Internal and external control of net photosynthesis and stomata1 conductance of mature eastern white pine (*Pinus* strobus)

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Leaf gas exchange and water relations were monitored in the upper canopy of two 25 m tall eastern white pine (*Pinus strobus* L.) trees over two consecutive growing seasons (1986 and 1987). Examination of the seasonal and diurnal patterns of net photosynthesis and leaf conductance showed that both internal and external (environmental) factors were controlling net photosynthesis and leaf conductance. Internal control was indicated by a rapid increase and then decrease in the photosynthetic capacity of l-year-old foliage during the development and maturation of current-year foliage, which was independent of environmental conditions. Large differences in net photosynthesis were observed between growing seasons due to seasonal differences in soil water availability, as indexed by predawn xylem pressure potential. Water stress reduced the maximum rate of net photosynthesis and altered the response of net photosynthesis and leaf conductance to absolute humidity deficit.

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Les échanges gazeux et les relations hydriques au niveau des feuilles furent suivis dans la partie suptrieure de deux pins blancs (*Pinus strobus* L.) de 25 m de haut au cours de deux saisons de croissance, en 1986 et 1987. L'examen du comportement saisonnier et diume de la photosynthese nette et de la conductance foliaire ont montré que des facteurs intemes autant qu'externes (environnementaux) contrôlent la photosynthese nette et la conductance foliaire. Le contrôle inteme se manifestait par une augmentation rapide suivie d'une diminution de la capacité photosynthétique du feuillage de 1 an, pendant le développement et la maturation des aiguilles de l'année courante qui Ctaient indépendants des conditions environnementales. Des differences importantes de la photosynthtse nette, dues à des variations saisonnibres de la disponibilité en eau du sol, telles qu'indiquées par la pression potentielle du xylème avant l'aube, furent observées entre les saisons de croissance. Le stress hvdriaue a réduit le taux maximum de la nhotosvnthèse nette et a change la réponse de la photosynthbse nette et de la conductance foliaire face au deficit d'humidité absolue.

[Traduit par la redaction]

Introduction

During the 1980s much of the southeastern United States was abnormally dry. Drought conditions were particularly severe during the spring and summer of 1986 in the mountains of western North Carolina. Total rainfall from winter through the middle of the growing season was the lowest on record (Karl and Young 1987), and temperatures during this period were above normal. This natural event provided an opportunity to measure the effects of a severe drought on the gas exchange characteristics of an important forest tree species, eastern white pine (*Pinus strobus* L.). Information on natural droughts is potentially very useful since it is likely that climate change will alter regional precipitation patterns. Tremendous uncertainty exists at the present time about the direction and magnitude of any precipitation change, and observations of plant response to extreme climatic events can help put the potential impacts to vegetation into perspective.

This study also provided some insight into the importance of internal factors in the regulation of the rate of net photosynthesis. This was not a planned component of the study, and the data resulted from fortuitous sampling. However, these data reveal the need for a better understanding of the relative contributions of internal and external controls on physiological processes in trees. The effects of external factors (light, temperature, water) have been described in detail for many tree species, but the role of internal regulators such as sink demand for carbohydrates may have had significant, but largely unrecognized, effects (Thomas and Strain 1991).

Materials and methods

Site location and characteristics

The study was conducted at the USDA Forest Service Coweeta Hydrologic Laboratory located in the southern Appalachian Mountains in western North Carolina (Otto, North Carolina). The Coweeta basin covers approximately 5000 acres (2024 ha) and is situated along the eastern slope of the Nantahala Range. Elevations in the basin range from 300 m to more than 1700 m. The climate is moderately cool and moist. Mean annual temperature is 13°C, and mean precipitation ranges from 170 cm· year-' at the lower elevations to 250 $\mathrm{cm \cdot year^{-1}}$ along the ridges. Annual rainfall is evenly distributed throughout the year, and droughts of long duration are rare. A detailed description of the climate of the region is given in Swift et *al. (1988).*

The study site was located in watershed 17 (WS 17), a white pine plantation established in 1956. The stand covers 13.4 ha, has a relief of 280 m, and generally has a northwest aspect (Swank and Douglas 1974). The study trees were located near the top of the watershed, at an elevation of 1100 m. The soil at the study site was an Evard-Cowee gravelly loam. Slopes at the site ranged from 30 to 50%. Stand basal area was 50 $\mathrm{m^2 \cdot ha^{-1}}$ (1100 stems/ha). A 30-m triangular television tower was constructed to gain access to the upper canopy of two dominant trees approximately 30 m in height.

