TRANSPIRATIONAL RELATIONSHIPS OF TULIP POPLAR[1]

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ABSTRACT

Leaf xylem water potential, stomatal diffusion resistance, and calculated transpiration of a mature *in situ* tulip poplar (*Liriodendron tulipifera* L.) canopy were examined and related to naturally occurring variations of the surrounding forest environment to determine their relative importance in affecting calculated transpiration rates. Data were collected at three crown levels during July and August. Transpiration values decreased from $32.0 \pm 15.3 \times 10^{-5}$ g cm^{-2} min^{-1} in the upper crown to $5.5 \pm 4.2 \times 10^{-5}$ g cm^{-2} min^{-1} in the lower crown in response to gradients in vapor pressure deficit, wind speed, and the difference between leaf and air temperature. Leaf water loss and resulting water deficits were not limited by stomatal control during the day. Stomatal diffusion resistance was controlled mainly by light intensity and did not increase as leaf xylem water potentials approached -22 bars. Transpiration rates were closely related to energy input and were influenced by morning dew deposition on leaves. These data indicate tulip poplar is a species in which photosynthesis proceeds at the expense of large transpirational losses and associated tissue water deficits.

[1]Research supported by the Eastern Deciduous Forest Biome, US/IBP, funded by the National Science Foundation under Interagency Agreement AG-199, DEB76-00761 with the U.S. Department of Energy under contract W-7405-eng-26 with Union Carbide Corporation, Oak Ridge National Laboratory. Publication No. 1253, Environmental Sciences Division, ORNL.

INTRODUCTION

Tulip poplar (Liriodendron tulipifera L.) is an important second growth species in eastern deciduous forests with a fast growth rate that is maximized on mesic sites. Maximum growth of forest trees normally requires a rapid uptake of atmospheric carbon dioxide with concomitant high rates of transpirational water loss. Resulting tissue water deficits may affect sensitive cellular growth processes (Hsaio 1973). Therefore, the balance of water and carbon dioxide exchange by leaves is crucial to maintenance of growth processes. This study examines the relationships between selected physiological parameters of *in situ* tulip poplar foliage and the environment. Calculated transpiration rates are compared with stomatal resistances, leaf water potentials, and various environmental parameters to elucidate factors influencing transpiration water losses.

METHODS

Study Site

The study area is in the Cesium 137 Forest Research Area, Oak Ridge National Laboratory, Oak Ridge, Tennessee. The forest is a second growth, bottomland, mesic hardwood stand dominated by tulip poplar (76% of the above ground biomass) (Sollins, et al. 1976). It is located in a karst depression in which an alluvial silt loam of the Emory series overlies dolomite bedrock. High humidity and dew deposition in early morning with dew evaporation from leaf surfaces completed by late morning is typical at this site. The site is described in detail by Sollins et al. (1976).

A co-dominant tulip poplar (DBH 24.6 cm, height 25.5 m, age 53) was selected for this study. A 30.5 meter walk-up tower next to the tree provided access to the eastern half of the tree crown.

Sample Procedure

Data were collected on seven days in the period July 9 to August 27, 1973 at three crown levels (top, middle, and bottom).

Individual measurements were made on leaves *in situ*. Data recorded for each leaf included: (1) time of day (eastern daylight saving time), (2) height of leaf above the ground, (3) relative humidity, (4) air temperature, (5) leaf temperature, (6) light intensity, (7) leaf xylem water potential, (8) leaf diffusion resistance, (9) leaf dimensions, and (10) wind speed.

Air temperature (^{o}C) and relative humidity were measured using a Bendix Psychron ventilated wet-dry bulb psychrometer equipped with mercury thermometers. The instrument was shaded and held at the same height as the leaves being sampled.

Leaf temperature (^{o}C) was measured using a 0.2 mm copper-constantan thermocouple held in contact with the lower leaf surface by a spring clip (Gale et al. 1970). Once in place, temperature measurement required less than 30 seconds. Between measurements, the sensor was shaded to prevent heating. Thermocouple output was measured with a Wescor Model MJ-55 Psychrometric Microvoltimeter.

