil tensiometers on the irrigated treatment plot had not dropped below -0.05 MPa so the plot was not irrigated. As planned, the plot was not irrigated after this time regardless of soil tensiometer readings. Since no irrigation took place in the designated irrigated plot and initial statistical analysis indicated no difference in the CER means of the two plots, the plots were considered to be similar and were combined in all further analysis. The plot factor was then disregarded and the readings from the six trees were combined.

The daily pattern of XPP (figs. 4-11) is consistent with those previously described for seedlings (Fites and Teskey 1988) and mature conifers (Hodges 1967, Leverenz 1980, Beadle et. al. 1985b). The needle water potential initially decreases with T_c and VPD reaching a low in the early afternoon, and then begins to recover in the evening. The two months with the lowest mean predawn water potential (PXP), an indicator of soil moisture, were May and November with needle water potentials of -0.81 and -0.75 MPa, respectively, while the two lowest monthly readings of XPP were those recorded in the upper crown during August and September with needle water potential values of -1.53 and -1.58 MPa, respectively.

The analysis of daily mean values of diurnal water potential showed crown position differences but no significant differences between age-flush classes within a crown position. Figure 12 illustrates the solar noon time values of needle water potential of '88-1 foliage by crown position. XPP tended to decrease from lower to upper crown position especially in the drier months of August, September, and October. This trend of decreasing XPP with increasing height has been previously recorded and explained through the increasing dynamic and static head required to provide water to evaporating sites at greater heights (Scholander et. al. 1965, Hellkvist et. al. 1974, Connor et. al. 1977, Rundel and Stecker 1977).

Crown Temperature and Vapor Pressure Deficit

The relationship of T_c and VPD with crown position and age-flush class varied with time of day and month. During daylight hours, average T_c readings for each measurement period were similar or slightly increased with decreasing foliage age (figs. 13 and 14). This increase from the oldest age-flush class to the youngest was never much more than 0.5°C and was usually considerably less. This is possibly explained by the increase in the daily amount of direct sunlight received by the younger age-flush classes due to being closer to the crown edge.

General trends in VPD between age-flush classes were difficult to discern (figs. 13 and 14). The relative

difference between average VPD per measurement period within a crown position was greater than that found in T_c .

Differences range up to 0.4 KPa between age-flush classes within a crown position.

The VPD crown profiles differed with months (fig. 15). Within a measurement period, average VPD differences between crown positions ranged up to 0.8 KPa. Differences between the VPD recorded in the upper crown and the lower two-thirds increased in the fall. This increase was also observed with T_c between crown positions and is possibly due to the seasonal differences in the amount of radiant energy absorbed at different crown positions. The lower angle of the sun in September, October, and November reduces the amount of radiant energy received by the middle and lower crown due to shading from surrounding trees.

Vertical crown T_c patterns also varied seasonally (fig. 15). The pattern was one of decreasing temperature with decreasing crown position or height, although differences were generally quite small and were only noticeable in the fall. The largest difference between the average T_c of two crown positions was approximately 3°C. This difference is similar to the temperature range of up to 2°C reported in an even-age lodgepole pine stand (Bergen 1974). This contrasts with Denmead's (1984) findings in a ponderosa pine (Pinus ponderosa Laws.) forest in Australia in which midday hourly average T_c was lowest at the top of the crown, reached a maximum between the middle and lower crown, and then slowly

decreased. Other researchers have found patterns that are similar to those observed in this study and have noted that these patterns can change with location in the stand (Bergen 1974), with seasons, and with time of day (Helms 1970). Differences between crown positions in T_c and also vapor pressure profiles can be explained by differences in foliage distribution and radiant energy absorption and loss, ambient temperature, humidity, wind conditions, and soil wetness (Landsberg 1986).

Chlorophyll Content

For each age-flush and crown position, total chl, chl a, and chl a:b content of the needles was plotted throughout the months (figs. 16 and 17). In conifers, some previous research has found chlorophyll content to reach a maximum in the summer and then decline in the winter (Bourdeau 1959). From a combination of both current and one-year-old foliage, McGregor and Kramer (1963) also reported this trend in loblolly and white pine seedlings while Higginbotham (1974) reported no decline in chlorophyll content during the winter months in the current year foliage of mature loblolly pine. In this study, the winter decline in needle chlorophyll content was apparent in only the chlorophyll content of the '88 flushes in the upper crown position. The decline was less noticeable with the '88 foliage from the middle crown position and non-existent in the bottom crown position. Perry and Baldwin (1966) noticed that with the first hard

frost chlorophyll breakdown was most severe in foliage that was exposed to direct sunlight and found shaded foliage tended to have more intact chloroplasts throughout the winter.

Within a given age, the chlorophyll content of the second flush was consistently lower than that determined for the first flush. An exception to this was the chlorophyll content in the upper crown where '88-1 and '88-2 were similar. The analysis of the mean values of total chlorophyll showed there was no significant crown position by age-flush interaction. Analysis of the mean values of total chlorophyll for each date averaged over crown positions found significant differences in chlorophyll content between foliage age but not between flushes within an age with the exception of the '89-1 and '89-2 foliage for October (table II). This exception might be explained by the immaturity of the '89-2 foliage. This pattern is supported by Higginbotham (1974) who also reported less chlorophyll in the second flush and found the difference in chlorophyll content between the two flushes to be not significant.

The '88 foliage consistently exhibited significantly higher total chlorophyll concentrations than the '89 foliage. This difference in chlorophyll content due to foliage age is in contrast to Blanche's (1978) observations of no differences in summer chlorophyll content between current and older needles of loblolly pine. A possible

TABLE II

TOTAL CHLOROPHYLL CONCENTRATIONS BY AGE AND FLUSH
AVERAGED OVER CROWN POSITION

Date (1989)	Age-Flush				
	87-1 ^a	88-1	88-2	89-1	89-2
	-----mmoles chl m ⁻² -----				
4/4	0.359	<u>0.369 e^b</u>	<u>0.361 b_c</u>	.	.
5/8	0.304	<u>0.422 abc</u>	<u>0.387 ab</u>	.	.
6/10	.	<u>0.453 a</u>	<u>0.423 a</u>	.	.
7/12	.	<u>0.406 bcd</u>	<u>0.413 ab</u>	0.203 b	.
8/8	.	0.424 abc	.	0.251 a	.
9/8	.	0.433 ab	.	0.264 a	.
10/3	.	0.389 cde	.	0.240 a	0.162 b
11/10	.	0.381 de	.	<u>0.254 a</u>	<u>0.216 a</u>

^a Statistical comparison for 87-1 not performed since n=1.

^b Letters compare mean chlorophyll concentrations among months within an age and flush. Concentrations followed by the same letter are not significantly different at the 0.05 level.

^c Underline compares mean chlorophyll concentrations among age and flushes within a row. Concentrations connected by the same line are not significantly different at the 0.05 level.

explanation for the difference in findings is that Blanche's values of chlorophyll content are on a unit weight basis. When converted to a leaf area basis his data would show a trend with age similar to what is reported in this study. This is because specific leaf area decreases with increasing level in crown (Lewandowska and Jarvis 1977). Others expressing chlorophyll content on a leaf area basis have also observed the chlorophyll content to be lower in the younger foliage (Higginbotham 1974, Vapaavuori and Vuorinen 1989).

Except in late fall, chlorophyll content was found to increase from lower to upper crown position (table III). On a leaf area basis, this trend has been observed by others (Lewandowska *et. al.* 1977). Shade grown needles tend to have a higher chlorophyll content than foliage grown at high light intensities when recorded on a fresh weight basis (Bourdeau and Laverick 1958, Lewandowska and Jarvis 1977). However, on a leaf area basis, Higginbotham (1974) recorded a slight but nonsignificant increase in chlorophyll content with decreasing crown position.

The seasonal pattern of chl b content was similar to that of chl a content, except the chl b peaks occurred one month before the chl a peaks. The observed chlorophyll ratio values from 2.3 to 4.0 are consistent with previous findings (Anderson 1967, Vapaavuori and Vuorinen 1989) although lower ratios have also been reported (Bourdeau and Laverick 1958, Lewandowska and Jarvis 1977). Except for the

TABLE III

TOTAL CHLOROPHYLL CONCENTRATIONS BY CROWN POSITION
AVERAGED OVER AGE AND FLUSH

Date	Crown Position		
(1989)	Upper	Middle	Lower
	-----mmoles chl m ⁻² -----		
4/4	0.374 a ^a	0.365 a	0.354 a
5/8	0.442 a	0.401 ab	0.385 b
6/10	0.487 a	0.426 b	0.401 b
7/12	0.364 a	0.351 a	0.308 b
8/8	0.374 a	0.347 a	0.291 b
9/8	0.379 a	0.359 a	0.308 b
10/3	0.282 a	0.284 a	0.224 b
11/10	0.273 b	0.332 a	0.254 b

^a Letters compare mean chlorophyll concentrations among crown positions within a row. Concentrations followed by the same letter are not significantly different at the 0.05 level.

'88 upper foliage where values of chl a:b were about the same, the second flush and younger foliage exhibited a higher ratio (fig. 17). The chl a:b also tended to increase with increasing crown position. A similar trend between chl a:b and crown position was recorded for willow (Salix cv. Aquatica gigantea) (Vapaavuori and Vuorinen 1989). The chl a:b patterns indicates a possible relationship with the amount of direct irradiation received. Kramer and Kozlowski (1979) state that higher ratios are found in sun than in shade leaves. This is supported by the findings of Alberte et. al. (1976) in which shade needles contained a greater proportion of the light-harvesting chlorophyll a/b-protein than those of sun needles which have a greater proportion of the P700-chlorophyll-a protein. However, Lewandowska and Jarvis (1977) reported chl a:b to be the same at all crown levels and similar results were noted by Bourdeau and Laverick (1958) in comparing sun and shade foliage.

The seasonal trend of the chlorophyll ratio has large variations that cannot be fully explained, especially the dip in August.

Photosynthetic Photon Flux Density and Carbon Exchange Rate

The average irradiation readings and standard errors obtained for each measurement period for the various age-flush and crown positions are shown in figures 18 through 25. PPFd was usually greatest at the upper crown position

in the youngest foliage; the youngest age-class being positioned on the outermost edge of the crown (table IV). Mutual shading at this point from other foliage in the tree and from other trees is the least. Light intensity was reported to decrease with crown height and depth in crown by Kramer and Kozlowski (1979). Over the growing season, the PPFD of the middle and lower crown positions was 57% and 39% respectively of the PPFD received by the upper crown. These percentages are similar to those obtained by Helms (1970), 67% for the middle and 41% for the lower crown as compared to the upper crown, from the south aspect of ponderosa pines. Until the near complete development of the '89-1 foliage, the middle crown received similar irradiation to that in the upper crown (fig. 26). This is partially explained by the relative openness of the stand and the criteria for the selection of measurement branches. The relative increase in October of PPFD in the middle crown position, as compared to the top, is possibly the result of senescence of the '88 foliage, and therefore a reduction in mutual shading. This is followed in November by the middle crown receiving its lowest percent of irradiation compared to the upper crown. This is likely due to the continuing decrease in the angle of the sun which would result in an increase in mutual shading from surrounding trees. The PPFD at the lower crown position follows a similar pattern as that seen in the middle position, with the exception of an unexplained increase in July. However, the lower crown

TABLE IV
 AVERAGE DAILY PHOTOSYNTHETIC PHOTON FLUX DENSITY
 BY AGE-FLUSH CLASS AND CROWN POSITION

Crown Position	Age-Flush	Date (1989)															
		4/4		5/8		6/10		7/12		8/8		9/8		10/3		11/10	
		PPFD ^a	% ^b	PPFD	%	PPFD	%	PPFD	%	PPFD	%	PPFD	%	PPFD	%	PPFD	%
Upper	'88-1	455 ^c	100	362	100	370	100	237	100	524	100	508	100	360	100	360	100
	'88-2	654	144	370	102	392	106	384	162
	'89-1	426	180	827	158	456	114	472	131	413	115
	'89-2	505	140	414	115
Middle	'88-1	490	108	288	80	356	98	296	125	367	70	253	50	325	90	97	27
	'88-2	504	111	304	106	404	112	222	94
	'89-1	255	108	388	74	294	58	355	99	165	46
	'89-2	379	105	144	40
Lower	'87-1	263	58	54	15
	'88-1	310	68	104	29	150	41	236	100	145	28	76	15	186	52	44	12
	'88-2	275	60	217	60	148	41	259	109
	'89-1	225	95	236	45	113	22	177	49	62	11
	'89-2	227	63	83	23

^aPhotosynthetic Photon Flux Density (PPFD) recorded in $\mu\text{moles m}^{-2} \text{s}^{-1}$.

^bPercentage of PPFD of '88-1 upper crown position for that date.

^cAverages exclude values recorded from post sunset to predawn periods inclusive

never receives more than 70% and usually receives less than 50% of the average daily PPFD of the upper crown position.

The combined effect of stand factors (shading by surrounding trees) and the changes in sun angle on PPFD are illustrated when comparing the direct irradiation received by the '88-1 foliage at the 9:30 measurement period for June and November. The PPFD for the upper crown position for both months is about $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, June's PPFD from the middle and lower crown is 600 and $350 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, while in November the middle crown position PPFD was $225 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the lower crown PPFD was $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ (figs. 20 and 25). Mutual shading from the fully developed '89 flush in November was not enough to account for this difference.

Compared to differences in crown position, differences in PPFD between age-flush classes was small (fig. 27). The youngest age-flush class generally had higher values of PPFD. This is likely due to less mutual shading of the younger age-flush class.

The values of P_n obtained are similar to those obtained for loblolly pine (Higginbotham 1974, Seiler and Johnson 1985, Fites and Teskey 1988), Scots pine (Beadle *et. al.* 1985b), and Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco) (Leverenz 1980). The daily P_n followed the general trend of increasing in the morning, reaching a maximum around midday, and then decreasing. This pattern has been observed by others (Schulze *et. al.* 1977, Leverenz 1980,

Troeng and Linder 1982b, Beadle et. al. 1985b). This pattern is erratic especially if P_n is measured on a continuous basis, often exhibiting a midday or afternoon depression that has been associated with moisture stress (Helms 1965, Hodges 1967), shading from overhead branches (Helms 1970), and large VPD and/or high leaf temperature (Hari and Luukanen 1973, Leverenz 1980). Figures 18 through 25 show both the general pattern and the variations in CER throughout the day.

The R_d rates obtained from the predawn and post sunset measurement periods were similar in regard to age-flush class and crown position. Slight if any differences in the rates of R_d were observed between crown positions. Compared to '88 foliage, the new foliage did not have a greater R_d rate as might have been expected. This is probably because the needle elongation was near completion by the time the needles were first measured for CER.

P_n rates also indicate that the photosynthetic ability of the new needles was well developed by the time the needles were first measured as the '89 needles generally exhibited higher rates than '88 even in July. Significant monthly differences in average daily P_n were found between '88 and '89 needles in the upper and usually in the middle crown (table V). There was no significant differences in P_n between ages in the lower crown, although the trend of higher P_n with younger age-flush class was still consistent. From a simulated model output of P_n for loblolly pine,

TABLE V
AVERAGE DAILY NET PHOTOSYNTHESIS BY AGE-FLUSH
CLASS AND CROWN POSITION

Crown Position	Age- Flush	Date (1989)															
		4/4		5/8		6/10		7/12		8/8		9/8		10/3		11/10	
		P_n ^a	% ^b	P_n	%	P_n	%	P_n	%	P_n	%	P_n	%	P_n	%	P_n	%
Upper	'88-1	2.72 ^{c,d}	100	2.05 a	100	1.95 a	100	1.53 c	100	1.74 b	100	1.68 a	100	1.23 b	100	0.92 b	100
	'88-2	2.97 a	109	2.27 a	111	2.27 a	116	2.11 b	138
	'89-1	2.88 a	188	2.90 a	167	2.29 a	136	2.59 a	210	1.59 a	173
	'89-2	2.70 a	220	1.96 a	213	.	.
Middle	'88-1	2.83 a	104	1.96 a	96	1.96 a	101	1.41 b	92	1.86 b	107	0.95 a	57	1.02 b	83	0.59 a	64
	'88-2	3.21 a	118	2.18 a	106	2.10 a	108	1.64 ab	107
	'89-1	2.02 a	132	2.69 a	155	1.37 a	82	1.62 ab	132	0.80 a	87
	'89-2	2.04 a	166	0.82 a	89	.	.
Lower	'87-1	1.11	41	0.02	1
	'88-1	2.01 a	74	1.20 a	59	1.06 a	54	1.11 a	73	1.50 a	86	0.45 a	27	0.59 a	48	0.27 a	29
	'88-2	2.26 a	83	1.57 a	77	1.44 a	74	1.18 a	77
	'89-1	1.34 a	88	1.25 a	72	0.77 a	46	0.93 a	76	0.35 a	38
	'89-2	1.00 a	81	0.37 a	40

^aNet photosynthesis (P_n) recorded in $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

^bPercentage of P_n of '88-1 upper crown position for that date.

^cAverages exclude values recorded from post sunset to predawn periods inclusive

^dLetters compare mean P_n among age-flush classes within a crown position and month. Rates followed by the same letter are not significantly different at the 0.05 level.

Reynolds et. al. (1980) found higher rates of P_n from the previous year's foliage until mid-September when the P_n rates for the current foliage surpassed that of the previous year's foliage. This difference is possibly due to differences in the rate at which the photosynthetic capacity of the current foliage increases with age, the degradation of the photosynthetic capacity of the '88 foliage, and/or the increase in shading of '88 foliage by the current needles. Higginbotham (1974) found that CO_2 uptake in mature loblolly pine under natural conditions reached a peak during the spring and early summer, and McGregor and Kramer (1963) observed maximum rates per unit fascicle in May in loblolly pine seedlings. The highest average P_n rates by measurement period recorded in this study occurred in April (fig. 18), though the actual peak is impossible to determine because of the few days per month that were sampled and the often less than optimum environmental conditions that occurred on these days. Troeng and Linder (1982a) working with Scots pine, found variation in both the date of peak P_n for one-year-old needles and the date at which current foliage surpassed the P_n of one-year-old foliage. This suggests that the date of these two occurrences will shift with the variation in yearly environmental conditions. Table V presents the average daily P_n for each measurement date for each crown position and needle age-flush. Each mean daily P_n was calculated by averaging the average P_n from the four to six daylight measurement periods, the

number of periods being dependent on weather and photoperiod. The values of P_n for each measurement period consists of data collected from three to six samples. Since the number of daytime measurement periods changed from month to month it is not advisable to compare the averages between months in table IV or table V. However, the values can be used to compare PPF_D or CER from crown positions and age-flush classes within a month. The values of P_n or PPF_D expressed as a percentage of the '88-1 upper crown position can be compared both across and within months.