Environmental and physiological measurements

Continuous measurements of precipitation: total irradiance; hourly mean, minimum, and maximum temperature; relative humidity; and

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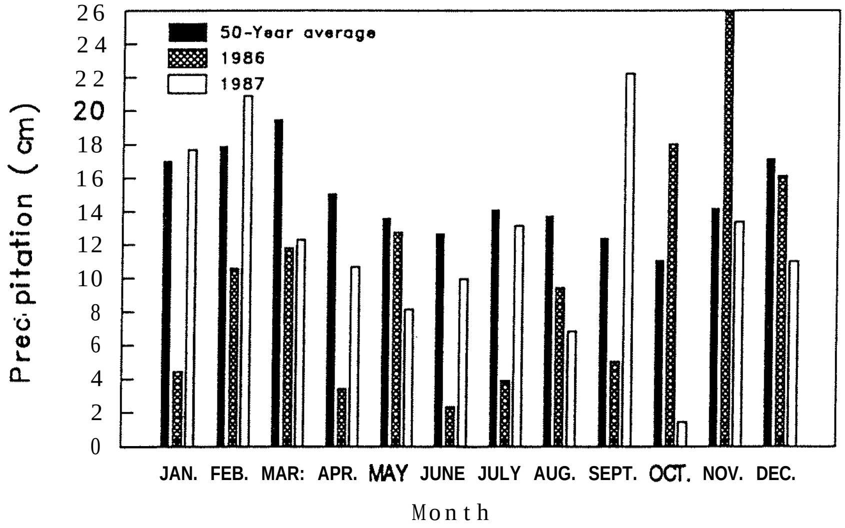

FIG. 1. Monthly precipitation in 1986 and 1987 compared with the 50-year average at the USDA Forest Service, Coweeta Hydrologic Laboratory.

vapor pressure deficit were made at a permanent USDA Forest Service meteorological station located within WS 17. Leaf gas exchange measurements were made with an ADC-LCA2 infrared gas analyzer (IRGA) (Analytical Development Company, Hoddeston, England) and a narrow-leaf Parkinson leaf chamber. The IRGA and chamber were operated in an open configuration. Ambient air was pumped into the chamber through a piece of long tubing, placed at least 5 m away from the tower, to ensure that chamber CO_2 concentrations were near ambient. The sample and reference air streams were dried just before entering the IRGA. Temperature (platinum resistance thermistor), relative humidity (capacitive sensor), and photosynthetically active radiation (PAR) (silicon photodiode) were measured with sensors mounted in the leaf chamber head. Barometric pressure was monitored using a hand-held barometer-altimeter (Thommen). Measurements of leaf xylem pressure potential (XPP) were made using a pressure chamber (PMS Instrument Company, Corvallis, Oregon) following techniques described by Ritchie and Hinckley (1975). Measurements of pressure potential were made on individual fascicles.

Sampling procedure

All measurements were made in the upper canopy on the second and third whorl of branches of the two sample trees. Each measurement day began with predawn xylem pressure potential (PXPP) measured approximately 30 min before sunrise. Measurements of gas exchange were taken on six branches, three on each tree. The same branches were used throughout both growing seasons. Measurements were made on 1-year-old foliage until early June, when concomitant measurements began on developing foliage (approximately 30% expanded). On each measurement day, one or two fascicles from each age-class on each sample branch were tagged and were used for gas exchange measurements. The needles were arranged in the leaf chamber so that self-shading was-minimized. Leaf chamber carbon dioxide concentrations were allowed to stabilize (30 to 90 s), then CO_2, chamber temperature, chamber relative humidity, and incident light were recorded. The foliage was then removed from the chamber, and the relative humidity and temperature of the airstream was measured. These measurements were needed for calculation of leaf conductance and transpiration. At the end of each measurement period, XPP was determined for each age-class on a nearby fascicle of the same shoot. Each measurement period required from 20 to 30 min to complete. Gas exchange measurements were taken every 1.5 h in 1986 and every 2 h in 1987 beginning at 06:30 and, weather permitting, continued until sunset. Fascicles were removed at the end of the day for leaf area determination.

Data analysis

Calculations of net photosynthesis (P_{net}), leaf conductance (g_l), and transpiration (E_t) were made using the formulas presented in Long and Hallgren (1985). Eastern white pine needles are triangular in *cross* section with three to five rows of stomata on the ventral surfaces. Physiological measurements were expressed on the area of these stomata-bearing surfaces. To convert to total leaf area, values should be reduced by one-third.

Means of P_{net}, g_l, and E_t were made by averaging the readings on both trees for each measurement period. Mean midday rates of net photosynthesis and leaf conductance were calculated by averaging measurements made between 10:30 and 14:00. Hourly mean XPP is the average of six pressure chamber readings for each foliage age-class.

Nonlinear regression (SAS Institute Inc. 1988) was used to model the relationship between P_{net} and light. A nonrectangular hyperbola (Marshall and Biscoe 1980; Lieth and Reynolds 1987) was used to fit the data and had the form

$$P_{net} = \frac{(\alpha \mathrm{PAR} + Mp_{net} + R_d) - (\alpha \mathrm{PAR} + Mp_{net} + R_d) - 4\alpha\ \mathrm{PAR}\ \Theta\ (Mp_{net} - R_d)}{2\Theta}$$

where α is apparent quantum yield, PAR is photosynthetically active radiation, Mp_{net} is maximum net photosynthesis, R_d is dark respiration, and Θ is degree of convexity. The relationships were developed using the mean P_{net} within discrete light intervals. Temperature and water stress produced large variations in P_{net} at high light intensities. Most of this variation was removed by excluding all data when P_{net} was less than 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at light intensities greater than 800 $\mu mol\ m^{-2} \cdot s^{-1}$.