A Weston Illumination Meter was used to measure illuminance. The meter was oriented with and held next to the leaf during measurements. Foot candle values obtained were divided by 7000 to estimate the solar radiation flux density in cal cm^{-2} min^{-1} (Reifsnyder and Lull 1965). Solar radiation flux density estimated in this way had a correlation coefficient of 0.99 with values measured by a Kipp and Zonen solarimeter (0.3 to 3.0 μ wave-lengths) (McConathy et al. 1976).

Stomatal diffusion resistance (sec cm^{-1}) was measured on the underside of leaves using a Lambda Diffusion Resistance Meter and Diffusion Resistance Porometer (Kanemasu et al. 1969, Lambda 1971).

Leaf diemensions were measured along the midvein (length) and at right angles to the midvein to the side lobe tips (width). Leaf area was estimated from the product of length and width using regression analysis (McConathy et al. 1976).

Wind speed (cm sec^{-1}) was measured with a cup anemometer installed at the top of the 30.5 meter tower. The anemometer was about 3 meters above the mean canopy height. Mean wind

speed was determined for each sampling period; thus, short-term variations are not reflected in this value. The wind speed profile through the plant canopy was calculated from wind speed at the top of the canopy and an extinction coefficient using the equation (Murphy and Knoerr 1972):

$$V = V_t \exp [k_2 (H_t - H)] \tag{1}$$

where V is the wind speed at height H in cm sec^{-1}, V_t is the wind speed above the canopy (cm sec^{-1}) at height H_t (3048 cm), k_2 is the extinction coefficient for wind speed [equal to 0.0017 (Shinn 1969)], and H is the height (cm) for which V is determined.

A Scholander-type pressure bomb was used to measure leaf xylem water potential (-bars) (Scholander et al. 1965). After all other measurements were completed xylem water potential was determined on each leaf within two minutes of excision. In this study, leaf xylem water potential becoming more negative is defined as "decreasing" and when becoming more positive is defined as "increasing" water potential.

Transpiration Calculations

Transpiration was calculated from measured parameters using the equation of Gates (1965):

$$E = \frac{SVD_1 - RH\ (SVD_a)}{R} \tag{2}$$

where E is the transpiration rate in g cm^{-2} min^{-1}, RH is the relative humidity of air, SVD_a is the saturated water vapor density of free air at air temperature (T_a) in g cm^{-3}, SVD_1 is the saturated water vapor density of air in the substomatal cavity at leaf temperature (T_1) in g cm^{-3} (relative humidity of the substomatal cavity is assumed to be 1.00), and R is the total resistance of the diffusion pathway in min cm^{-1}. R is composed of mesophyll, stomatal, and boundary layer resistances.

Richardson, Dinger, and Harris (1973) found mesophyll resistance in tulip poplar a relatively constant, small fraction of total resistance; therefore, for use in Equation 2 R was considered to be the sum of stomatal (r_s) and boundary layer (r_a) resistances. Stomatal diffusion resistance was easily measured using a sensitive hygrometer, the Lambda diffusion resistance porometer, that was attached to the in situ leaf. The formulation of boundary layer resistance used for calculating tulip poplar transpiration rates (Gates 1968) is:

$$r_a = k_1 \, (D^{0.35} \, W^{0.20} / V^{0.55}) \qquad (3)$$

where r_a is the boundary layer resistance in min cm^{-1}, k_1 is the leaf dimensional coefficient equal to 0.042 (Gates 1968), D is the leaf dimension in the direction of the wind in cm, W is the leaf dimension at right angles to wind direction in cm, and V is the wind speed in cm sec^{-1} (calculated using Equation 1).