The differences in P_n between age-flush classes tended to increase toward midday and then decreased. Again, this is most likely explained by the increase in mutual shading at all age-flush classes during the time in which the sun's angle is lower. In comparing the daily percentages of P_n based on '88-1 foliage, the second flush had a higher percentage of P_n than the first flush but the difference was not as great as that associated between '88 and '89 foliage (fig. 28). Reynolds *et. al.* (1980) calculated a similar relationship between the P_n rates of two flushes of the same year's foliage. Throughout the study, the differences in P_n between the two flushes remained fairly constant while the differences in P_n between foliage age classes increased. This is attributed to the increase in shading of '88 needles by the growth of the '89 needles, the decline in P_n rates of the '88 needles and the continued maturation of the current needles.

In general, the lower crown position exhibited a lower average daily P_n than the other two crown positions. This trend has been recorded by others (Helms 1970, Higginbotham 1974, Beadle et. al. 1985b). Over the growing season, the P_n of the middle and lower crown positions was 82% and 52% respectively of the P_n received by the upper crown. These percentages are similar to those obtained in ponderosa pine by Helms (1970), 72% for the middle and 51% for the lower crown as compared to the upper crown, and in loblolly pine by Higginbotham (1974), 76% and 51% for the middle and lower crown position respectively of the P_n of the upper crown. Up until September, the average daily P_n from the middle crown was similar to that of the upper crown (fig. 29). Thereafter, the percentage of daily P_n of the middle crown as compared to the upper crown was drastically reduced to less than 60% in September rising to 72% in October and falling to 49% in November. This pattern was similar to the variation in PPF_D observed between crown positions. A similar but less erratic pattern in P_n was observed in the lower crown where the percentage of the average daily P_n rates as compared to the upper crown was 75% in April and declining to a low of 22% in November.

CER Regression Models

In the previous figures and tables, a strong relationship between CER and PPF_D was observed. It was of interest to determine if the variation in light could

explain the differences in measured CER between crown position and age-flush classes.

Figure 30 illustrates the crown position and/or age-flush grouping of CER regression models where the CER for each group can be explained by the same regression model. Within a month, the rectangular enclosure of age-flush and/or crown position categories indicate where the response of CER to irradiance (PPFD, $PPFD^{0.5}$) and/or the intercept were not found to be significantly different at the 0.05 level. Changes in the intercept could be the result of changes in the relationships to CER by any of the independent variables in the models including those that deal with irradiance such as PPFD and $PPFD^{0.5}$. However, except for chlorophyll content, variation of the non-irradiance variables among crown positions and/or age-flush classes were small. Table VI shows the chlorophyll variables to be weakly correlated with the models. Therefore, it seems reasonable to assume the models are differentiated by changes in the CER-PPFD relationship and further discussion will assume this to hold true.

There was a consistent differences in the CER-PPFD relationship due to foliage age. Except for the first and final month, there was insufficient evidence to differentiate the response of CER to PPFD based on the flush type within an age class. In light response curves presented by Higginbotham (1974) little difference was seen between the first and second flush of the middle level of

TABLE VI
R-SQUARED VALUES FOR CARBON EXCHANGE
RATE REGRESSION MODELS^a

Month (1989)	Age-Flush	Crown Position	PPFD ^{.5}	PPFD	XPP	VPD	Stress	Air Temp	Total Chl	Chl a	Chl a:b	Model Total	N
Apr	'88-1	Upper	.743	.562	.155	.055	.078	.089	.003	.003	.003	.937	35
		Mid & Lower	.929	.808	.383	.215	.308	.230	.002	.002	.003	.960	66
	'88-2	Upper	.789	.619	.113	.160	.155	.164	.001	.002	.000	.914	34
		Mid & Lower	.852	.687	.301	.208	.263	.200	.002	.002	.016	.895	61
May	all	all	.826	.604	.240	.384	.382	.230	.000	.001	.012	.880	209
Jun	all	all	.806	.583	.414	.411	.431	.379	.003	.004	.010	.864	230
Jul	'88-1 & 2	all	.840	.606	.317	.511	.477	.462	.018	.019	.002	.885	224
		Upper & Mid	.854	.597	.211	.464	.407	.422	.022	.024	.005	.917	77
Aug	'89-2	Lower	.799	.580	.278	.380	.411	.447	.067	.066	.000	.856	38
		all	.933	.760	.604	.766	.689	.538	.016	.019	.022	.958	60
	'89-1	Upper	.952	.885	.713	.728	.716	.537	.169	.182	.001	.988	21
		Mid & Lower	.888	.711	.521	.756	.639	.563	.057	.057	.011	.959	43
Sep	'88-1	all	.822	.638	.384	.420	.448	.441	.009	.017	.073	.868	95
		all	.852	.710	.264	.347	.320	.392	.001	.002	.022	.876	97
Oct	'88-1	all	.824	.677	.306	.351	.322	.336	.009	.011	.008	.869	98
		Upper	.800	.643	.213	.271	.209	.312	.026	.028	.005	.911	35
Nov	'88-1	Mid & Lower	.905	.829	.341	.433	.419	.391	.000	.000	.010	.916	117
		all	.636	.422	.141	.053	.063	.087	.032	.035	.002	.771	66
		all	.763	.616	.092	.050	.059	.080	.013	.011	.038	.862	102
	'89-2	all	.711	.589	.152	.093	.107	.119	.000	.000	.115	.823	87

^aThe R² value under each variable is the R² for a simple linear regression model between CER and the column heading. The R² value under "Model Total" is an R² for a multiple regression model that includes all variables.

the canopy. However, at the top level of the canopy, he recorded a greater capacity for CO₂ exchange in the second flush. He concluded that this might have been the result of a slightly higher level of chlorophyll found in the second flush and/or the different environmental conditions in which the two flushes were formed and developed. In this study, all regression models included chlorophyll variables even though similar chlorophyll content was found between flushes in the '88 upper crown foliage. The consistent difference in the response to light between '88 and '89 foliage is supported by Higginbotham's finding of differences in light response curves between needle age groups.

The inability of one model to explain the relationship of CER to light among flushes at the first and last month of this study is possibly explained by the different effect subfreezing temperatures might have had on the two flushes. Subfreezing temperatures can injure the photosynthetic apparatus, but with time the damage is usually repaired during periods of above freezing temperatures (Kramer and Kozlowski 1979). Perry and Baldwin (1966) found chloroplast breakdown to be more severe in foliage that was exposed to direct sunlight than foliage from shaded branches. The chlorophyll content of the flushes were similar in April though, according to Perry and Baldwin, it is the disruption of the chloroplasts that is important. It is possible that some of the chlorophyll content recorded might have been free chlorophyll released into the cytoplasm from disrupted

chloroplasts. Also, as the second flush had less time to harden for winter, it might have sustained greater damage, and hence would require a longer period of time in spring for recovery.

Differences in chloroplast damage and in rates of repair of the frost damaged photosynthetic mechanism would also explain the need for separate CER models for the upper crown and the lower two-thirds in April. The significant differences in CER-PPFD relationship by crown position in July and August for the '89-1 foliage is possibly due to differences in the physiological maturation of the new foliage. In October, the ecophysiological reason for the statistically separate models for the upper crown foliage and the lower two-thirds is unknown.

Within an age-flush, most of the crown positions could be combined into one regression model. When models could be combined, the result was that the CER response to PPFD was not significantly different within the range of environmental variables observed. This contrasts with much of the previous research that has found differences in the photosynthetic capacity and/or the photosynthetic efficiency of foliage by crown position (Troeng and Linder 1982b, Kull and Koppel 1987) or shade/unshaded foliage (Bourdeau and Laverick 1958, Leverenz and Jarvis 1980, Ginn *et. al.* 1988). However, under natural conditions, Beadle *et. al.* (1985a) found the relationship between photosynthesis and light to be independent of crown position and capable of being

described by a single hyperbola. They concluded that since light saturated rates of P_n decrease with canopy depth (Jarvis et. al. 1976), the P_n rates among crown positions may be similar under conditions where light is less than saturating.

Lewandowska et. al. (1977) suggested that the photosystem activity might be limiting photosynthesis in foliage at the lower canopy of Sitka spruce (Picea sitchensis (Bong.) Carr.). Since chlorophyll content was found to differ in age-flush classes and crown position, it is possible that the chlorophyll variables in the models account for some of the differences in CER-PPFD relationship that occur throughout the crown that would otherwise have been detected. Chlorophyll content or ratio did not account for the separation of CER regression models by age, though. Anderson (1967) concluded that normal field variation in chlorophyll content between individual leaves had very little effect on the photosynthetic rate. McGregor and Kramer (1963) reported that seasonal variations existed in chlorophyll content in loblolly pine seedlings but the differences were not large enough to account for the seasonal variations in photosynthetic rates based on fascicle length. In contrast, Higginbotham (1974) reported the variability in chlorophyll content between flushes and crown positions to be insignificant. However, he did find that the seasonal variation in the concentration of total

chlorophyll to be the second most important regression variable in describing the seasonal differences of P_n .

Models were not compared between months since the purpose was not to produce models to predict CER but to compare light response between crown positions and age-flush classes. The coefficient of determination (R-squared) for the models ranged from 0.77 to 0.99 (table VI). $PPFD^{0.5}$ and PPFD were the two variables that consistently explained the greatest amount of variation in CER. Higginbotham (1974) found that most of the variability in CER in all canopy positions and flushes could be explained by light intensity. The models were also checked for biases by plotting the residuals or the error of the prediction against both the dependent and the independent variables as suggested by Reed et. al. (1977). No bias was noticed in the models for either the dependent or independent variables.

There is some limitations to the data and models. First, as previously mentioned, there are other variables in the models other than irradiation that can cause differences in CER. These variables are small or they are weakly correlated to CER when looking at the variation of CER among crown positions and/or age-flush classes within a month. Second, if the model does not fit the data, there could be differences in CER among crown positions or age-flush classes that are not explained by irradiation. The model total R^2 s (Table VI) and the lack of biases in the plotting of the residuals indicate that these models fit the data

well. Finally, the data was obtained in a year when moisture stress was not a major factor during the growing season. The R^2 's' of the irradiation and other variables and possibly the grouping of the models could change under different environmental conditions than those recorded during this study.

CONCLUSION

The effect of summer moisture stress on the CER was unable to be determined due to the unusually wet summer.

Under the environmental conditions experienced, the variation of CER within different crown positions and age-flush classes could be categorized by whether these variations could be explained by changes in the relationship of CER with irradiation, XPP, VPD, T_c , and chlorophyll content and ratio into effect. PPF_D and PPF_D^{0.5} was more strongly correlated to CER than any other variable. Usually the correlation was much stronger than that exhibited by other variables. A different response to irradiance seems evident between foliage age classes while during the growing season the models suggest that the response to light is similar between flushes. The different CER-PPFD relationships as it relates to crown position seems to vary with crown phenology and frost damage, but during the majority of the growing season, the response of mature foliage CER to PPF_D is similar among crown positions under natural conditions.

Though further study is needed, these relationships suggest the possibility of predicting crown CER by monitoring environmental variables, especially irradiance, throughout the vertical and horizontal crown locations and

then relating these to a few CER measurements sampled at strategic crown locations and/or age-flush classes like current and previous year's foliage. A similar model has been developed for Monterey pine (Pinus radiata D. Don) (Grace et. al. 1987).

Further investigations are also needed to determine if the CER-PPFD relationships change under moisture stress. The effects of subfreezing temperatures on CER and winter CER rates also require further study.

Over the growing season, rates of P_n across all age classes of foliage in the middle and lower crown positions were 82% and 52%, respectively of that measured for the upper canopy. Over a similar time span, PPFD was 57% and 39% for the middle and lower crown positions respectively of the PPFD received by the upper crown. The results indicate the importance of irradiation to CER. This suggests that increasing the wood quality by pruning the lower one-third of the crown would only have a relatively small effect on the total CER of the tree. Assuming a constant transpiration rate throughout the crown and under droughty conditions, the removal of the lower crown could also provide a decrease in tree moisture stress. Therefore, it is hoped that a better understanding of CER and its relationship to environmental factors, crown position, and age-flush classes will aid in the future management of loblolly pine.

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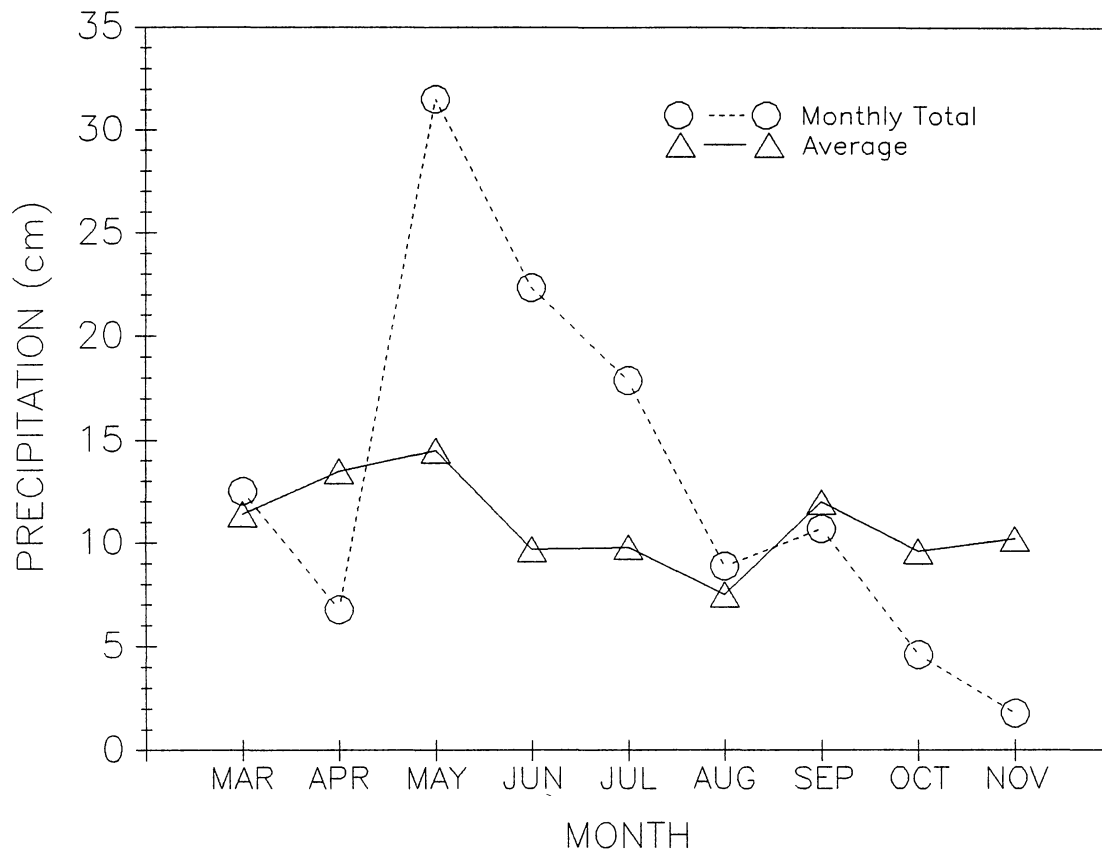


Figure 1. Monthly on-site precipitation for 1989 and average monthly precipitation. Average monthly precipitation based on data recorded from 1951-1980 at Broken Bow, OK, 16 km northwest of the site.

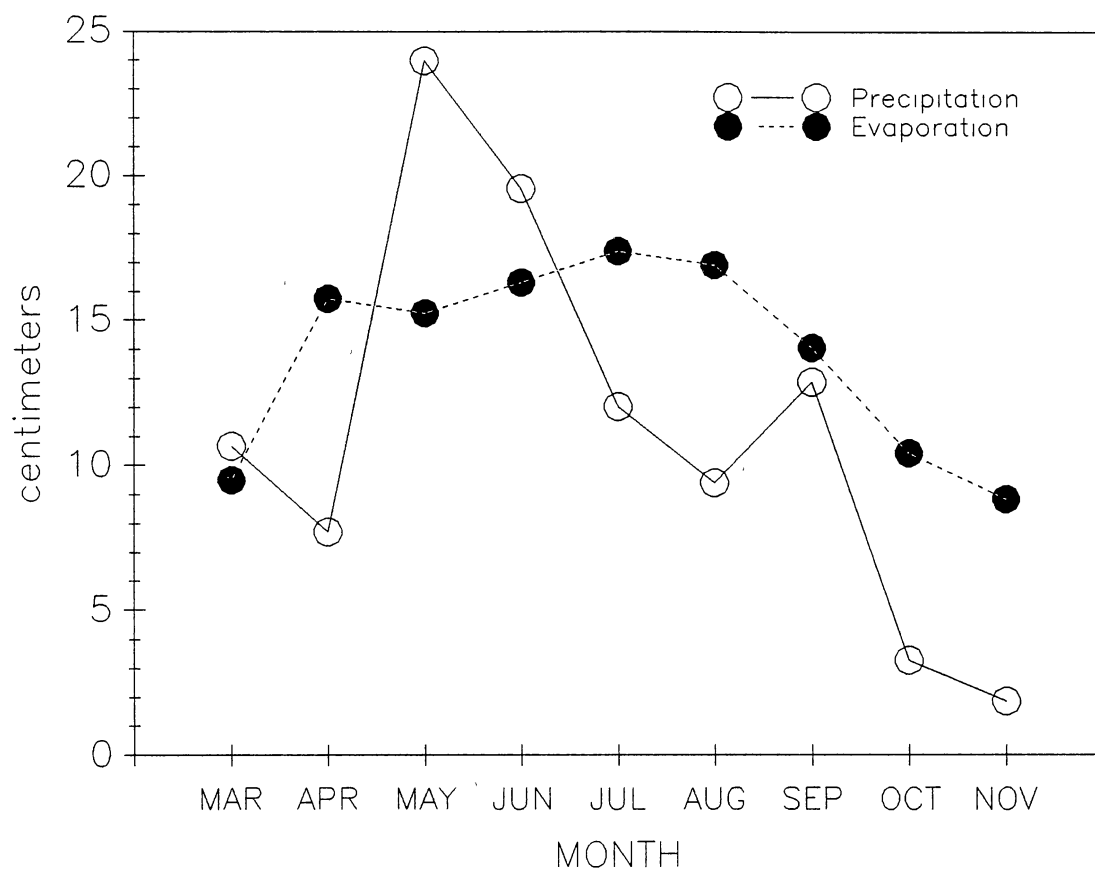


Figure 2. Monthly precipitation and pan evaporation from Broken Bow Dam, 27 km north of study site.