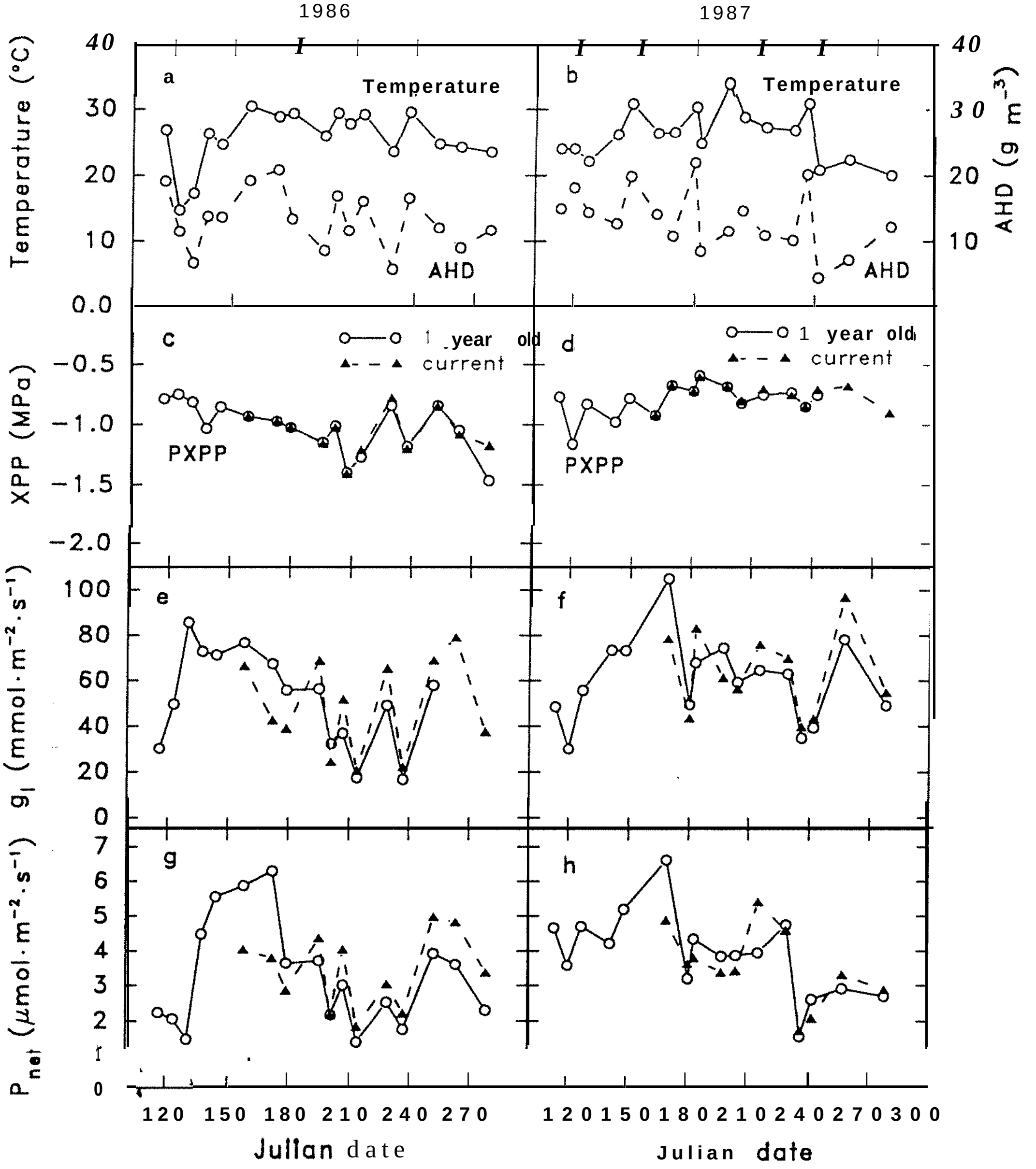

FIG. 2. Seasonal trends in midday temperature and absolute humidity deficit (AHD), predawn xylem pressure potential (PXPP), midday leaf conductance (g_l), and midday net photosynthesis (P_{net}) in the canopy of 31-year-old white pine trees during two growing seasons. Each point is the mean of 12-16 measurements from two trees made between 10:30 and 14:00, except for PXPP, which was measured 30 min before sunrise.

Results

Seasonal patterns

Environmental conditions

Precipitation in 1986 and 1987 was 31 and 17%, respectively, below that of the 50-year average at Coweeta (Fig. 1). The monthly distribution of rainfall also varied between the two years. The differences were most notable during the dormant season (November – February) and during periods of rapid growth (May -July). The first 6 months of 1986 were very dry, receiving only 49.4 cm of rainfall, which created severe drought conditions. The same period in 1987 was much wetter, receiving almost twice the amount of precipitation (92.9 cm).