The values for saturation water vapor density were calculated using an equation derived from statements of Shaw (1930) presented by Idle (1970).

$$SVD = 217/{}^{\circ}K \times \exp\,[(5427 \times (0.00366 - 1/{}^{\circ}K)) + 1.809]/1 \times 10^{6} \qquad (4)$$

where SVD is the saturated water vapor density in g cm^{-3}, and °K is the temperature of air or leaf in °K. The equation gives exact values of SVD at 20°C, a 1% negative error at 0°C, and a 5.3% positive error at 50°C (Idle 1970). The range of air and leaf temperature encountered in tulip poplar stands allows use of this equation with a small error.

Total radiation absorbed by a tulip poplar leaf was calculated using the formula of Gates (1968). Further discussion of the use of the formula and its terms can be found in Gates (1962), Gates (1965), Gates and Tantraporn (1952), Geiger (1965), Idle (1970), McConathy et al. 1976, and Reifsnyder and Lull (1965).

Previous attempts to correlate physiological parameters with particular environmental variables in the field have not been entirely successful because physiological parameters are simultaneously affected by more than one environmental variable (Jarvis 1976). Some parameters may show a diurnal hysteresis when correlated, leading to increased scatter in the plotted data.

In this study 167 complete leaf-environment measurements were collected. The lack of independence of some of the variables measured did not permit the use of multiple regression analysis procedures to isolate influences of individual parameters. Thus, linear regression equations are presented only to indicate the general trends of the data while the corresponding regression coefficients (r^2) indicate dispersion of data about the regression line.

RESULTS AND DISCUSSION

Calculated transpiration rates (equation 2) during the study ranged from 1.7 to 67.7 x 10^{-5} g cm^{-2} min^{-1} with the mean equal to 20 ± 16 x 10^{-5} g cm^{-2} min^{-1}. This compares favorably with published daily average values for tulip poplar ranging from 16 to 20 x 10^{-5} g cm^{-2} min^{-1} (Kramer and Kozlowski 1960). These tulip poplar transpiration rates are equivalent to or slightly higher than those for red oak (13 g cm^{-2} min^{-1} x 10^{-5}), buckeye (12 g cm^{-2} min^{-1} x 10^{-5}), and boxelder (10 g cm^{-2} min^{-1} x 10^{-5}) reported by Salisbury and Ross (1969). Thus, tulip poplar appears to have a rather high transpiration rate compared to these species.

Studies have shown correlations between transpiration and the environmental variables, leaf temperature, vapor pressure deficit (VPD), and light intensity (Kramer and Kozlowski 1960, Lange et al. 1971). Plant variables, such as stomatal resistance and water stress, have also been correlated with transpiration (Jarvis 1976, Meidner and Mansfield 1968).

Environmental Variables

Air and leaf temperature affected transpiration rate through the establishment of vapor-pressure gradients between the leaf and atmosphere. During this study, VPD values were significantly correlated with leaf temperature (TLEAF):

$$TLEAF = 22.21 + 0.58\ (VPD)$$

$$r^2 = 0.74 \qquad (5)$$

where TLEAF is in °C and VPD is in millibars. As air temperature increased, the difference between leaf and air temperature (TDIFF) increased (Figure 1). Air and leaf temperatures were greatest in the afternoon in the upper crown, the time and crown position where insolation was greatest. In the upper crown TDIFF increased with increasing air temperature. Lower crown leaves were shaded and TDIFF decreased with increasing air temperature, possibly in response to increased transpiration and convective cooling during the warmest period of the day. As air temperature increased above 22°C, the difference between leaf temperature in the upper and lower crown increased. This resulted in higher VPD's in the upper crown.

The linearity of a relationship between two variables over their naturally fluctuating range measures the degree of control one variable has over another. Of all the variables we examined, transpiration rate was most linearly related to VPD (over the range 0 to 24 millibars):

$$E = 0.000021\ (VPD) - 0.000016$$

$$r^2 = 0.48 \qquad (6)$$

where E is in g cm^{-2} min^{-1} and VPD is in millibars. Any nonlinearity in this relationship would be due to changes in plant resistances to transpiration (O'Leary 1975) or temporal changes in other controlling variables.