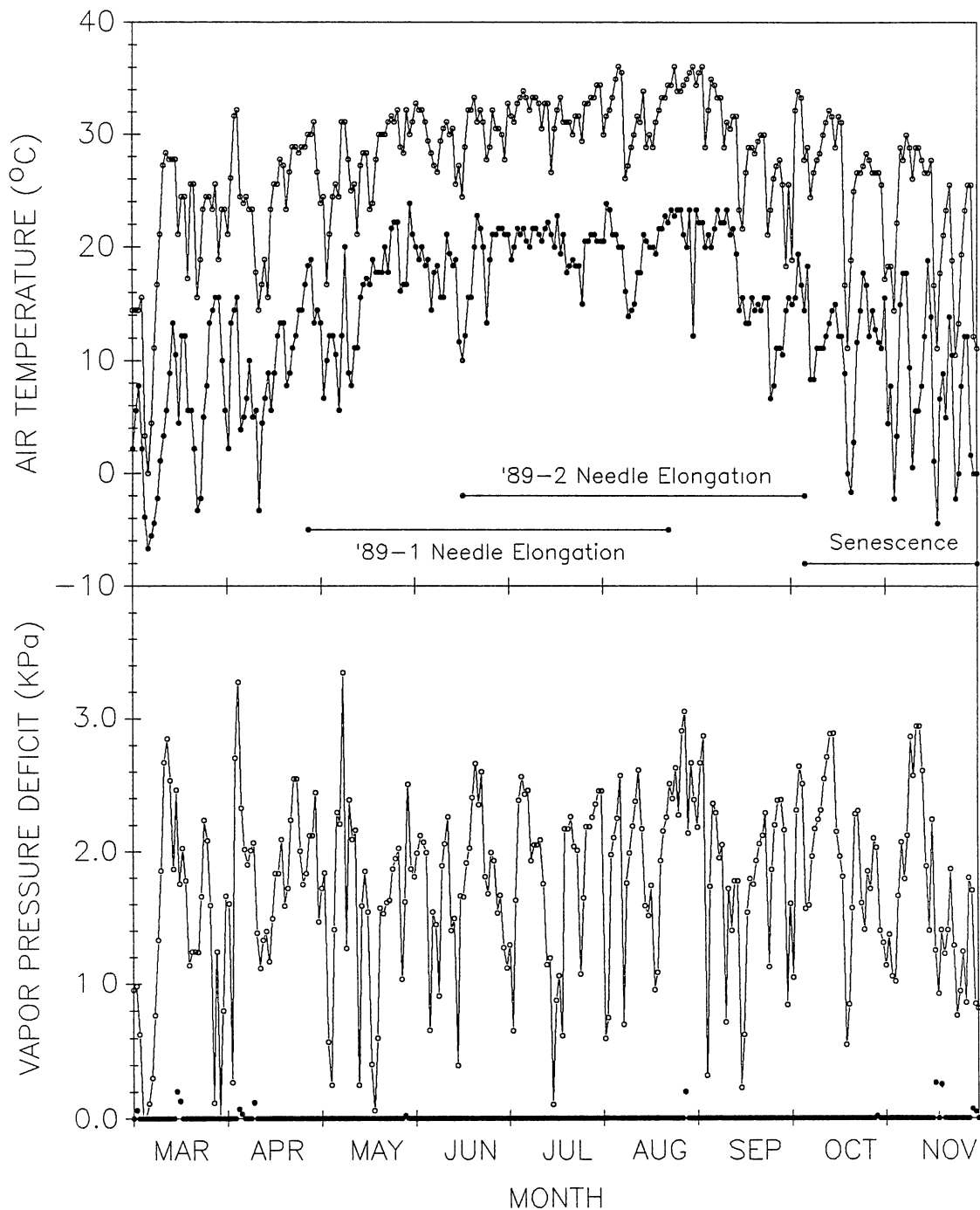


Figure 3. Daily minimum and maximum air temperatures and vapor pressure deficits for 1989 recorded at Broken Bow, OK, 16 km northwest of the research site along with the inception and termination of needle elongation for the two flushes of 1989 and the period of senescence for 1988 foliage.

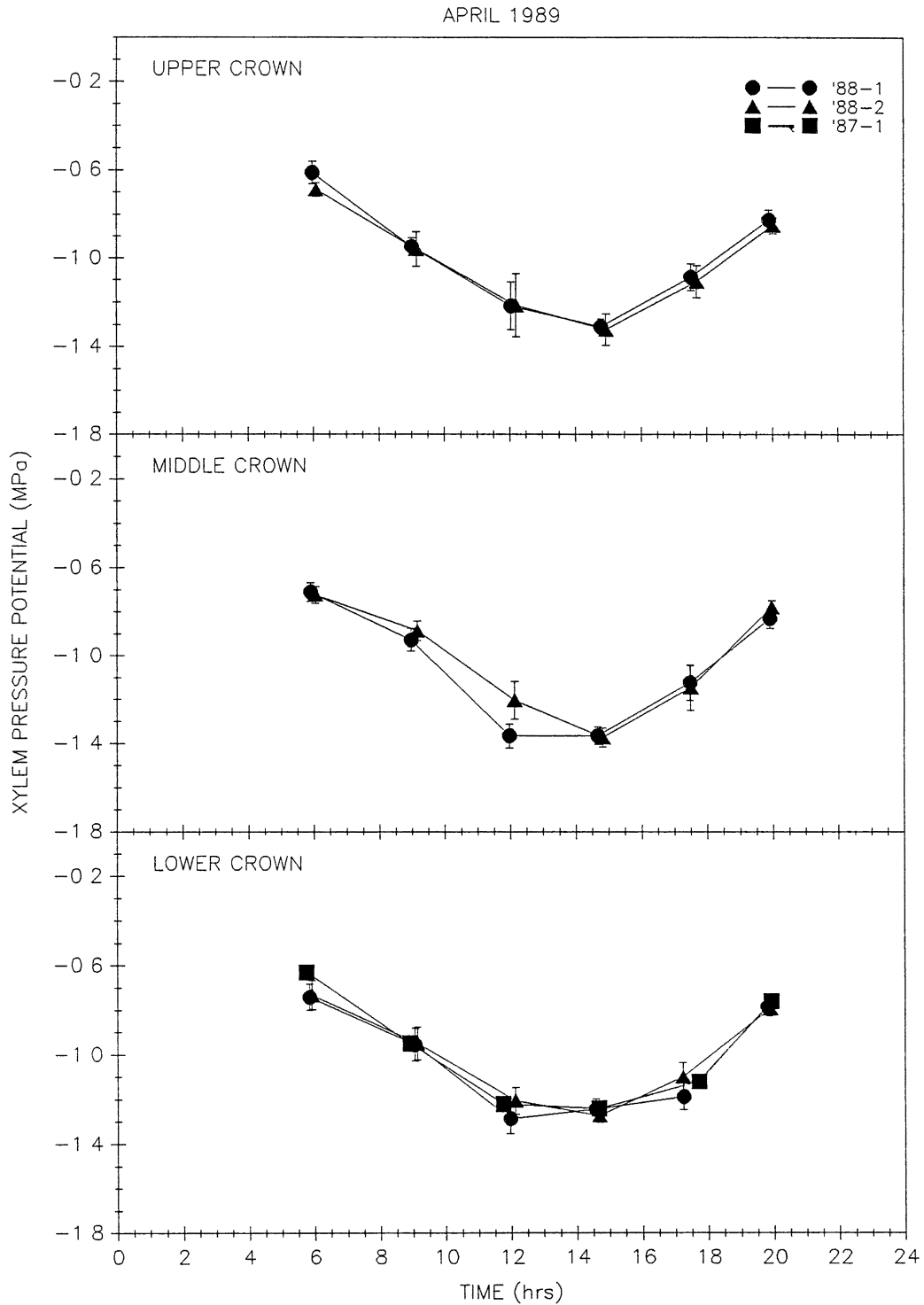


Figure 4. Diurnal patterns of XPP for April. Each bar represents one standard error and each point represents the mean of five to six trees measured on March 31 and on April 5 and 6.

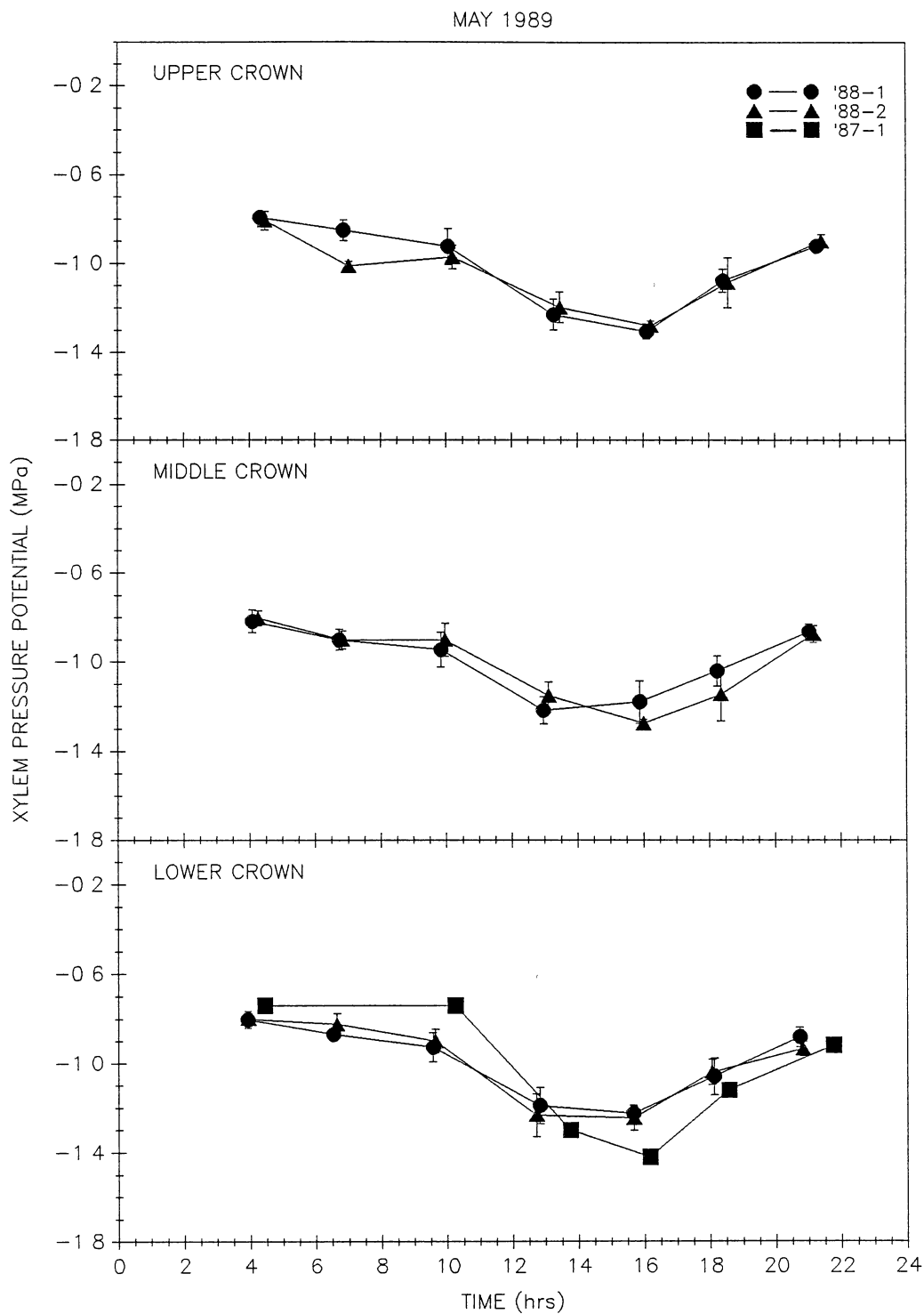


Figure 5. Diurnal patterns of XPP for May. Each bar represents one standard error and each point represents the mean of five to six trees measured on May 9, 10, and 11.

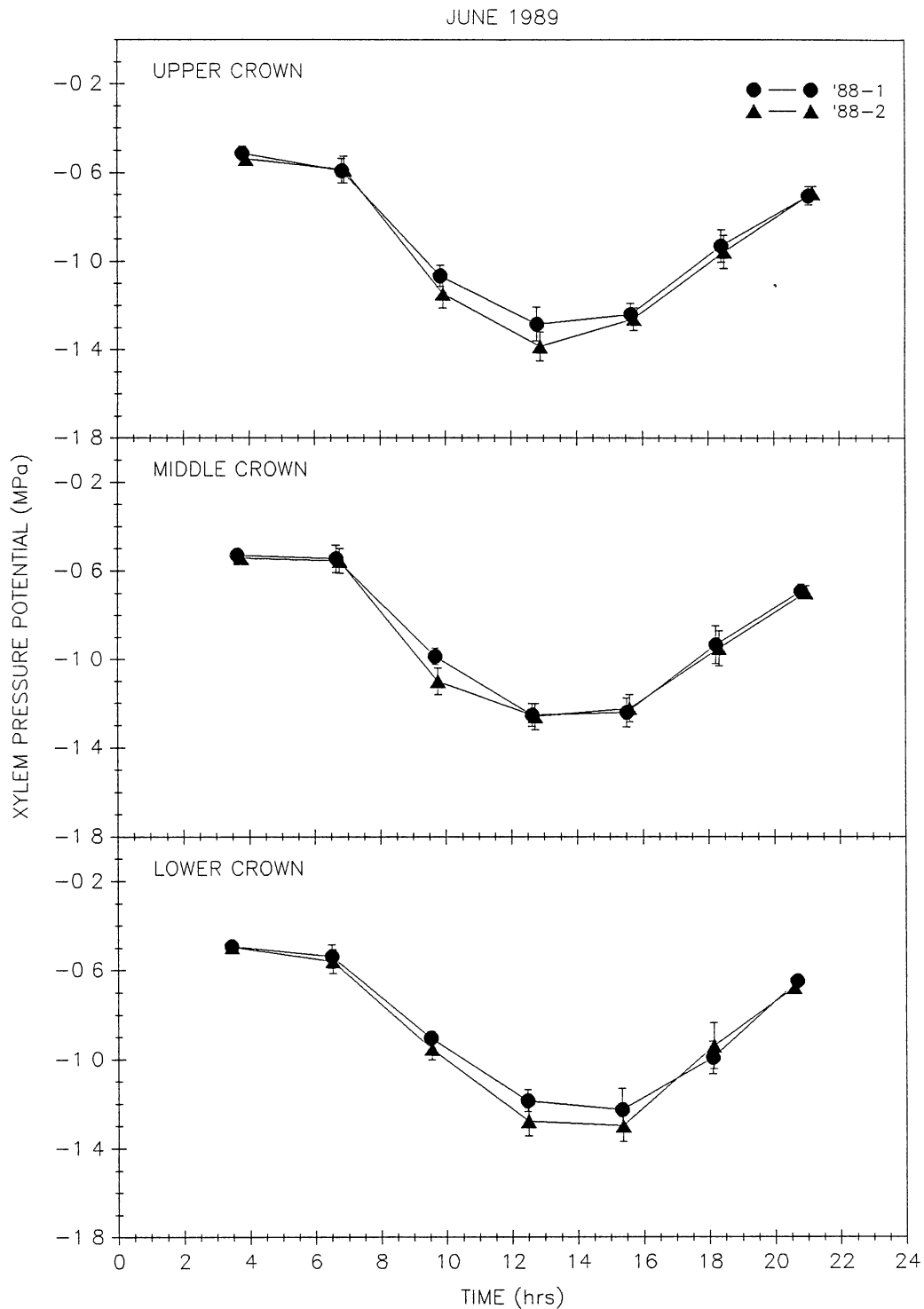


Figure 6. Diurnal patterns of XPP for June. Each bar represents one standard error and each point represents the mean of six trees measured on June 6, 7, and 15.