Xylem pressure potentials

PXPP reflected rainfall patterns in both growing seasons. In early spring, PXPP were relatively high, generally above -1.0 MPa (Figs. 2*c* and *2d*). In 1986 PXPP began to decline owing to the lack of rainfall and reached a summer low of -1.4 MPa on day 207. In late summer and fall, PXPP fluctuated with rain events. In 1987 PXPP remained high throughout the growing season. Current-year and l-year-old foliage had similar values of PXPP in both years.

Leaf conductance

Midday g_l in l-year-old foliage rapidly increased in the early spring to the yearly maximum (Figs. 2e and 2*f*). On subsequent dates midday g_l fluctuated with rainfall events (most evident in 1986) or other variations in environmental conditions. Owing to the drought in 1986, midday g_l was as low as 17 mmol·m^{-2}·s^{-1} (day 237) and was correlated with low PXPP. The seasonal trend of midday g_l in current-year foliage was similar to that of l-year-old foliage. After needle maturity,

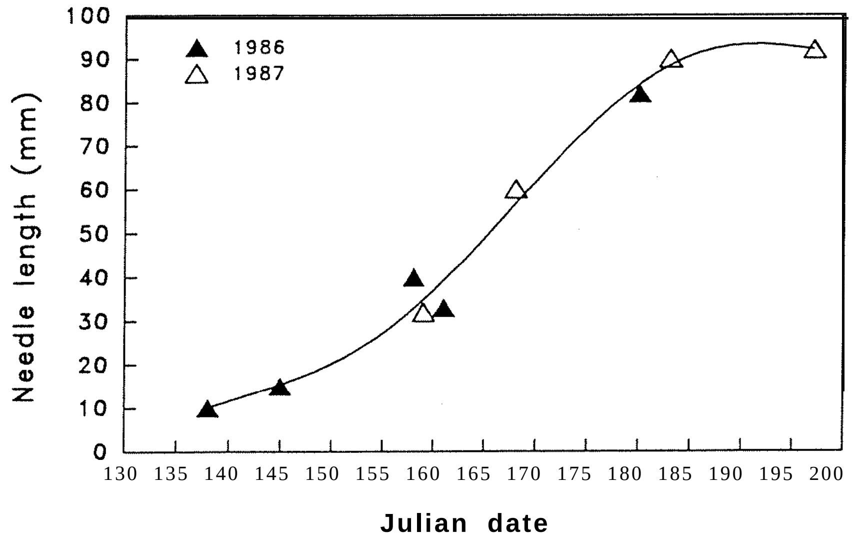

FIG. 3. Expansion of current-year foliage in 1986 and 1987.

g_{l} of current-year foliage was generally higher than that of older foliage. This was especially noticeable on days when temperatures were mild and absolute humidity deficits were low.

Net photosynthesis

In early spring (days 110–130), midday rates of P_{net} were quite different in the two growing seasons. This was correlated with seasonal temperatures. In spring 1986, which was much cooler than spring 1987, midday P_{net} ranged from 1 to 2.5 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$, well below the 3.5 to 4.5 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ recorded in 1987 (Figs. 2g and *2h*). A rapid increase in net photosynthesis occurred in both growing seasons in late spring, and midday P_{net} peaked between 6 and 7 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ in late June. This peak in midday net photosynthesis of 1-year-old foliage coincided with rapid growth of current-year foliage, which was approximately 70% expanded (Fig. 3). Following the seasonal peak, an abrupt decline in P_{net} occurred in both growing seasons, dropping about 50% within 10 days. This rapid decline in midday P_{net} in 1-year-old foliage coincided with the maturation of current-year foliage (>80% expanded) and was not correlated with the environmental conditions at the time (Figs. *2a–2d*), which were favorable for net photosynthesis.

Midday P_{net} continued to decline in the summer of 1986 and reached a seasonal low of 1.4 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ on day 214. Positive midday P_{net} were observed throughout the summer drought period, although at quite low rates. Late-summer rain showers that increased PXPP also caused a partial recovery in P_{net}; however, the magnitude of the recovery was not as great as in g_{l} (Figs. 2e and 2g). During the summer of 1987, which was much wetter, midday P_{net} was maintained at 50 to 60% of the spring peak until fall, when rates declined, apparently owing to low temperatures.

Midday P_{net} in fully expanded current foliage peaked at 5.0 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ in early September 1986 and at 5.4 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ in early August 1987. Rates of midday P_{net} of current-year foliage were significantly greater than 1-year-old foliage in the fall of 1986. This difference was not observed in 1987.