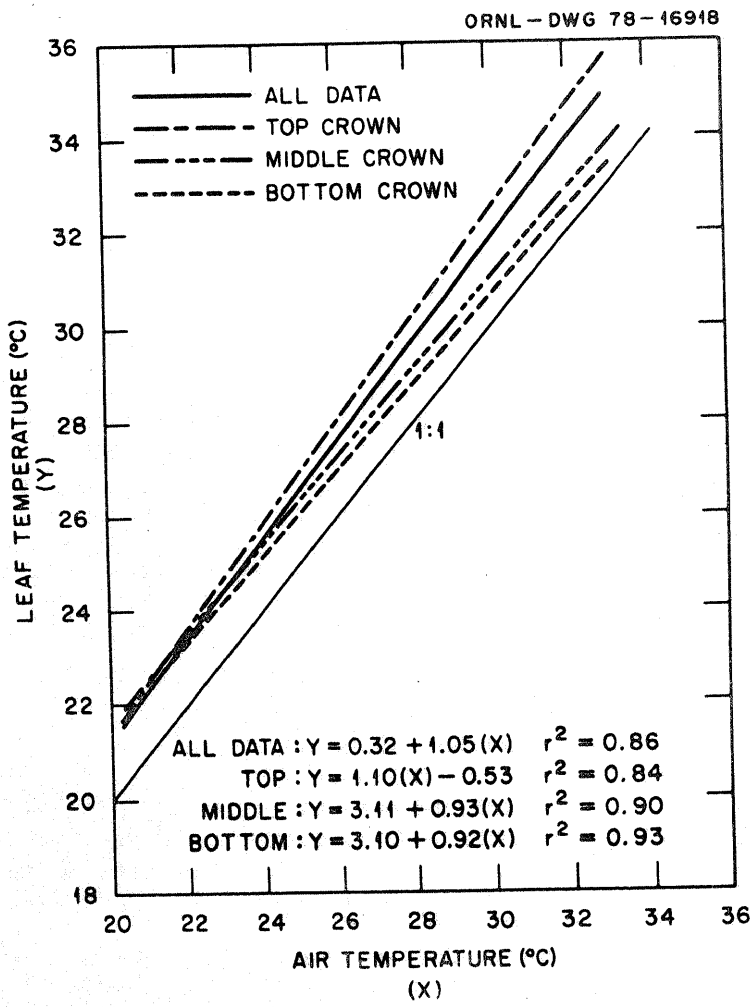

Figure 1. The relationship between air temperature and leaf temperature for tulip poplar leaves at three crown levels.

The relationship between total radiation absorbed by the leaf and TDIFF was slightly non-linear with TDIFF (± SD) values of 0.9 ± 0.9°C and 3.8 ± 1.8°C associated with values of 0.55 and 1.05 cal cm^{-2} min^{-1} total radiation absorbed, respectively. Between 1.05 cal cm^{-2} min^{-1} and a full sunlight value of 1.2 cal cm^{-2} min^{-1}, TDIFF (± SD) values increased nonlinearly to 5.8 ± 1.2°C. The increase in TDIFF with higher radiation input increased the vapor-pressure gradients driving transpiration.

Plant Variables

Hinckley et al. (1978b) reported stomata react strongly to temporal radiation patterns, apparently a universal pattern in forest trees, with minimum leaf resistance reached at radiation levels exceeding 10% of full sunlight (e.g., about 0.15 cal cm^{-2} min^{-1}). In tulip poplar the minimum radiant flux density that initiated stomatal opening (r_s = 4.0 sec cm^{-1}) was about 0.04 cal cm^{-2} min^{-1}. Diffusion resistance reached a minimum ($r_s \approx 1.0$ sec cm^{-1}) at about 0.6 cal cm^{-2} min^{-1} and did not decrease significantly at higher radiation flux densities. These light values correspond to those found by Shimshi (unpublished) where photosynthesis increased rapidly below 4.0 sec cm^{-1} diffusion resistance (stomatal opening) and peaked at light levels of 0.7 cal cm^{-2} min^{-1} (minimum diffusion resistance). Other plant species may attain a minimum diffusion resistance at lower radiation flux densities (e.g., 0.15 to 0.3 cal cm^{-2} min^{-1}) (Hinckley et al. 1978, Slatyer and Bierhuizen 1964) than tulip poplar. Thus, the high light threshold for maximum stomatal opening is a partial explanation for the shade intolerance of tulip poplar.