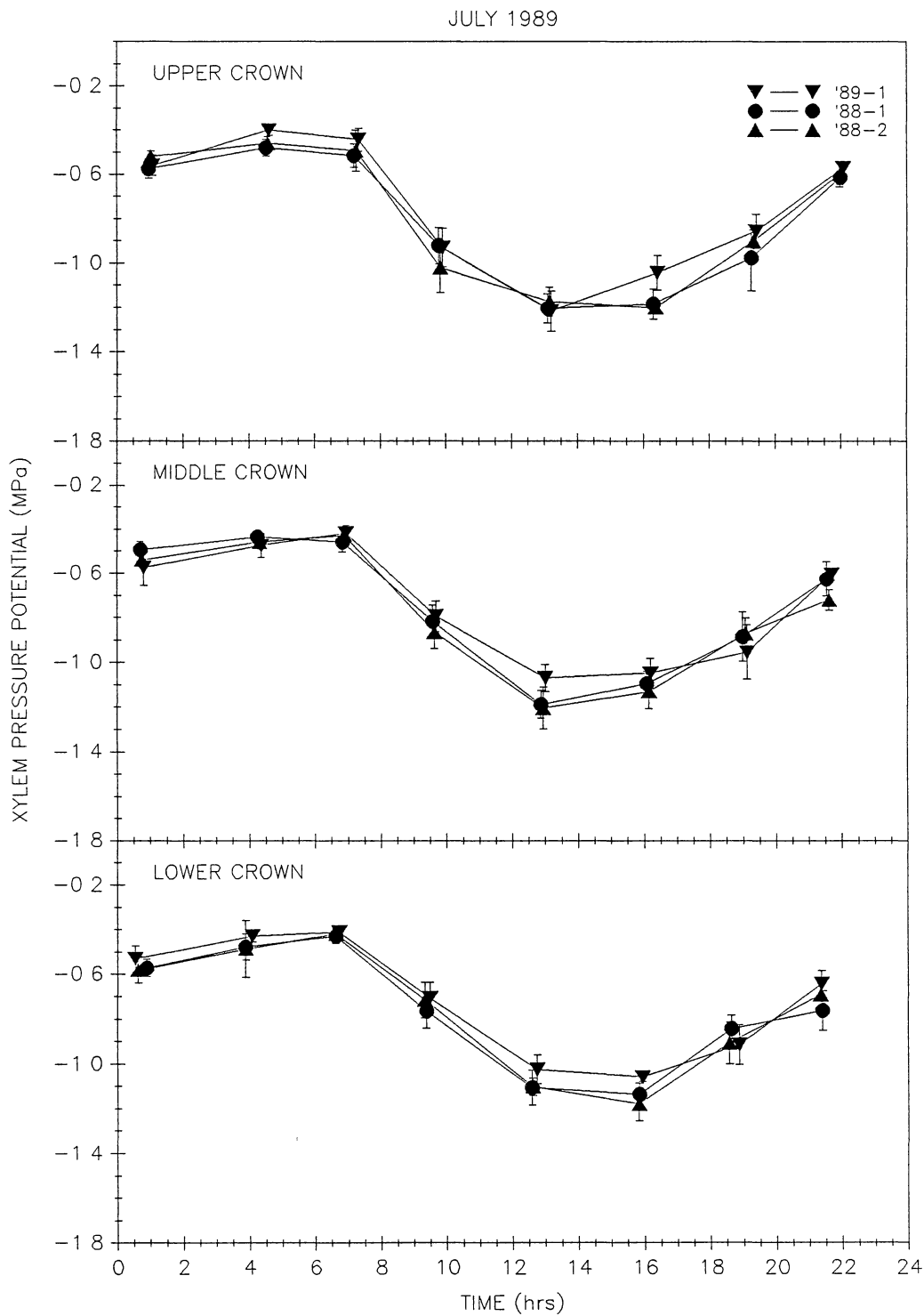


Figure 7. Diurnal patterns of XPP for July. Each bar represents one standard error and each point represents the mean of four to six trees measured on July 11, 12, and 13.

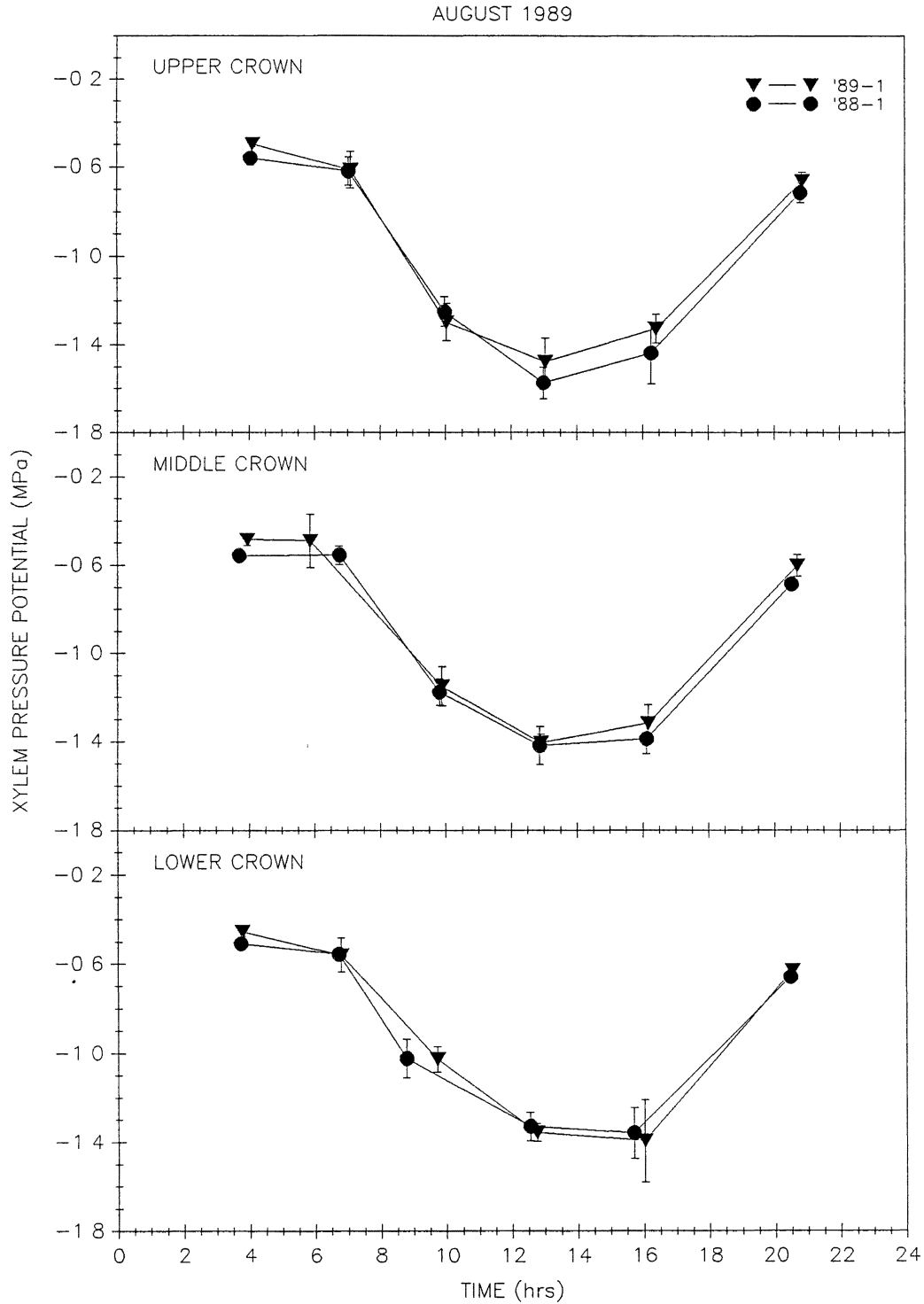


Figure 8. Diurnal patterns of XPP for August. Each bar represents one standard error and each point represents the mean of five to six trees measured on August 8.

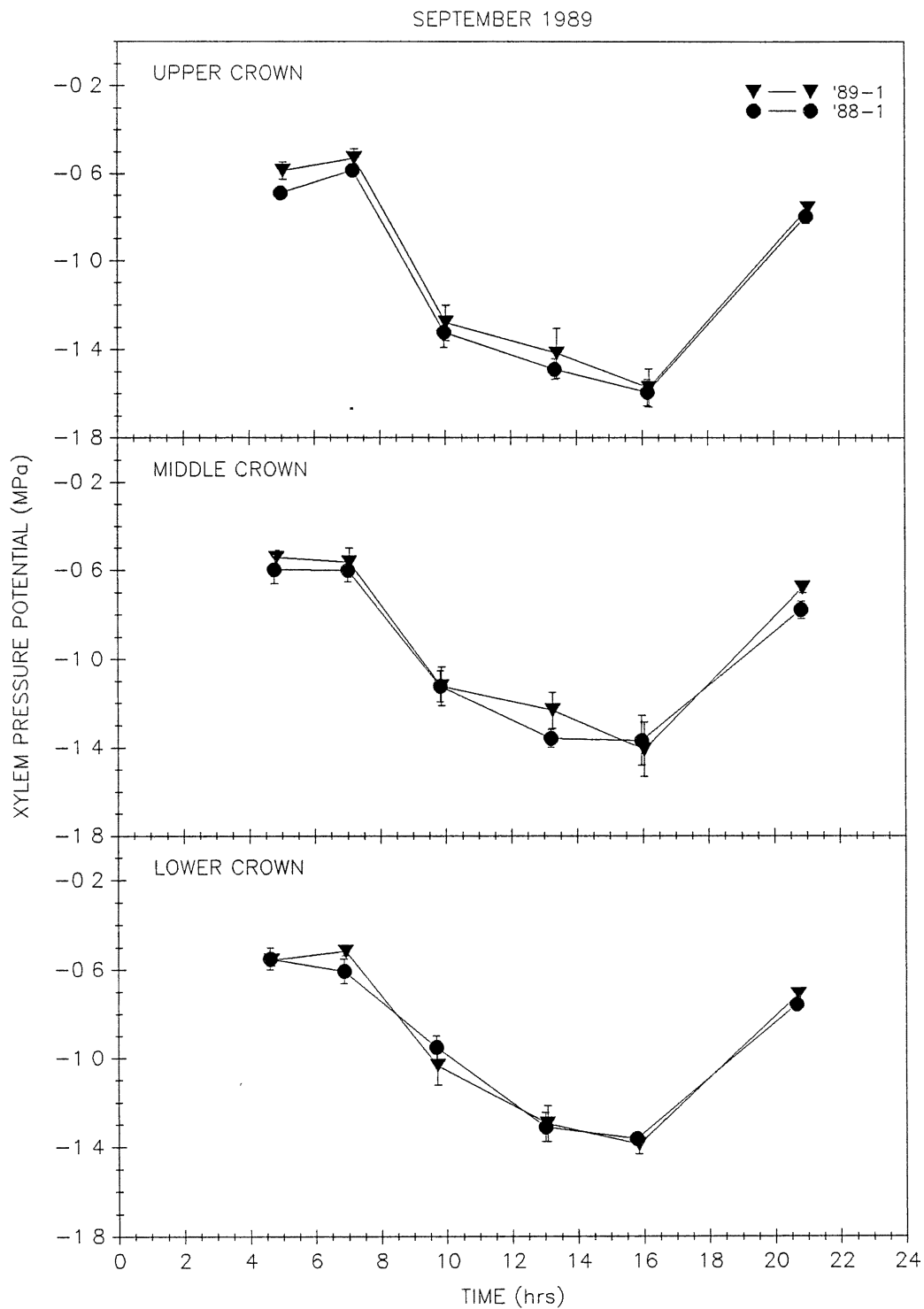


Figure 9. Diurnal patterns of XPP for September. Each bar represents one standard error and each point represents the mean of six trees measured on September 8.

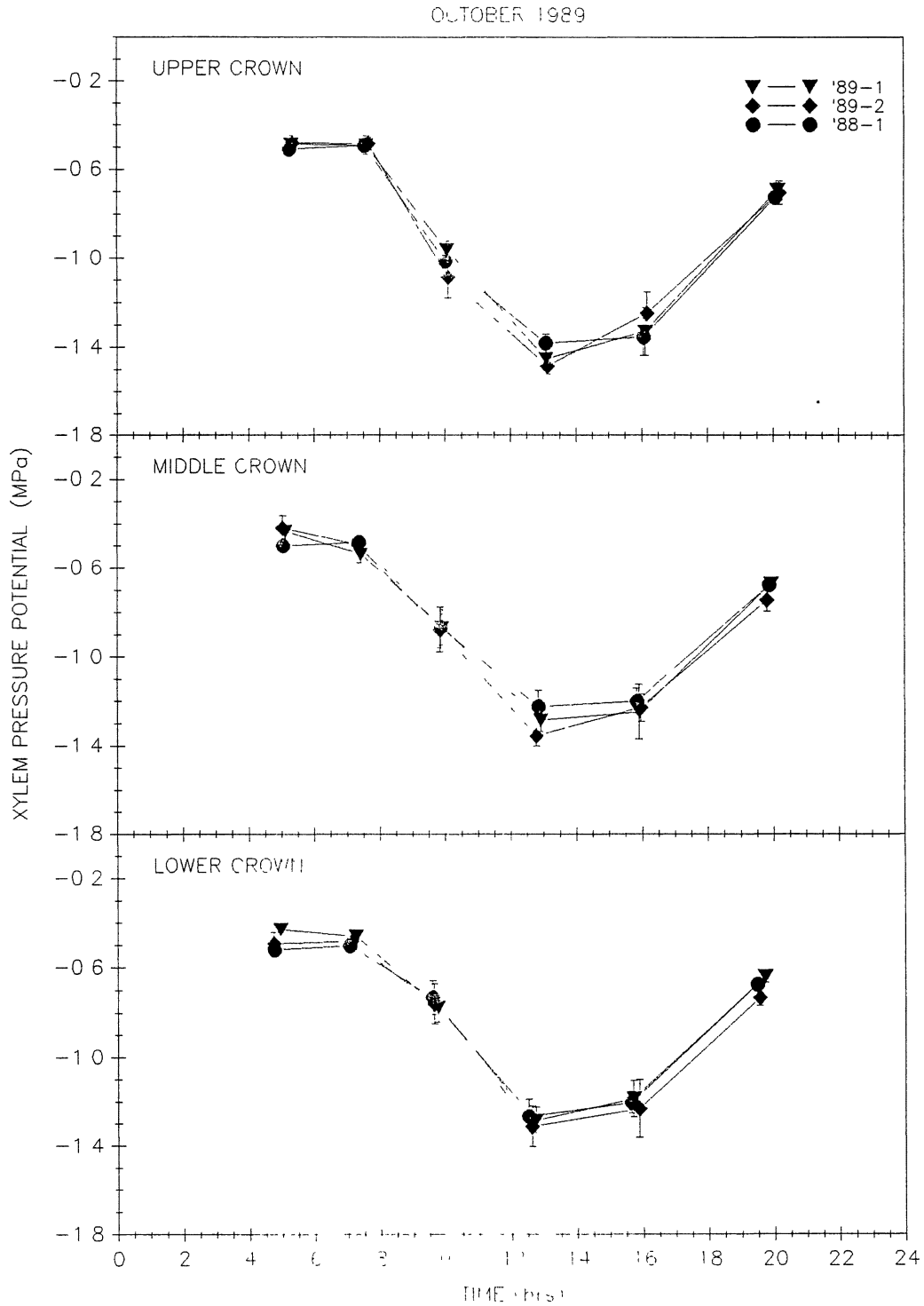


Figure 10. Diurnal patterns of XPP for October. Each bar represents one standard error and each point represents the mean of three to six trees measured on October 3.

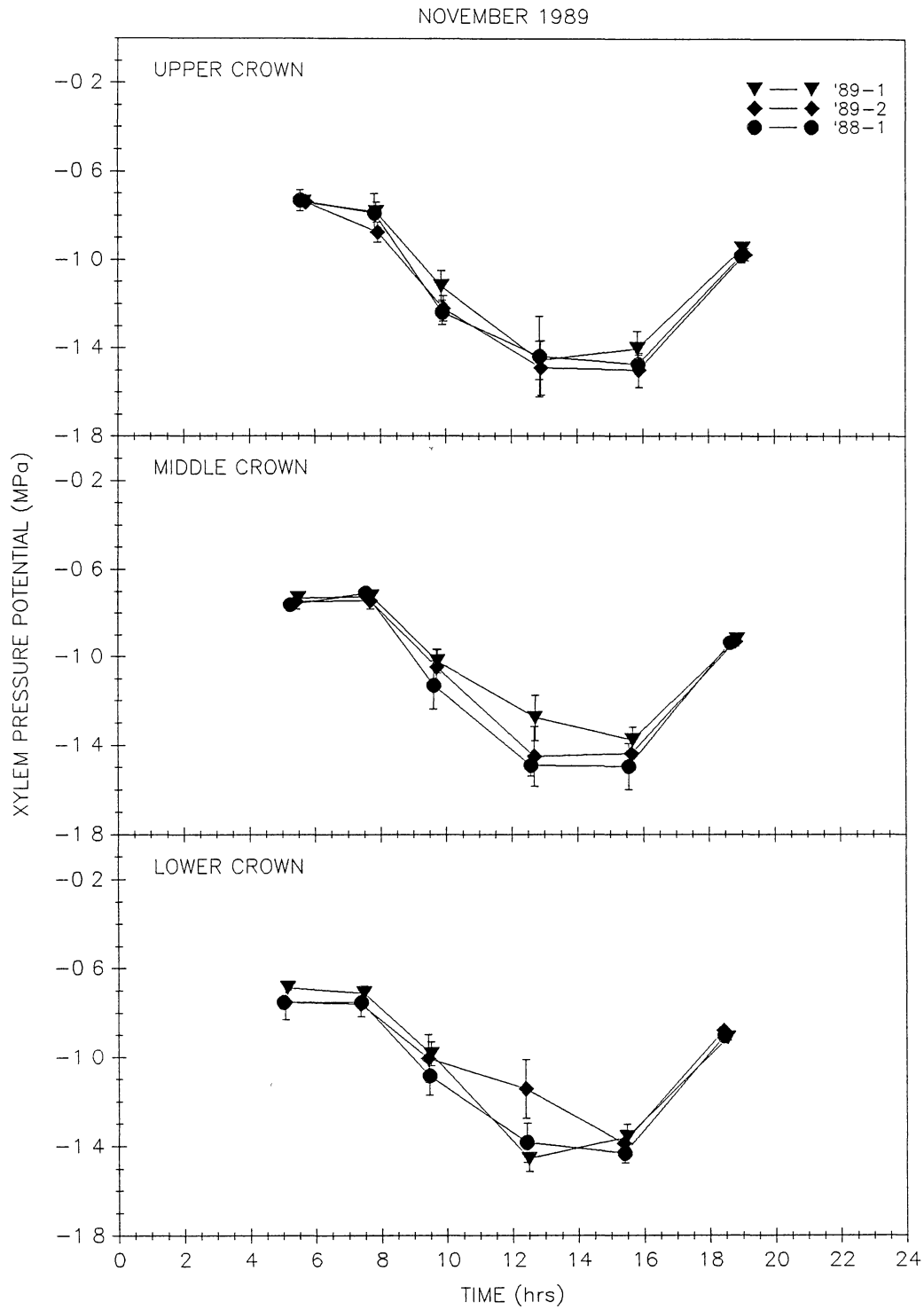


Figure 11. Diurnal patterns of XPP for November. Each bar represents one standard error and each point represents the mean of three to six trees measured on November 10.