Internal regulation

The seasonal patterns indicated that both internal (physiological) and external (environmental) factors exert control over the rate of P_{net} and g_{l}. An illustration of the internal control of gas exchange can be seen in the diurnal patterns of P_{net} and water relations for 2 days in 1986 that had very similar environmental conditions: day 172 (June 21), when current-year foliage was actively growing, and day 201 (July 20) when current-year foliage was fully expanded (Fig. 4). Both days were clear and warm. Irradiance (PAR) and air temperature were nearly identical (Fig. *4a*). The absolute humidity deficit (AHD) was slightly higher at midday on day 172 and slightly higher in the late afternoon on day 201. Predawn XPP were the same on both days (-1.0 MPa). P_{net} was markedly higher on day 172 than on day 201, especially in 1-year-old foliage. On day 172, P_{net} reached a maximum of 7.8 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ around midday. The maximum P_{net} on day 201 was only 3.5 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ and occurred in the early morning when temperature and AHD were low. For any given hour when light was not limiting (PAR > 500 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ P_{net} in 1-year-old foliage was approximately twice as high on day 172 as on day 201, even though the environmental conditions were very similar. Associated with the high rates of P_{net} on day 172 were high g_{l} and E_{t} (Figs. *4c* and *4d*). Although g_{l} was higher on day 172, strong stomatal limitations to P_{net} were suggested by the very low internal CO_2, concentration (110–120 ppm) at midday (Fig. 4e). Even current-year foliage, which was only partially developed on day 172, had somewhat higher P_{net}, g_{l}, and E_{t} than it had on day 201, when it was fully expanded. Midday XPP was much lower on day 172 (-2.00 MPa) than on day 201 (-1.68 MPa); therefore reduced P_{net} on day 201 cannot be attributed to leaf water potentials (Fig. 2*c*). Since the environmental conditions were similar on both days, the data indicate that the variation in P_{net} was due to internal controls. It is likely that a strong sink for carbon provided by the new growth produced the higher photosynthetic rates.

Response to environmental variables

The strong internal control of photosynthesis was also evident when P_{net} in growing and nongrowing periods was related to light (Fig. 5). It was apparent that the response of P_{net} to light differed between periods of high and low metabolic activity. Maximum rates of P_{net} during active growth periods were 5 to 6 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$, and saturation