Leaf xylem potential values decreased as stomatal resistance decreased and transpiration increased. A rapid drop in xylem potential occurred at a stomatal resistance of 3.5 sec cm^{-1}, the point where stomata opened in response to increasing radiation. Thus, the point at which transpiration losses exceeded water uptake was reflected in a decreasing leaf xylem potential. Decreases in leaf xylem potential values from -3 to -18 bars did not cause stomatal closure, i.e., increased stomatal resistance. A few observations with xylem potentials above -22 bars, however, indicated a possible reduction in transpiration rates.

Threshold xylem potential values causing stomatal closure in trees have been found over a range from -15 to -24.5 bars (Hinckley et al. 1978a, Federer 1977). This threshold value is influenced by the growing environment and stage of maturity and growth (Hinckley et al. 1978b, Sullivan 1974, Watts 1977). Higher threshold water potentials have been found in Douglas fir seedlings and greenhouse grown trees (-16 bars) than in forest trees (-22 bars) of the same species (Waring and Running 1978). Hinckley et al. (1978b) and Hsiao (1973) report similar findings for other species. Richardson et al. (1973) found the stomatal closing threshold for tulip poplar seedling was -18 bars. Seedlings in their study were allowed to experience cumulative increases in water stress, i.e., morning xylem potentials of -15 bars. The absence of a cumulative water stress in our study tree may explain the apparent stomatal closure at a lower potential of around -22 bars. This tree occupied a moist site that rarely developed soil water potentials below -5 bars. Leaves routinely exhibited early morning leaf xylem potentials between -4 and -7 bars indicating almost complete recovery from daily moisture deficits.

Tulip poplar has been shown to exhibit a seasonal osmotic adjustment of -1.7 bars thereby maintaining favorable cell water relations for stomatal opening and cell growth (Federer and Gee 1976, Roberts 1977). In the forest, tulip poplar is able to maintain internal water potentials below threshold values for stomatal closure, thus maintaining photosynthesis at a high rate.

Crown Height Variations

Vertical changes in stomatal diffusion resistance, leaf xylem potential, and transpiration rate are shown on Figure 2. The crown was sampled as three zones (top, middle, bottom) based on leaf morphology and exposure. Fully exposed upper crown leaves were the smallest leaves on the tree and, in addition, were more vertically oriented than other leaves. This leaf orientation suggested the possibility of a photomorphogenetic response. Phototropism has been observed in tulip poplar, but the small angular change noted was not associated with any diurnal pattern nor was it synchronized among leaves (Hutchison, personal communication). The vertical leaf orientation is