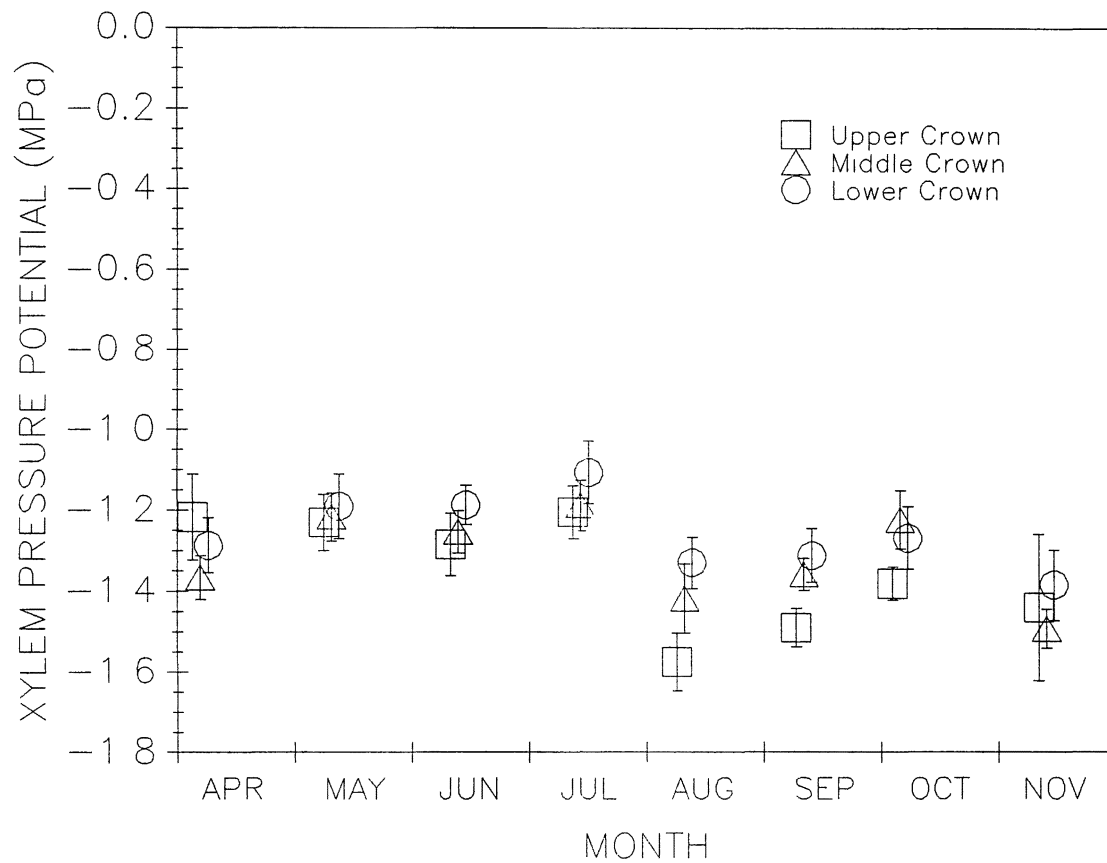


Figure 12. Seasonal patterns of xylem pressure potential (XPP) for '88-1 foliage. Each bar represents one standard error and each point represents the mean of four to six trees.

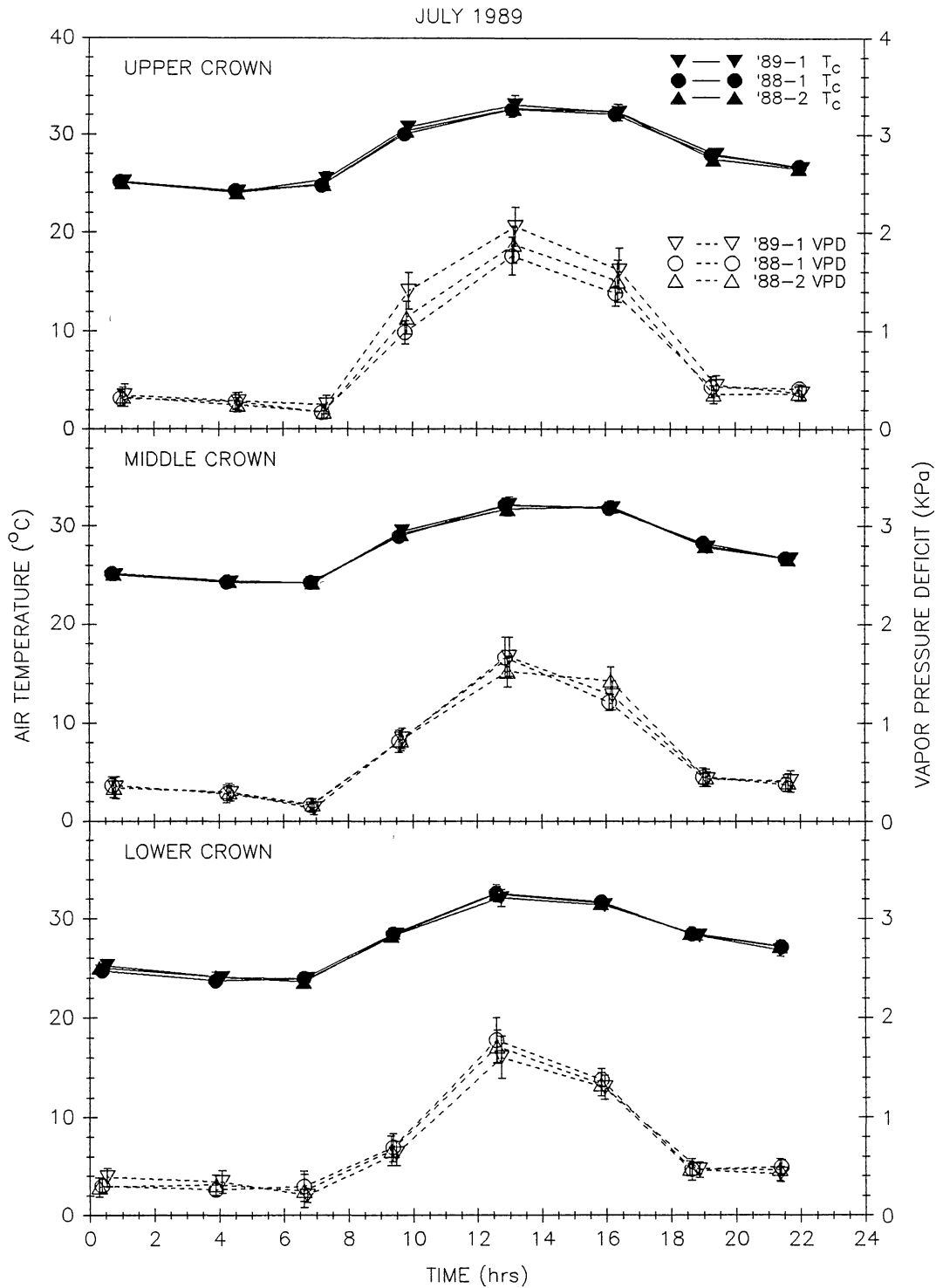


Figure 13. Diurnal patterns of crown air temperature (T_c) and VPD for July. Each bar represents one standard error and each point represents the mean of five to six trees measured on July 11, 12, and 13.

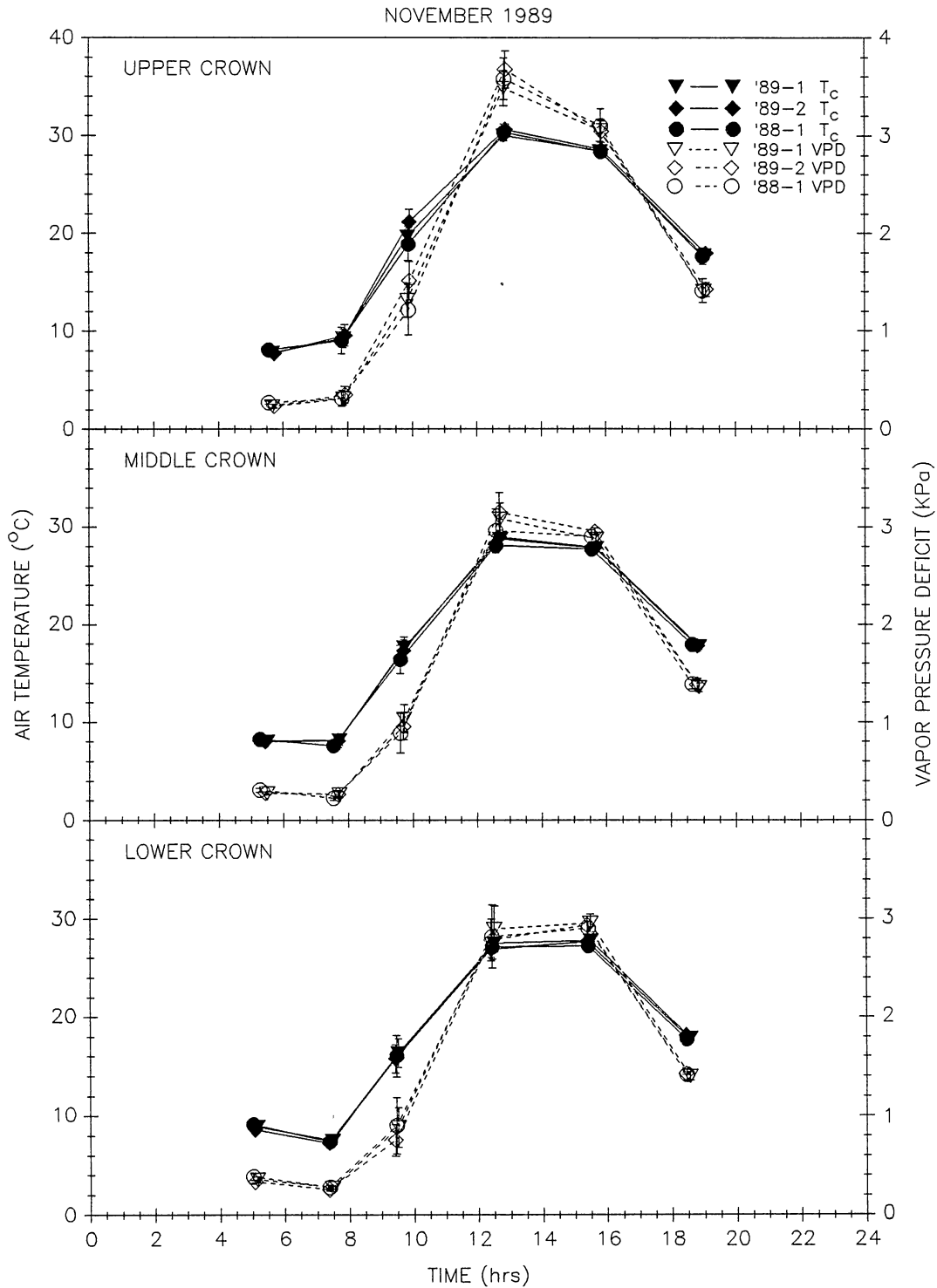


Figure 14. Diurnal patterns of crown air temperature (T_c) and VPD for November. Each bar represents one standard error and each point represents the mean of three to six trees measured on November 10.

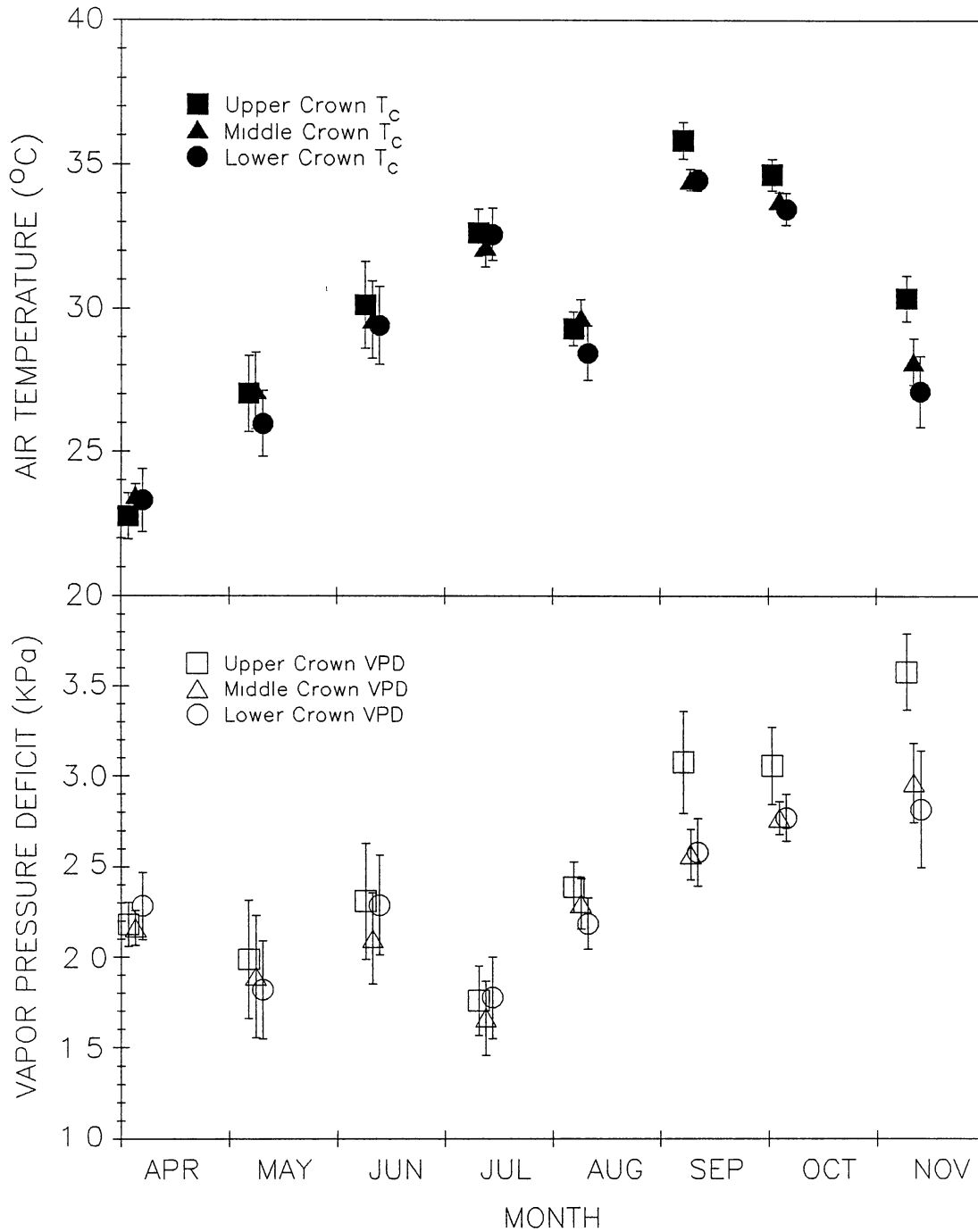


Figure 15. Seasonal patterns of crown air temperature (T_c) and vapor pressure deficit (VPD) for '88-1 foliage measured at solar noon. Each bar represents one standard error and each point represents the mean of three to six trees.

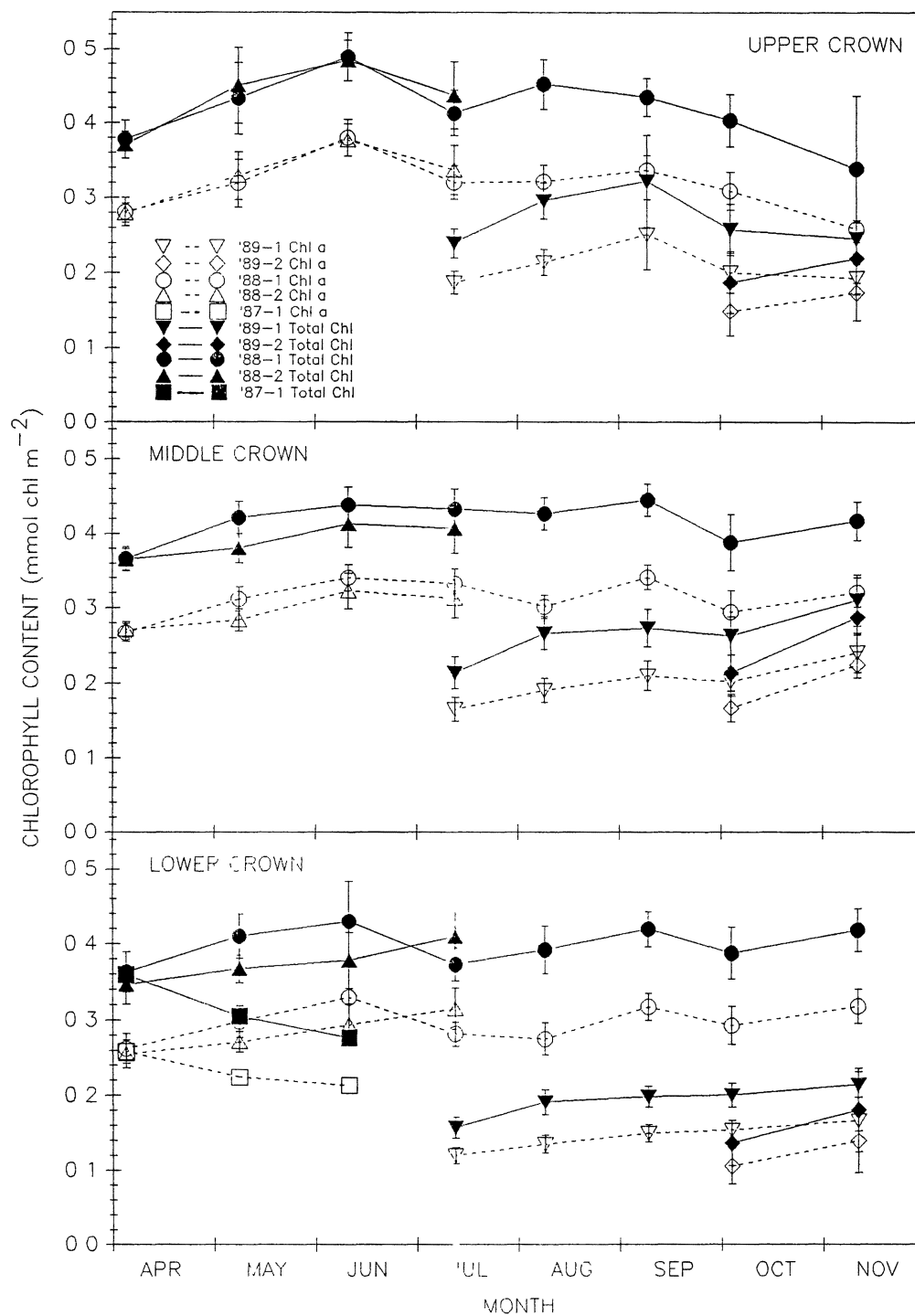


Figure 16. Seasonal patterns of total chlorophyll and chlorophyll a content. Each bar represents one standard error and each point represents the mean of five to six trees except '87-1 which is from one sample only.