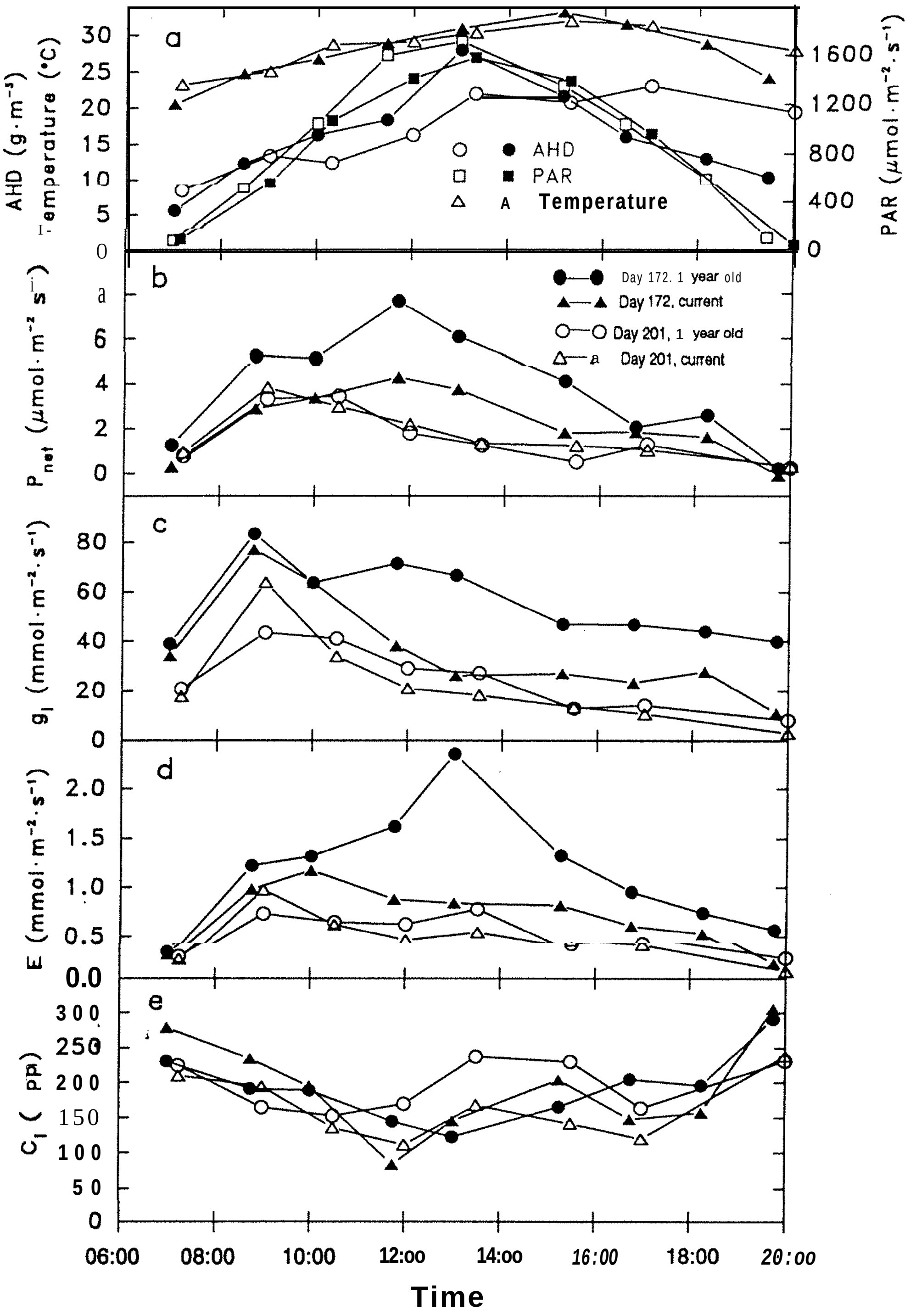

FIG. 4. Diurnal patterns of temperature, absolute humidity deficit (AHD), photosynthetically active radiation (PAR), net photosynthesis (P_{net}), leaf conductance (g_l), transpiration (E_t), and internal CO_2 concentration (C_i) on 2 days during the spring and summer of 1986. Each data point is the mean of four to six measurements (two or three per tree).

appeared to be at intensities greater than 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. During nongrowth periods maximum P_{net} was considerably lower, 3 to 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and light saturation was evident at intensities less than 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The most obvious environmental factors limiting P_{net} and g_l were light and water, but many factors simultaneously influenced gas exchange (Fig. 6). In addition, water stress significantly modified the response to other environmental factors, and decreased variability. For example, under saturating light, P_{net} showed no relation to AHD at PXPP levels greater than -1.0 MPa (Fig. 6*a*), but a good correlation existed for both foliage age-classes during periods of water stress (PXPP < -1.0 MPa) (Fig. 6*b*). This relationship is similar for g_l (Figs. 6*c* and 6d). A weak correlation existed between g_l and AHD at PXPP > -1.0 MPa, but a strong correlation could be found at lower PXPP.

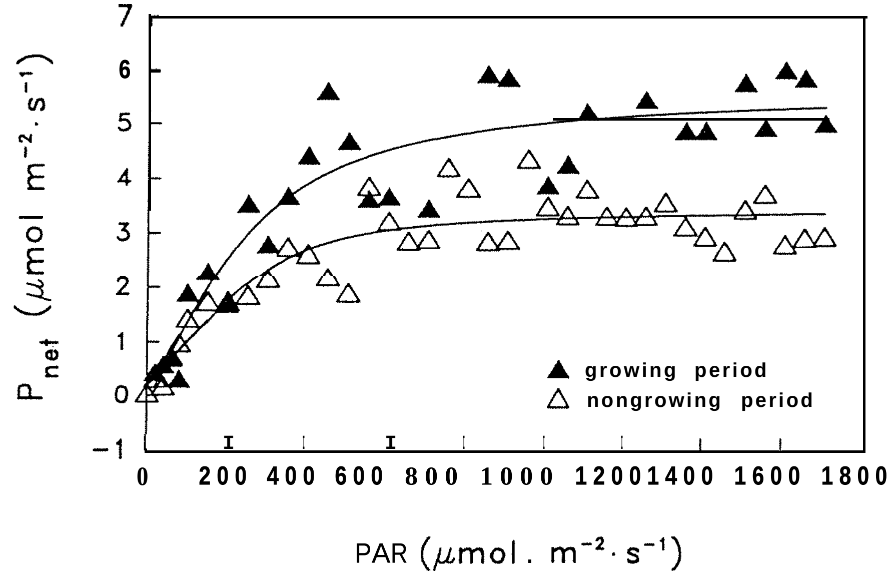

FIG. 5. The relationship between net photosynthesis (P_{net}) and light (photosynthetically active radiation, PAR) during periods of high growth activity (days 110–175) and low growth activity (days 175-290). Each point is the mean P_{net} within a PAR interval. Means were calculated in 50-μmol increments for light intensities above 100 μmol·m^{-2}·s^{-1}, and 20-μmol increments for light intensities below 100 μmol·m^{-2}·s^{-1}. Relationships were derived from combined 1986 and 1987 data sets.

Discussion

The results of this study demonstrate that the seasonal and diurnal variation in P_{net} and g_l in these white pine trees was due to both internal and external factors. The range of maximum P_{net} of 6-8 μmol·m^{-2}·s^{-1} was within the range reported for conifers (Larcher 1980) and was similar to the photosynthetic rates reported for loblolly pine (*Pinus taeda* L.) in the southeastern United States (Teskey *et al.* 1987). Light was the variable that was most highly correlated with P_{net}, although maximum P_{net} under light-saturated conditions ranged from 2.5 to 8.0 μmol·m^{-2}·s^{-1} owing to limitations from factors other than light. When foliage and branches were growing, midday P_{net} sharply increased, particularly in 1-year-old foliage. This increase was thought to be controlled by internal factors. The extent to which the maximum photosynthetic rates were controlled by internal factors at other times of the year could not be determined from these data. Seasonal variations in P_{net} and g_l were correlated with many factors whose relative importance changed as the growing season progressed. These included effects that are difficult to assess: foliage development, foliage ageing, and carbon demand, as well as the easily measured environmental factors water, temperature, AHD, and light.