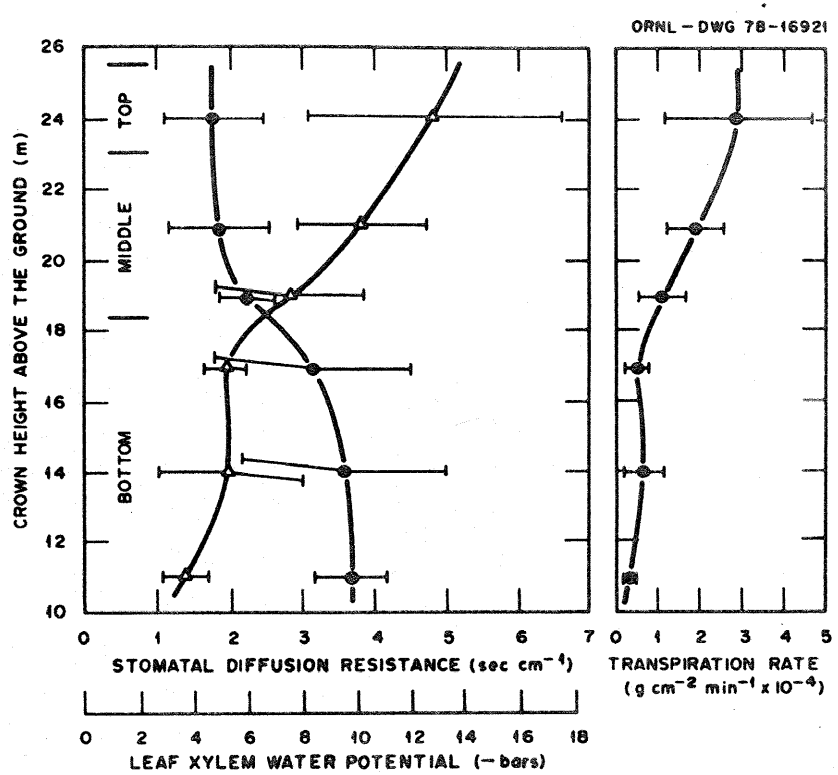

Figure 2. Tulip poplar stomatal diffusion resistance (●), leaf xylem water potential (△), and transpiration rate variations (± 1 SD) with height above the ground.

probably a mechanism that reduces the leaf angle to incoming solar radiation, thus minimizing heat build-up and admitting light to the lower canopy that is usually under less stress (Horn 1971). This would then increase photosynthesis in the lower layers. Middle zone leaves were slightly larger than top zone leaves and experienced more shading than the fully exposed upper crown leaves. Crown closure with adjacent trees occurred at about 18 to 19 meters (8 meters below the crown tip). The bottom zone was almost in complete shade, below the level of canopy closure and large shade leaves predominated.

Leaves in the top and middle zone had about the same stomatal diffusion resistance values (Figure 2). Diffusion resistance began to change at the height of crown closure with neighboring tree crowns. This supports the hypothesis that tulip poplar stomata react strongly to light and remain open above a threshold intensity. Woods and Turner (1971) have reported a gradual stomatal closing in tulip poplar as light decreases, with rapid closure beginning at around 0.14 cal cm^{-2} min^{-1} on the adaxial surface. Hutchison (1977) reported rapid light extinction through the zone of crown closure from 450 to 250 ly day^{-1}, or close to 50%. Thus, rapidly increasing stomatal resistances at around 18 meters resulted from a 50%, or greater, decrease in light intensity through the zone of crown closure. High resistance values in the lower crown probably resulted from low light levels, increased humidity, and a greater sensitivity to water loss than in sunleaves (Hall 1975, Kozlowski 1976, Zobel 1978).

The mean stomatal resistance in the lower crown was 3.75 sec cm^{-1}, very near the 4.0 sec cm^{-1} value associated with the CO_2 compensation point for tulip poplar. Hutchison (1977) estimated lower crown light levels to be about 0.16 cal cm^{-2} min^{-1}, or near the light level reported by Woods and Turner (1971) where rapid stomatal closure begins. This suggests that leaves at the base of the crown may be photosynthesizing near their compensation point and thus, may be parasitic on the upper crown at times of low light intensity.

Leaf xylem water potential rapidly decreased with height in the upper two zones (Figure 2). Potentials were uniform in the bottom crown. Xylem potentials in the top and middle zones

followed transpiration indicating that the water supply to upper leaves was unable to replace water losses. Diffusion resistance values were unaffected even though there was a decrease in xylem potential from -6 to -13 bars in the upper two zones. This indicated that at this site normal water potentials did not cause stomatal closure in the upper crown and therefore stomata did not control transpiration. This agrees with other results that show stomatal control of transpiration occurs in the morning and evening when stomata are opening and closing, but during the day when stomata remain open VPD determines transpiration rates (Kozlowski 1976, Landsberg 1975, Watts 1977). Good correlation between water potential and VPD has been reported, with the relationship usually forming a hysteresis loop when plotted by time of day (Hinckley 1974, Jarvis 1976, Landsberg 1975). The water potential versus VPD hysteresis relationship observed during this study agrees with those reported by Jarvis (1976) who attributed the hysteresis effect to diurnal changes in VPD lagging behind changes in available energy input.