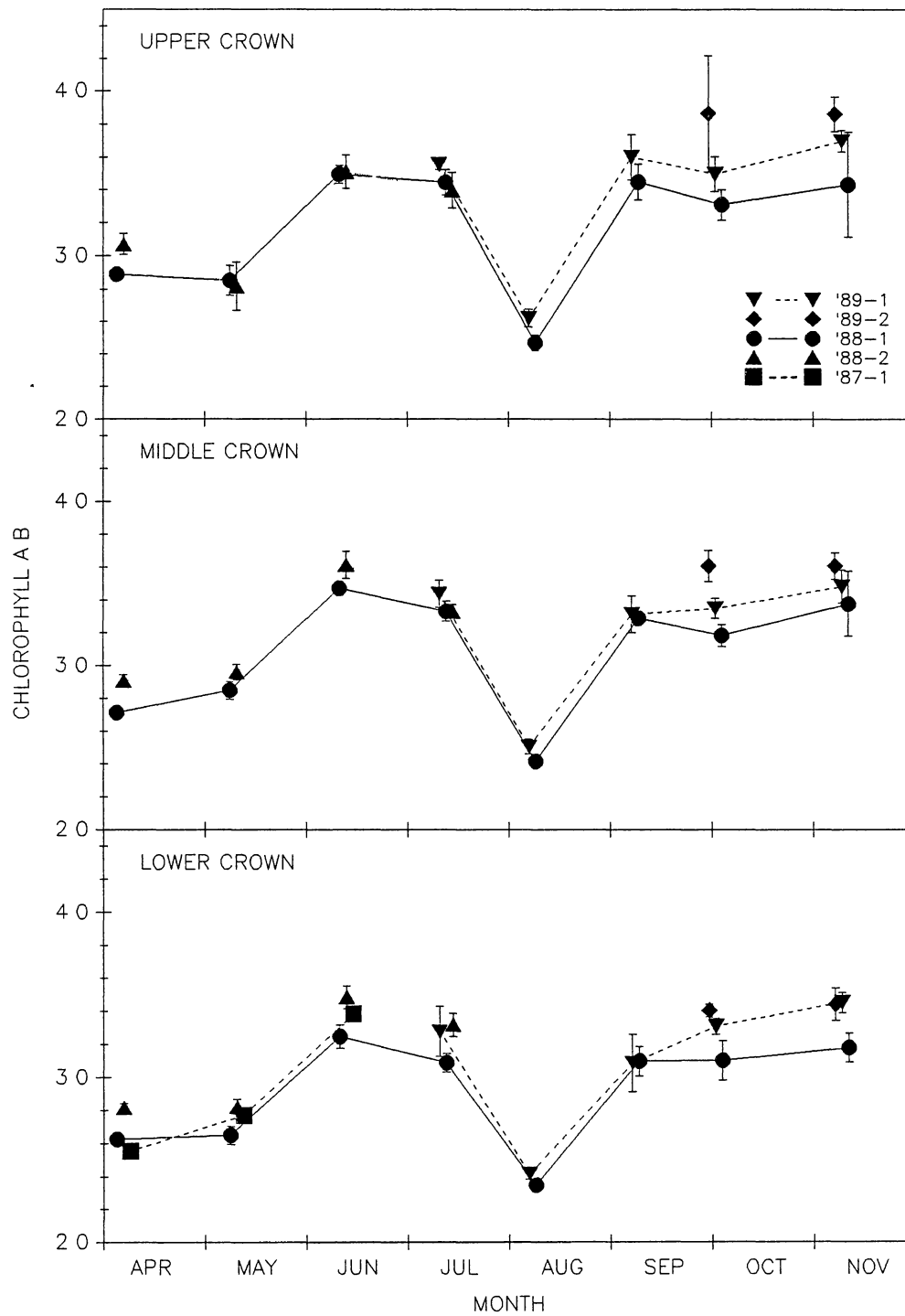


Figure 17. Seasonal patterns of chlorophyll a:b. Each bar represents one standard error and each point represents the mean of five to six trees except '87-1 which is from one sample only.

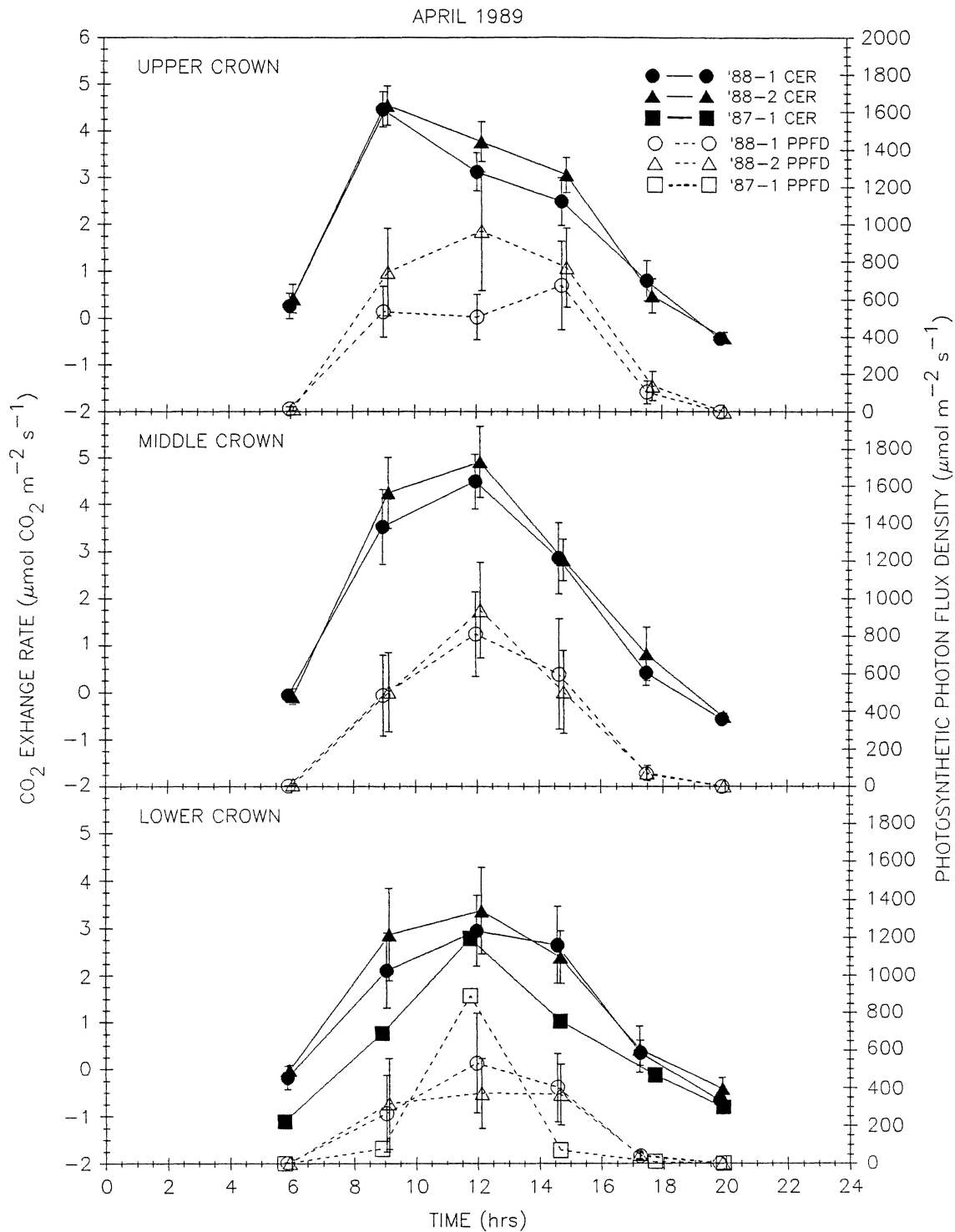


Figure 18. Diurnal patterns of CER and PPFD for April. Each bar represents one standard error and each point represents the mean of five to six trees measured on March 31 and on April 5 and 6.

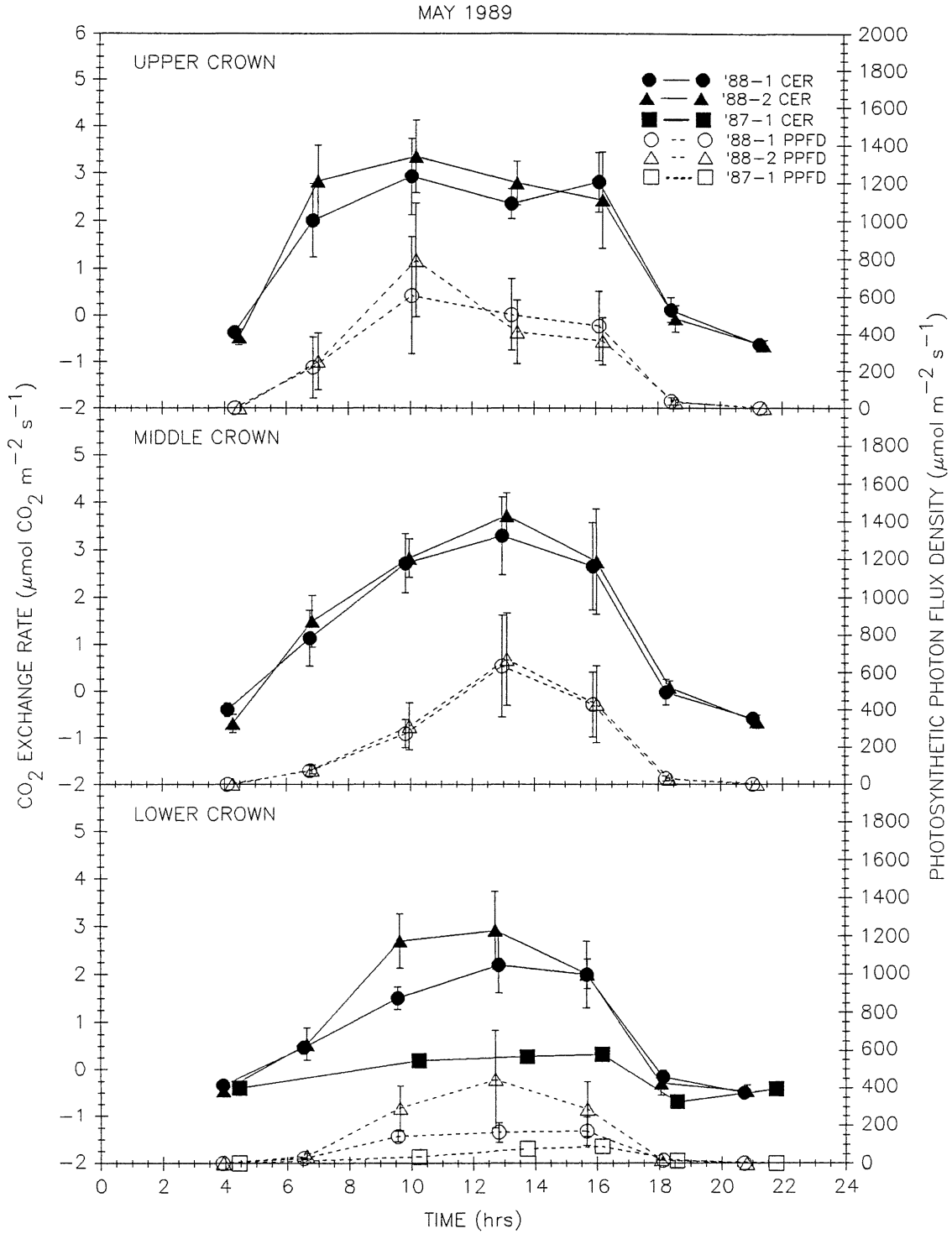


Figure 19. Diurnal patterns of CER and PPFD for May. Each bar represents one standard error and each point represents the mean of five to six trees measured on May 9, 10, and 11.

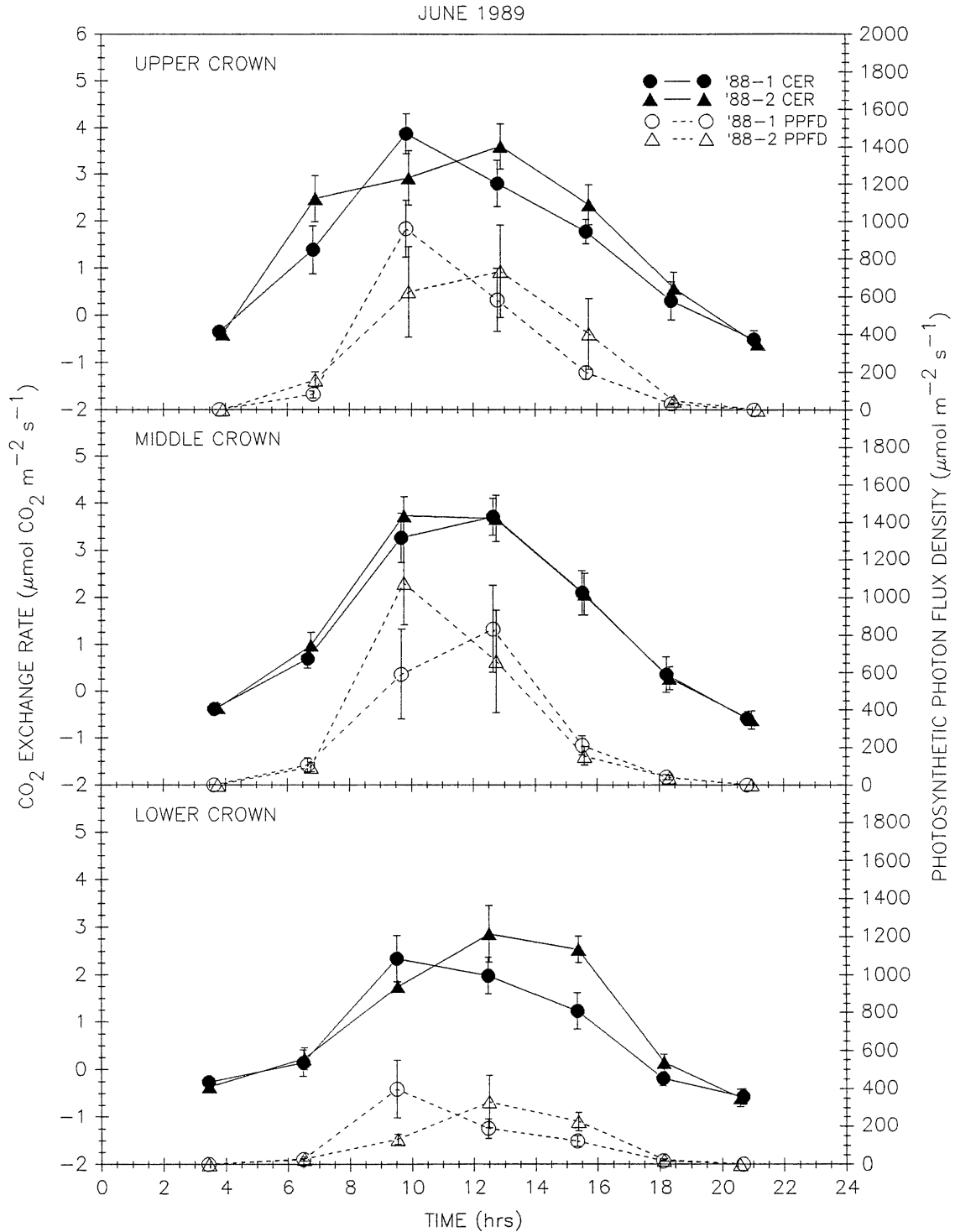


Figure 20. Diurnal patterns of CER and PPFD for June. Each bar represents one standard error and each point represents the mean of six trees measured on June 6, 7, and 15.