White pine has a determinate growth pattern and usually has only one shoot flush per growing season. Shoot extension and needle growth in the study trees was rapid, being fully developed in 60 to 80 days, resulting in a doubling of leaf area in a span of 10 weeks. Interestingly, the developmental trend for new foliage was the same for both growing seasons despite the differences in rainfall. The white pine stands at Coweeta carry approximately 11 300 kg·ha^{-1} of foliage at the peak of development, as opposed to 6300 kg·ha^{-1} during the winter (W. Swank, personal communication). This means that developing foliage represents an extremely strong carbon sink in the spring. The rapid spring increase in P_{net} and the seasonal maximum in 1-year-old foliage coincided with the rapid growth of new foliage. When new foliage was 70 to 80% expanded, P_{net} in 1-year-old foliage began to decline and a 50% reduction occurred over a 10-day period. In early July, new and old foliage had similar rates of P_{net}, indicating that the new foliage probably was no longer a significant carbon sink. This pattern was similar in both growing seasons. McLaughlin et al. (1982) followed the fate of photosynthetically fixed ^{14}C in branches of 25-year-old white pine trees in eastern Tennessee. In June, older needles lost 80% of the initial ^{14}C photosynthate, while current-year foliage increased in activity, indicating that older needles were exporting photosynthate to these active sinks. However, by August both age-classes were sources of photosynthate and were exporting ^{14}C at similar rates. Increases in photosynthetic activity in older foliage during early spring growth have been reported in other mature conifers (*Picea sitchensis* (Bong.) Carr., Ludlow and Jarvis 1971; *Tsuga heterophylla* (Raf.) Sarg. and *Abies grandis* (Dougl.) Lindl., Fry and Phillips 1977; *Picea abies* (L.) Karst., Fuch et al. 1977; *Abies amabilis* (Dougl.) Forbes, Teskey *et al.* 1984).

These results suggest that growth has a major impact on the photosynthetic capacity of existing foliage. Young expanding needles are heterotrophic and are dependent upon carbohydrates imported from other parts of the tree, primarily older, mature foliage (Turgeon 1989). Even though the developing white pine foliage had positive P_{net} when it was partly expanded, this should not be interpreted to mean that it was self sufficient, because the rates of dark respiration of developing foliage are extremely high (Teskey et al. 1984). Developing foliage, fruit, and reproductive structures are strong carbon sinks and can affect the photosynthetic capacity of source foliage (Woodward and Rawson 1976; Jarvis and Leverenz 1983). If these carbon sinks are suddenly removed, photosynthesis is sometimes inhibited (Gifford and Evans 1981). Removal of developing foliage in *Pinus resinosa* Ait. shoots significantly reduced the rate of photosynthesis in