Diurnal Variations

Generalized observations can be made about diurnal trends in the data. Diurnal trends were driven by the total radiation absorbed by the leaves with peak radiation occurring at solar noon (around 1:00 PM EDT). Leaf temperature closely followed solar radiation values as TDIFF values increased with increasing leaf temperature thereby increasing the moisture gradient between the leaf and atmosphere. VPD increased with a slight lag behind solar radiation input and, combined with larger TDIFF, resulted in maximum transpiration in the period around solar noon.

Other factors also influenced these diurnal cycles. The study tree was located in a valley where direct sun did not strike the upper crown until midmorning, around 9:30 to 10:00 AM. Heavy dew was common on leaves in the morning. Dew evaporation would tend to form a sink for heat absorbed early in the morning. This could explain the gradual changes in variables during the early morning. In the early afternoon the eastern portion of the tree where sampling was done became shaded. This

resulted in the steep decline of environmental and plant values after solar noon.

Diurnal trends are represented by the means for morning (0900 to 1200 hrs.) and afternoon (1330 to 1600 hrs.) data in Table 1. These data represent all the data collected and statistically there appear to be significant changes due to "date," thus the standard deviations may be inflated by this effect. Also, the response of some variables to crown position does not appear to be the same with date, indicating an interaction between data and crown position.

Temperature values between AM and PM showed a general increase throughout the crown. TDIFF values showed an increase from AM to PM in the upper crown only, with no change in the middle crown and a decrease in the lower crown. These results indicate the effect of direct solar heating in the upper crown and the relatively constant sun and shade conditions in the middle canopy. Increased transpiration rates and wind speeds in the lower canopy reduced TDIFF through increased evaporative and convective heat loss. VPD showed a large percentage change from AM to PM and maintained a gradient that decreased with height down through the crown. Solar radiation showed a similar trend.

Transpiration rates increased from AM to PM with the percent increase in the upper and lower crown being the same. The PM stomatal resistance increased slightly in the upper and middle crown and, while not significant, may have been a response to decreased water potentials. These results are similar to those of Landsberg (1975) who found that little change in stomatal resistance occurred from 11:30 till 4:00. Lower crown stomatal resistance decreased from an AM value close to 3.75 sec cm^{-1}, an apparent threshold value for physiological functioning, to a lower PM resistance that resulted in increased transpiration. Change in stomatal resistance with height was probably a response to changing light values (Pereira and Kozlowski 1974, Turner 1969, Watts 1977) with stomatal opening occurring last in the lower crown. This was reflected in the large percentage decrease in PM water potential in the lower crown that resulted from increased transpirational water loss.

Table 1. Environmental and plant variable means (± SD) by crown position during two periods of the day (AM = 0900 to 1200 and PM = 1330 to 1600)