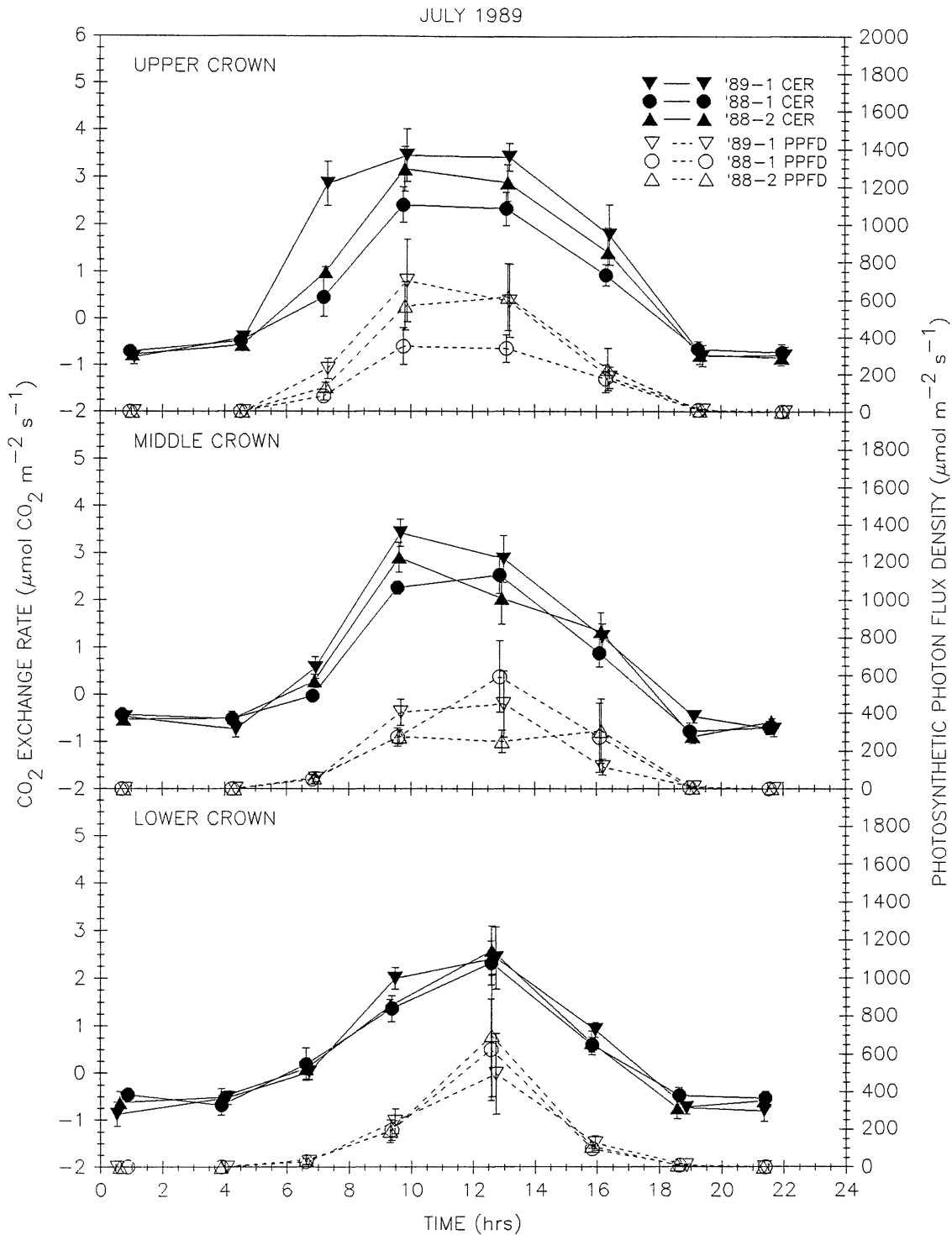


Figure 21. Diurnal patterns of CER and PPFD for July. Each bar represents one standard error and each point represents the mean of four to six trees measured on July 11, 12, and 13.

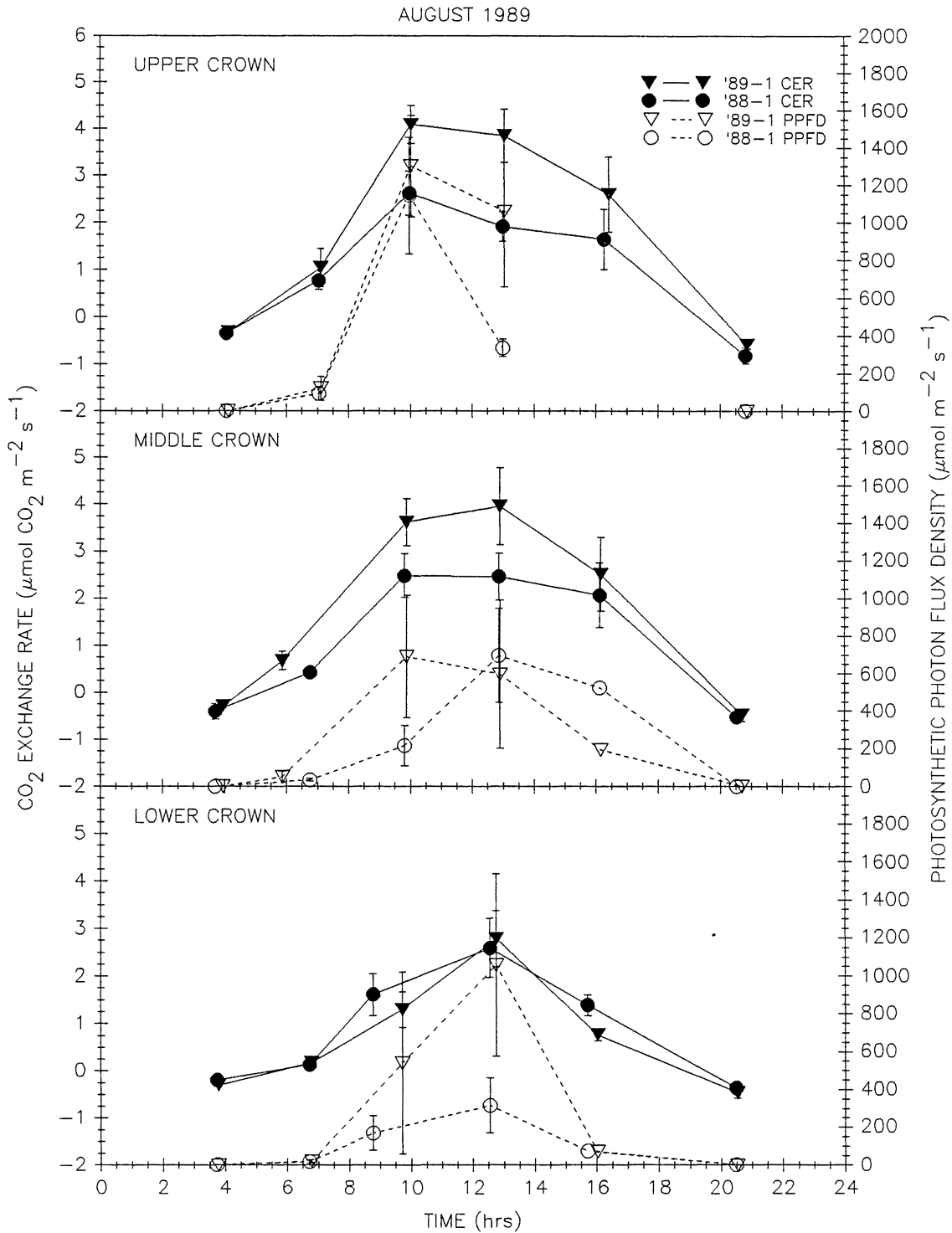


Figure 22. Diurnal patterns of CER and PPFD for August. Each bar represents one standard error and each point represents the mean of three trees measured on August 8.

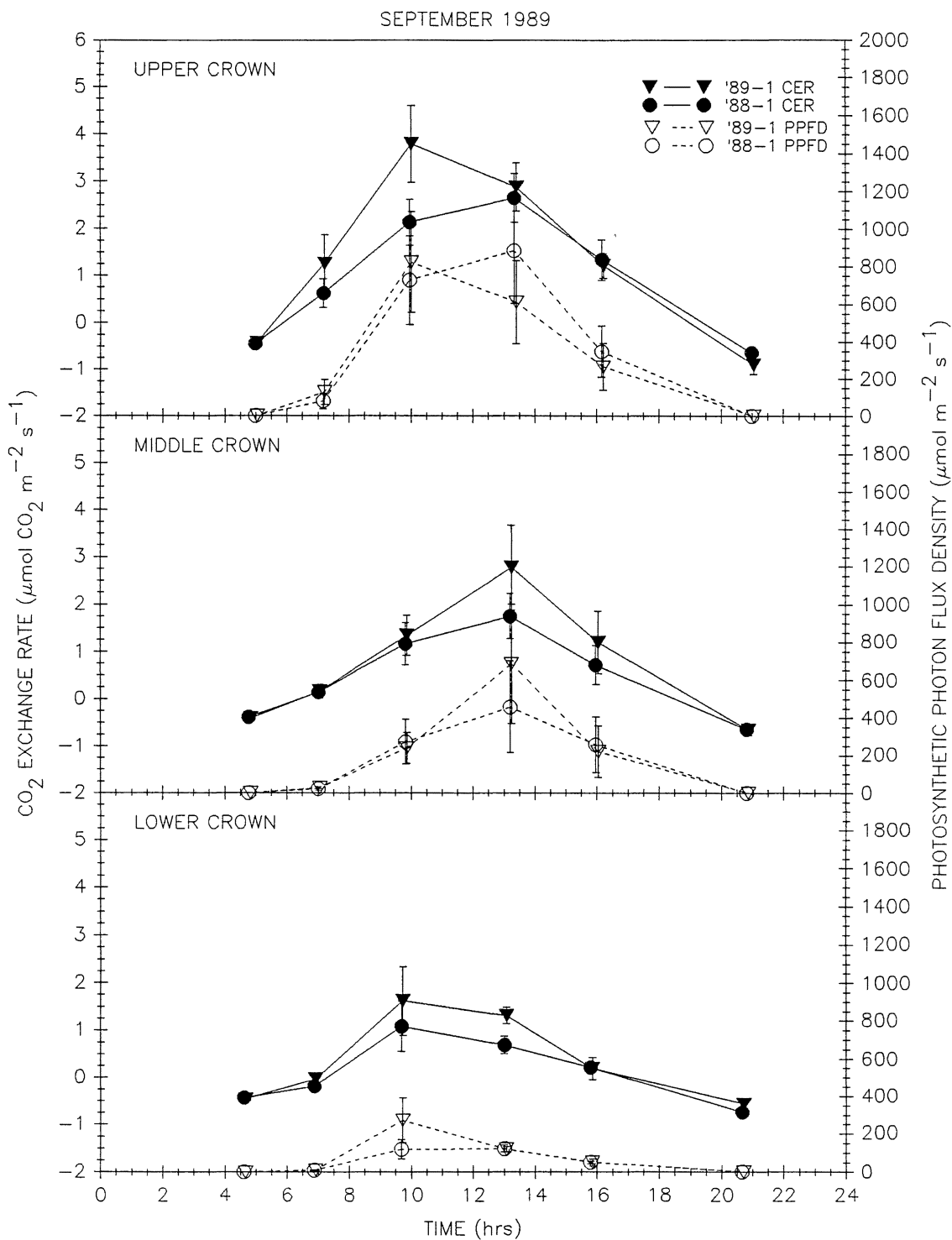


Figure 23. Diurnal patterns of CER and PPFD for September. Each bar represents one standard error and each point represents the mean of six trees measured on September 8.

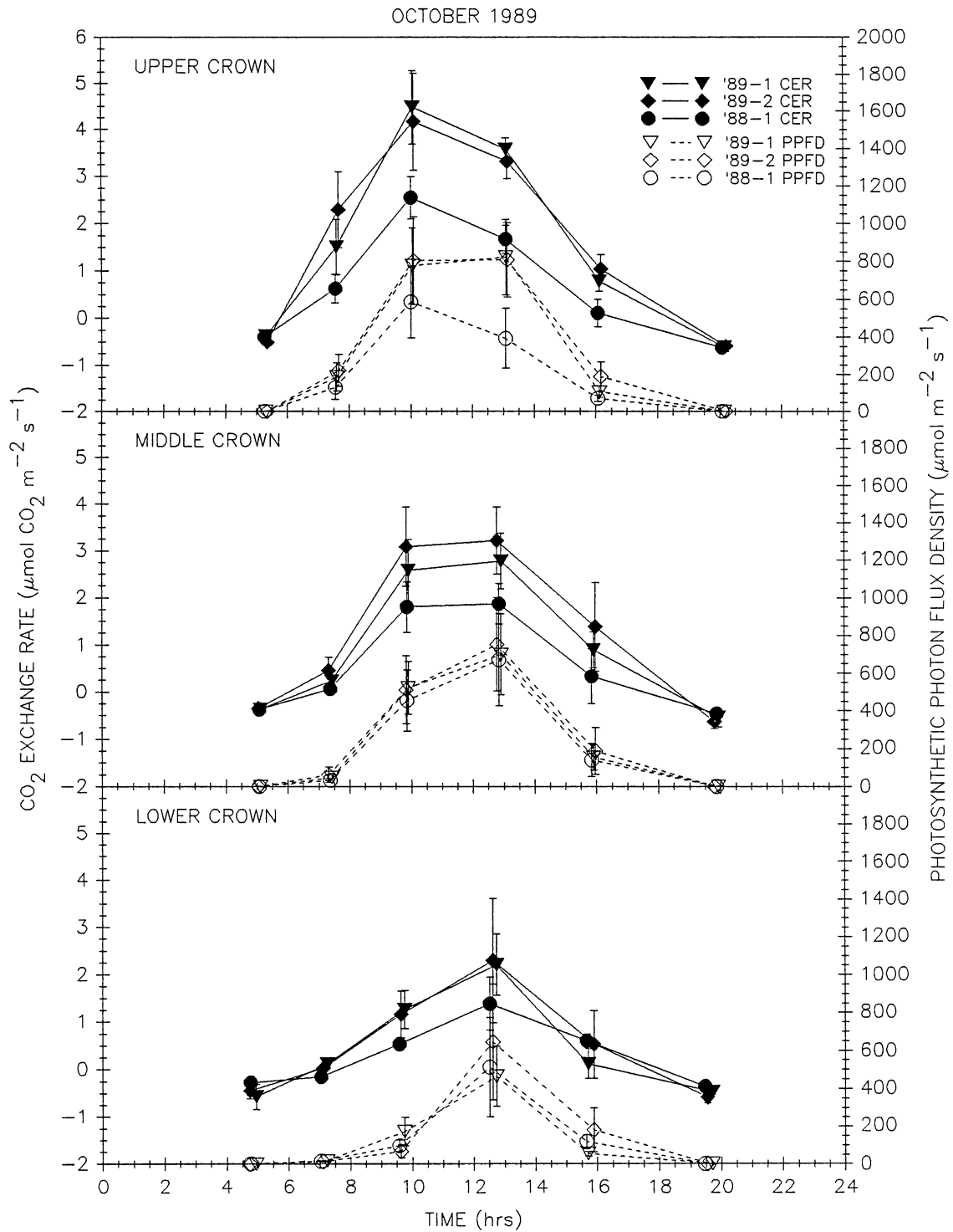


Figure 24. Diurnal patterns of CER and PPFD for October. Each bar represents one standard error and each point represents the mean of four to six trees measured on October 3.

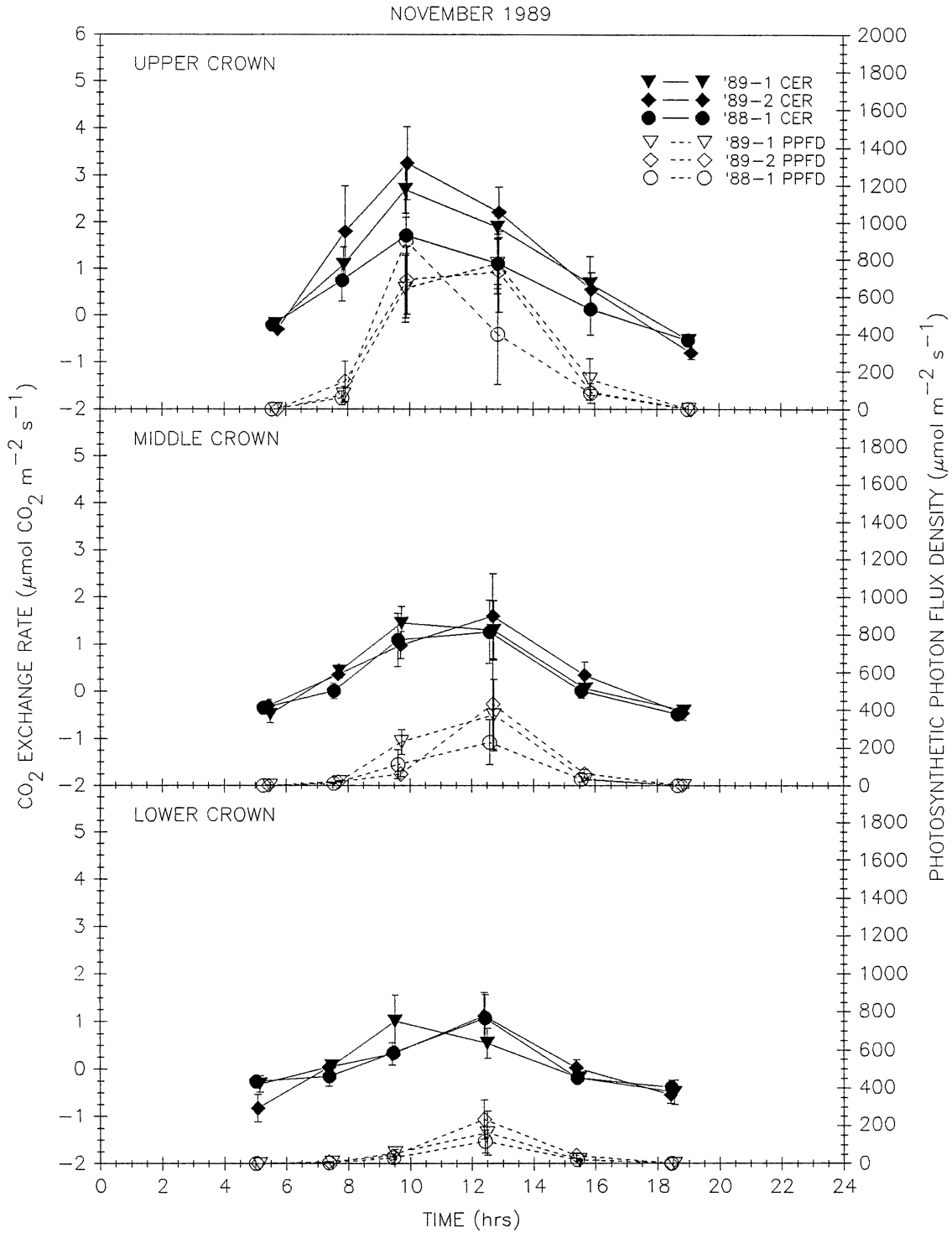


Figure 25. Diurnal patterns of CER and PPFD for November. Each bar represents one standard error and each point represents the mean of three to six trees measured on November 10.