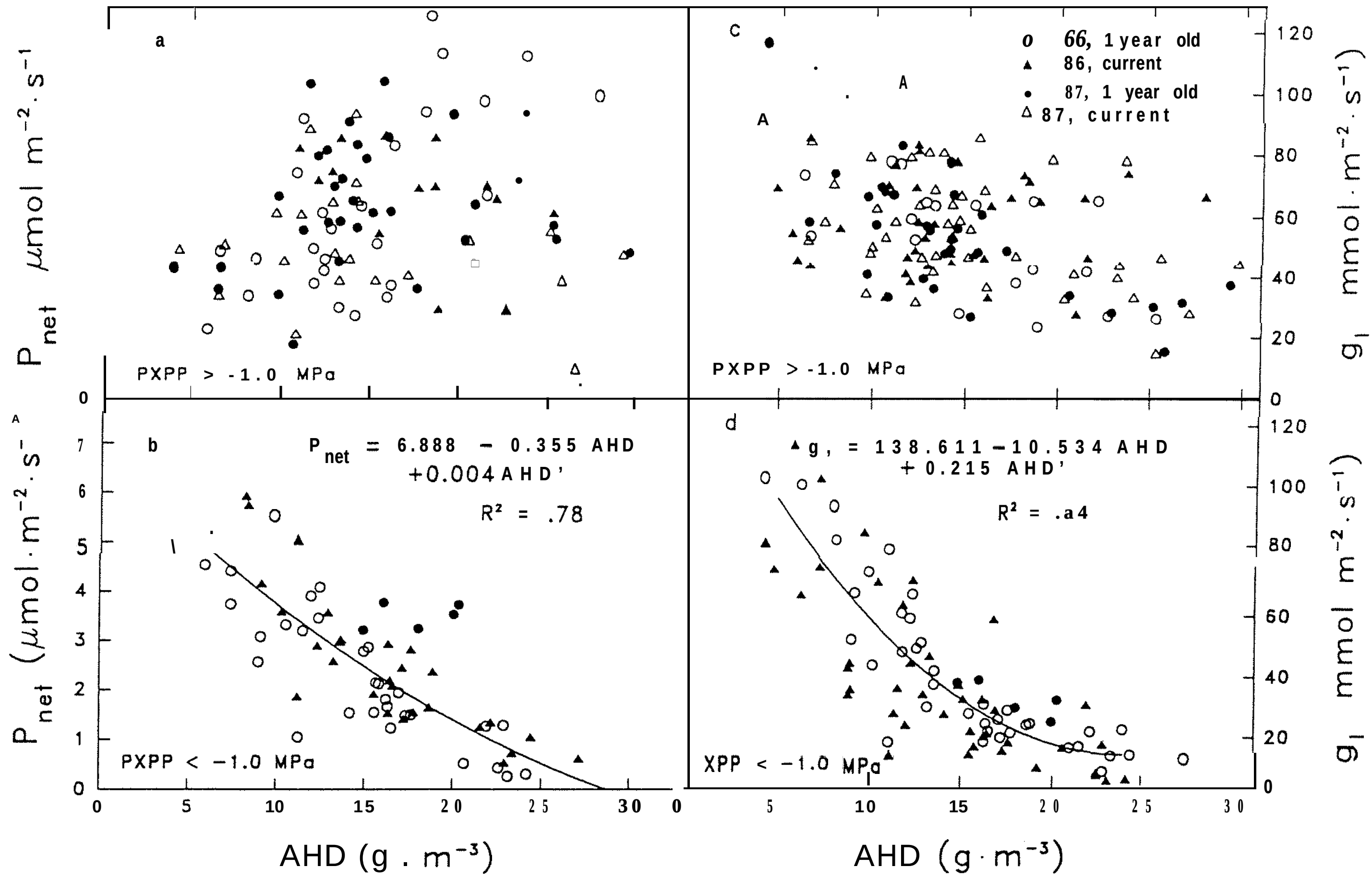

FIG. 6. Response of net photosynthesis (P_{net}) and leaf conductance (g_l) to absolute humidity deficit (AHD) when predawn xylem pressure potential (PXPP) > -1.0 MPa and when PXPP < -1.0 MPa. In all cases PAR > 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

1-year-old foliage (Gordon and Larson 1968). In this study, the rapid decline in P_{net} in late ‘June in 1-year-old foliage suggested a sudden change in carbohydrate sink-source relationships. Turgeon (1989) concluded that the transition of developing leaves from a sink for carbohydrates to a source was due to changes in leaf carbon balance and to a maturing vascular system. Starch accumulation as a result of reduced sink activity during this transition period probably regulates source photosynthesis through feedback inhibition (Thome and Koller 1974; Acock and Allen 1985), although the mechanisms of feedback inhibition that control P_{net} in existing foliage are not well understood. Accumulation of starch in chloroplasts may also explain the reduction in light-saturated P_{net}. Thome and Koller (1974) suggested that large starch granules in chloroplasts may disrupt grana and shade the lamella, reducing P_{net}. A better understanding of nonenvironmental limitations to photosynthetic capacity is needed to improve our understanding of how photosynthesis is regulated in trees.

Although it is often difficult, and sometimes inappropriate, to ascribe specific changes in rates of gas exchange to individual influences, clearly the drought during the summer of 1986 had a significant and overriding impact on gas exchange. Midday P_{net} ranged from 10 to 75% below those measured in 1987 during the same period. Both soil water availability (PXPP) and AHD affected g_l and P_{net} during the drought period. When soil moisture was low (PXPP < -1.0 MPa), P_{net} and g_l were strongly reduced at high AHD, but when there was adequate moisture, AHD appeared to have little effect on gas exchange. This indicates that the stomata were not responding directly to AHD, but that the higher rates of transpiration under high AHD were inducing water stress in the leaf when soil water was limited (Sharkey 1984). The sensitivity of tree species to AHD on gas exchange appears to be quite variable. Some conifers show little response to AHD regardless of soil moisture levels (P. *taeda*, Teskey *et* al. 1987), while others have a strong response (*Pinus contorta* Dougl., Running 1980; *Pinus radiata* D. Don, Benecke 1980). Eastern white pine appears to be intermediate, showing little response when soil moisture is adequate but a strong response in water-limited conditions.

In conclusion, environmental factors were responsible for the large variation in gas exchange seen between years, but internal factors had a strong influence on the seasonal pattern of P_{net} within a growing season. Photosynthetic capacity of 1-year-old foliage in the spring appeared to be primarily controlled by assimilate demand in growing tissues. This “sink-strength” effect appears to be of importance, and should be accounted for when attempting to isolate controlling influences on photosynthesis.

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