Variable	Crown* zone	AM	PM	Percent† change
Time of day (hr)		1014 ± 56	1455 ± 48	
Air temperature (°C)	T	24.3 ± 1.6	29.1 ± 2.0	19.8
	M	24.1 ± 2.0	28.5 ± 2.4	18.3
	B	23.1 ± 2.6	27.5 ± 2.7	19.0
Leaf temperature (°C)	T	26.0 ± 1.7	31.3 ± 2.6	20.4
	M	25.2 ± 1.7	29.7 ± 2.4	17.9
	B	24.3 ± 2.4	28.3 ± 2.7	16.5
TDIFF (°C)	T	1.7 ± 1.0	2.2 ± 1.5	29.4
	M	1.1 ± 0.8	1.1 ± 1.1	0.0
	B	1.2 ± 1.0	0.8 ± 0.8	-50.0
Calculated wind speed (cm sec^{-1})	T	58.5 ± 6.3	48.7 ± 29.6	-20.1
	M	24.0 ± 1.7	19.8 ± 17.1	-21.2
	B	6.5 ± 4.1	10.8 ± 9.7	66.2
Radiation input (cal cm^{-2} min^{-1})	T	0.75 ± 0.05	0.89 ± 0.13	18.7
	M	0.69 ± 0.03	0.77 ± 0.07	11.6
	B	0.65 ± 0.04	0.71 ± 0.07	9.2
Vapor pressure deficit (millibars)	T	6.4 ± 2.8	14.9 ± 2.9	132.6
	M	6.3 ± 3.4	13.4 ± 4.2	114.4
	B	5.3 ± 3.3	10.2 ± 5.1	92.5
Transpiration rate (g cm^{-2} min^{-1} x 10^{-4})	T	1.67 ± 0.68	3.20 ± 1.53	91.6
	M	1.06 ± 0.40	1.69 ± 0.83	59.4
	B	0.55 ± 0.42	1.06 ± 0.74	92.7
Stomatal resistance (sec cm^{-1})	T	1.73 ± 0.57	1.97 ± 0.76	13.9
	M	1.93 ± 0.52	2.22 ± 0.55	15.0
	B	3.44 ± 1.23	2.77 ± 1.13	-24.2
Xylem water potential (-bars)	T	8.58 ± 2.61	13.27 ± 2.37	54.7
	M	6.88 ± 2.37	9.93 ± 2.68	44.3
	B	4.36 ± 1.87	7.43 ± 3.02	70.4

*T = top; M = middle; B = bottom.

†Positive = increase from AM to PM; negative = decrease from AM to PM.

The tulip poplar canopy microclimate is essentially "light dependent." Changes in temperature, relative humidity, and ambient CO_2 occur in direct proportions to fluctuation in radiant flux density (Burgess and O'Neill 1975). Stomata open in response to increasing light levels. VPD increases as a result of temperature rises induced by solar heating. This promotes increased transpiration resulting in water potential deficits in transpiring leaves. Temporal water potential values during the study were not of sufficient magnitude to cause stomatal closure.

These interpretations agree with those drawn from studies with other species, where water potentials and transpiration rates responded primarily to changing VPD, temperature, and solar radiation values (Federer and Gee 1976, Jarvis 1976, Llepper 1968, Landsberg 1975, Pereira and Kozlowski 1977). Jarvis (1976) found linear regressions of air temperature, VPD, and light in combination accounted for 70 to 95% of water potential variations over short-time intervals. Stomata have been shown to respond primarily to light with little change above threshold values, and to exhibit responses to environmental conditions which vary with crown positions (Keller and Tregunna 1976, Kozlowski 1972, Landsberg 1975, Pereira and Kozlowski 1974, Watts 1977, Woods and Turner 1971).

CONCLUSIONS

This study describes responses of tulip poplar foliage to spatial and temporal variations of canopy environmental variables. The data indicate that tulip poplar tolerates high moisture stress with a high threshold for stomatal closure and with overnight recovery from daily water losses. Transpiration in the upper and middle crown is most closely related to VPD values, which is the controlling variable during the midday period when stomatal resistance is minimum. Stomata only control transpiration during opening and closing in the early morning and late afternoon. A comparatively high light intensity required for minimum diffusion resistance relates to the shade intolerance of tulip poplar. Changes in leaf xylem water potential follow the temporal trend of transpiration, reflecting water losses in excess of leaf water supply.

Stomatal diffusion resistance in the lower crown is higher than in the upper crown in response to light attenuation below the level of crown closure. Early-to-mid morning and mid-to-late afternoon diffusion resistance values in the lower crown approach a value corresponding to the carbon dioxide compensation point. This implies that photosynthetic production in the lower crown at these times may just be sufficient to provide for its own maintenance.

Early successional species, such as tulip poplar, enhance photosynthesis and growth by keeping stomata open longer than later successional species under conditions of decreasing water potential (Phelps et al. 1977). Data from this study indicate that tulip poplar follows a behavior pattern in which open stomata maximize photosynthesis at the expense of large transpirational losses and resulting tissue water deficits. Thus, the poor performance of yellow poplar on drier sites may be a function of high transpirational losses leading to tissue moisture deficits that limit growth.

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