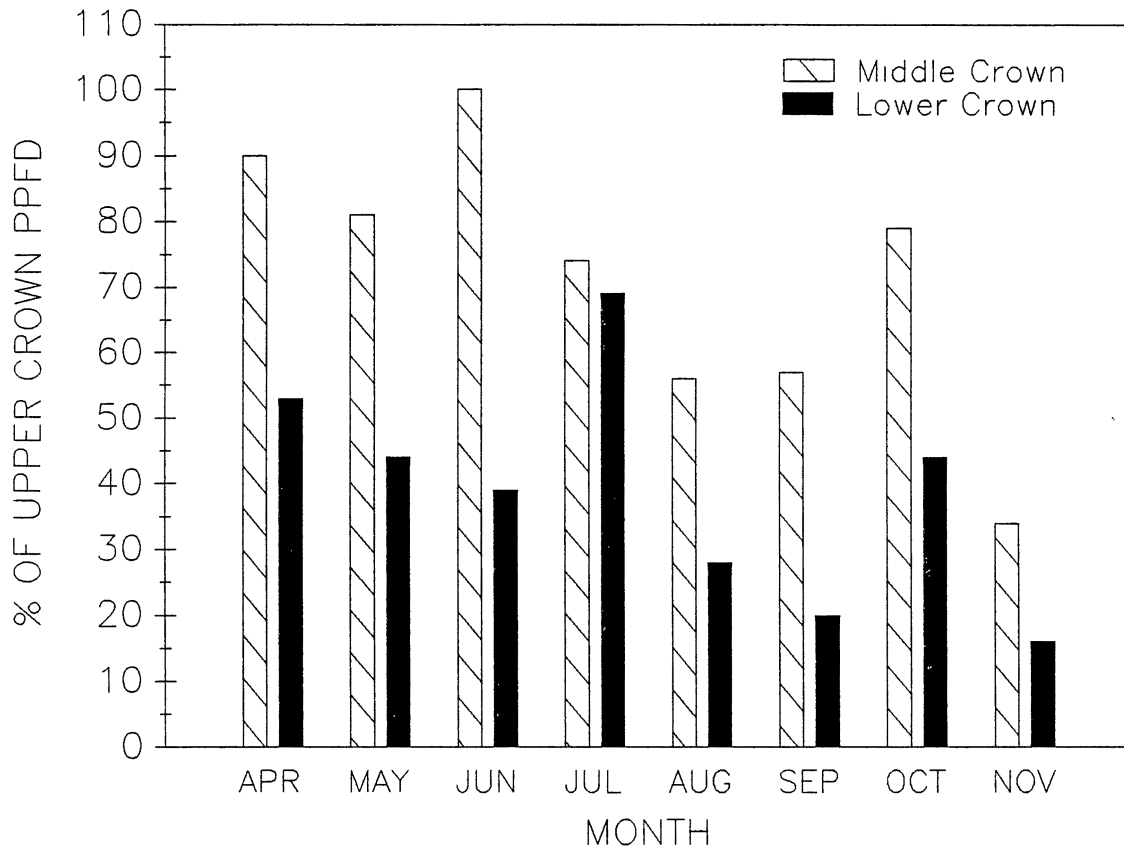


Figure 26. Photosynthetic photon flux density (PPFD) averaged over age-flush classes of middle and lower crown based on the percent of PPFD recorded in the upper crown by month.

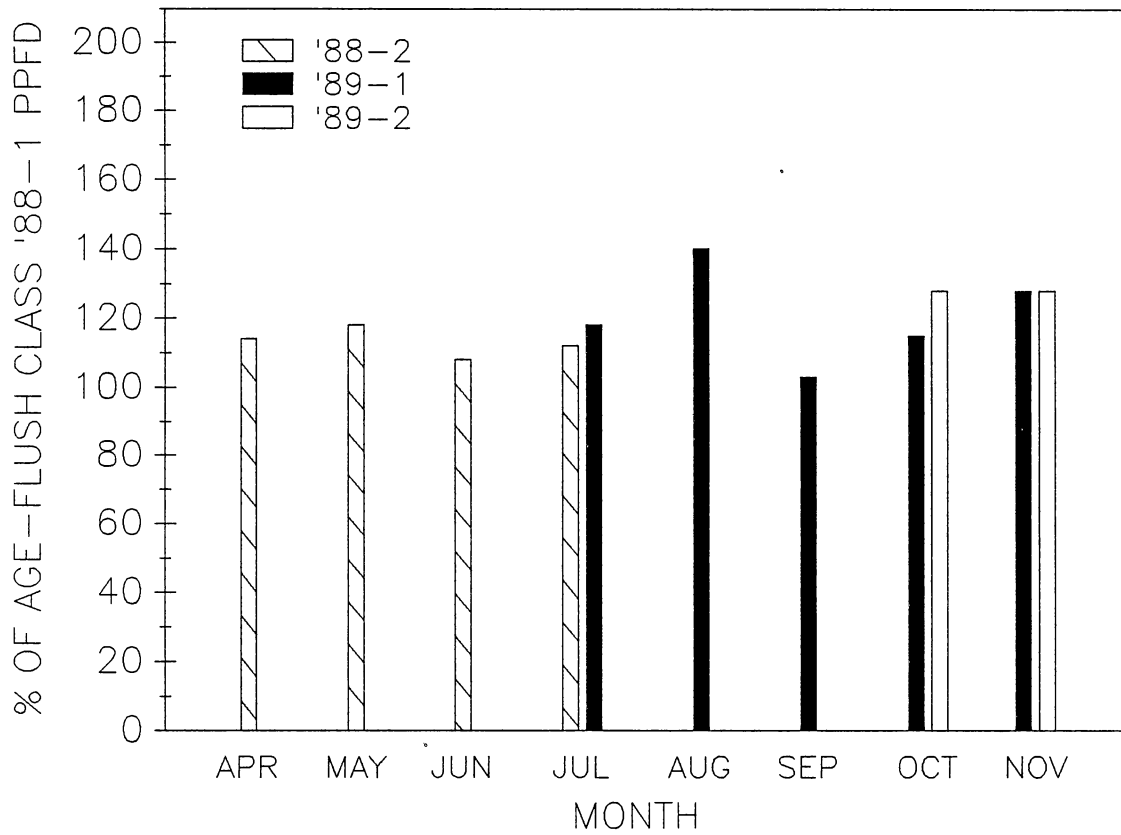


Figure 27. Monthly photosynthetic photon flux density (PPFD) of age-flush classes based on the percent of PPFD of the '88-1 foliage.

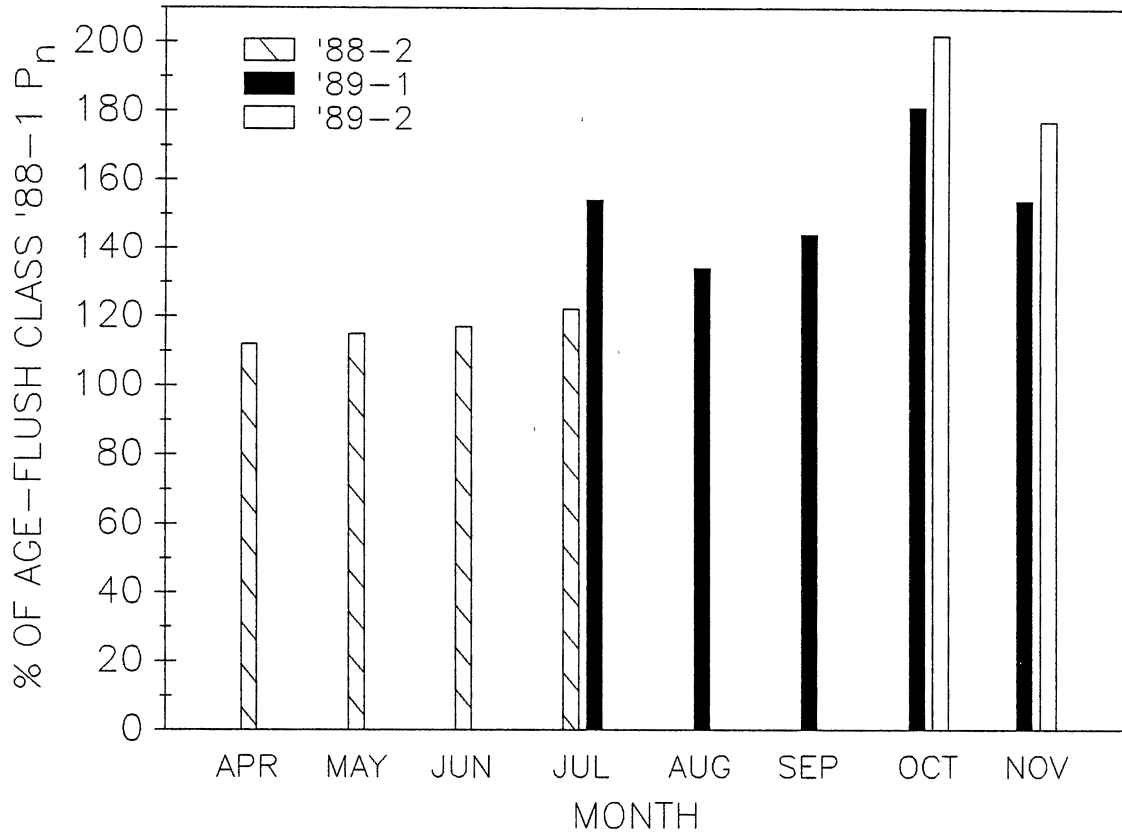


Figure 28. Monthly net photosynthesis (P_n) averaged over crown positions of age-flush classes based on the percent of P_n of the '88-1 foliage.

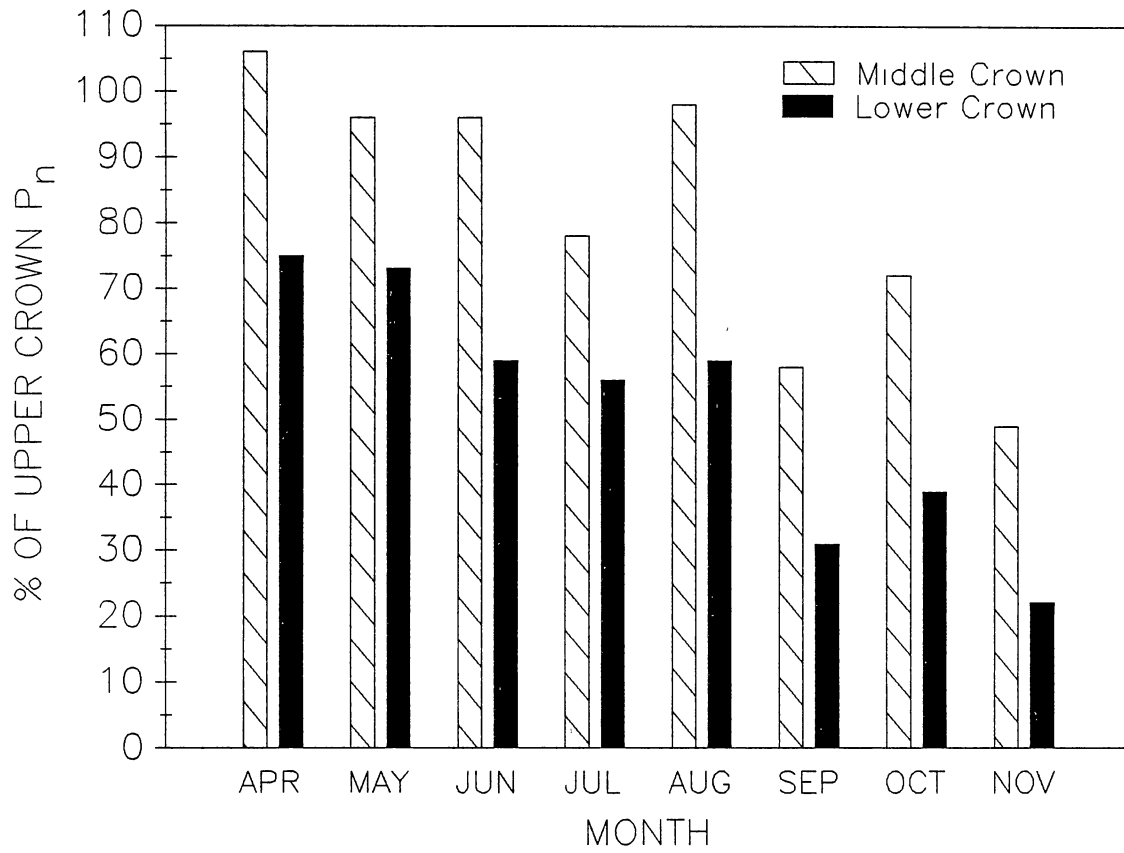


Figure 29. Monthly net photosynthesis (P_n) averaged over age-flush classes of middle and lower crown positions based on the percent of P_n recorded in the upper crown.

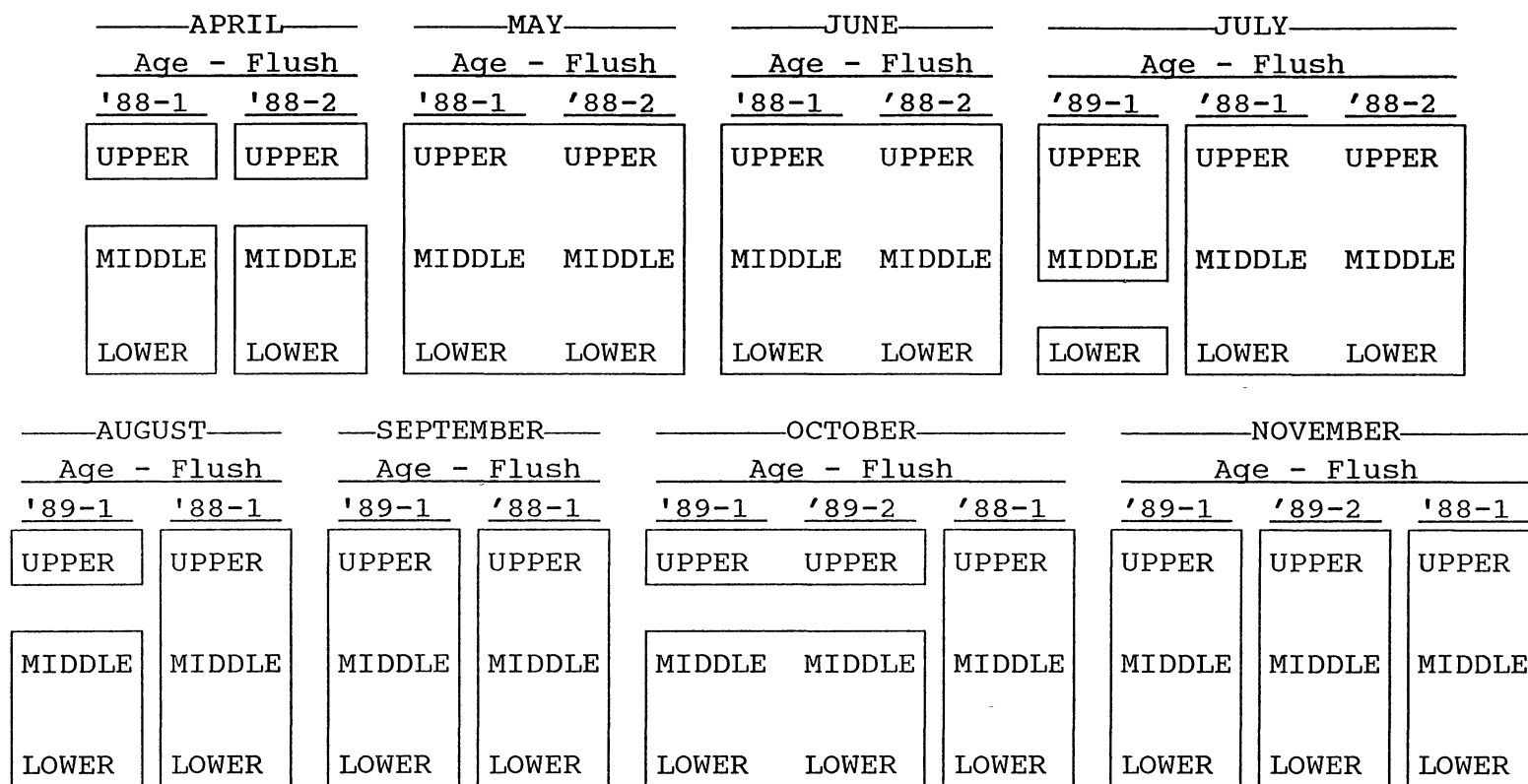


Figure 30. Statistical grouping of carbon exchange rate-photosynthetic photon flux density (CER-PPFD) by date, crown position, and age-flush class. Crown positions and age-flush classes enclosed by a rectangle indicate that pair-wise comparisons of the developed CER-PPFD relationships are not significantly different at the 0.05 level.

2
VITA

Paul Edward Chapman

Candidate for the Degree of
Master of Science

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LOBLOLLY PINE (Pinus taeda L.) STAND

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