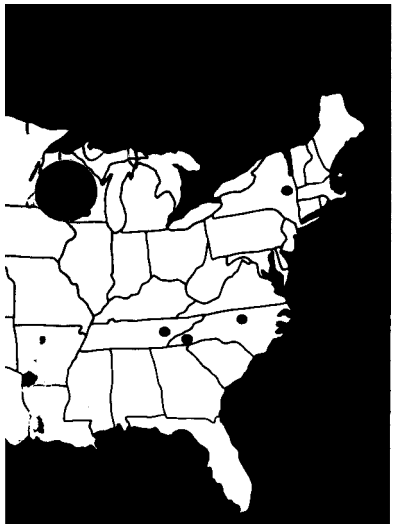

Eastern Deciduous Forest Biome

Analysis of Ecosystems

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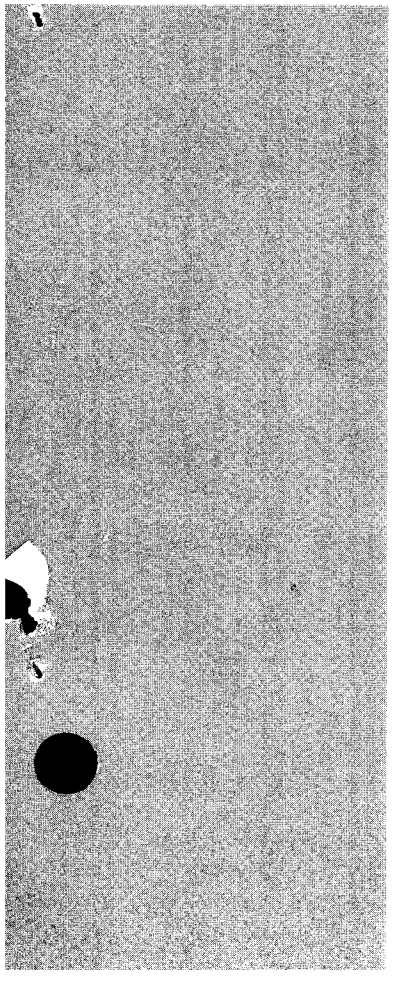
LEAF ENERGY BALANCE and TRANSPIRATIONAL RELATIONSHIPS of TULIP POPLAR (Liriodendron Tulipifera)

R. K. McConathy - S. B. McLaughlin - D. E. Reichle - B. E. Dinger

Environmental Sciences Division Publication No. 918



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R. K. McConathy, S. B. McLaughlin, D. E. Reichle
and B. E. Dinger

Environmental Sciences Division
Publication No. 918

Submitted as a dissertation by R. K. McConathy to the Graduate Council of The University of Tennessee in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

McCONATHY, R. K., S. B. McLAUGHLIN, Jr., D. E. REICHLE, and B. E. DINGER. 1976. Leaf energy balance and transpirational relationships of tulip poplar (Liriodendron tulipifera). EDFB/IBP-76/6. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 118 pp.

Relationships between several physiological parameters of in situ tulip poplar (Liriodendron tulipifera L.) foliage, and its surrounding forest environment were examined, with emphasis on the transpirational process. Objectives were to (1) measure and compare stomatal relationships with environmental and plant morphological variables, (2) determine and assess the relative importance of factors affecting transpiration and leaf energy balance of a mature tulip poplar, (3) examine and describe the diurnal kinetics of transpiration and leaf energy balance under forest conditions, and (4) examine and develop equations describing these processes and relationships.

Tulip poplar leaves were examined at three crown heights. Stomatal distribution, density, and dimensions were measured, then these data were used to predict leaf diffusion layer resistance. Stomatal dimensions decreased with crown height while stomatal density increased, but neither varied over individual leaf surfaces. Numbers of stomata per leaf were constant throughout the crown.

Calculated transpiration rates were compared with stomatal diffusion resistance, leaf xylem water potential, and environmental parameters. Calculated transpiration rate was not limited by water potentials less negative than -22 bars, and increased with decreasing stomatal diffusion resistance. Stomatal diffusion resistance was mainly controlled by light intensity and was not increased by high levels of measured water potential. Transpirational water loss, and resulting water deficits, were not under stomatal control during the study. Diurnal leaf heat loss, water stress, and stomatal resistance measurements followed the diurnal variation of the radiation absorbed by the leaf. Heat loss by radiation, evaporation, and convection varied with crown height in response to variations in stomatal diffusion resistance, transpiration, vapor pressure deficit, leaf temperature, and wind speed.

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INTRODUCTION

Energy exchange between the plant and its environment is a primary feature of the ecological dynamics of plant communities. Solar radiation is the energy source of the ecosystem and is partitioned into short-wave and long-wave radiation inputs. Absorption of radiant energy by the forest and the flow of heat energy through the forest provides the "driving force" for chemical and physical processes responsible for growth and life itself. In a mesic forest almost all net radiation energy is used in the evaporation process (Rutter, 1968). As a result, energy flow in the forest is coupled to the water relations of forest trees through the transpirational process. A tree's capacity to control the transpirational loss of water during periods of high solar radiation is important in avoiding desiccation while allowing essential physiological processes to continue. Forest trees must be adapted to two opposing conditions: maximum growth requires intensive uptake of atmospheric carbon dioxide while the maintenance of optimum cell water content requires that loss of water to the atmosphere be kept low. The regulatory function of the stomata serves to reconcile these two opposing constraints. Successful forest species have evolved physiological mechanisms that

minimize transpirational losses during photosynthesis. One of the most important of these mechanisms is stomatal regulation. Studying the nature of these physiological mechanisms and their relationship to the forest environment is basic to understanding and describing the functions of a forest ecosystem.

This study was undertaken to examine the relationships between several physiological parameters of *in situ* tulip poplar (*Liriodendron tulipifera* L.) foliage and the surrounding forest environment, with emphasis on the transpirational process. The specific objectives were:

a) to measure and compare stomatal relationships with environmental and plant morphological variables,

b) to determine and assess the relative importance of factors affecting transpiration and leaf energy balance of a mature *in situ* tulip poplar,

c) to examine and describe the diurnal kinetics of transpiration and leaf energy balance under forest conditions,

d) to examine and develop equations describing these processes and relationships.

I. METHODS

Introduction

Because of their role as the major site of photosynthesis and transpiration, leaves were chosen as the study material in this investigation. Stomata on the underside of the tulip poplar leaf are responsible for controlling gas and vapor exchange between the leaf and the atmosphere, and for this reason the distribution, density, and dimensions of stomata were examined. These parameters were then used in established formulations to predict stomatal resistances to vapor diffusion in relation to stomatal width and the wind-speed-related boundary layer resistance. Predicted stomatal and boundary layer resistances were compared with field measurements. Calculations of transpiration rate were made and compared with stomatal resistance, leaf water potential, and environmental parameters to establish relationships that would elucidate strategies the plant has evolved to regulate transpirational water losses. The coupling of evaporation, i.e. transpiration, with energy flow in the forest was examined using an energy balance approach applied to a single leaf. Diurnal trends were then examined to establish the dynamic relationships between the leaf and its changing environment.

This study identifies the parameters that are important in driving and controlling the transpirational process. Such information reveals the manner in which a tulip poplar leaf reacts to and optimizes its environment. Models to describe and simulate forest growth and physiological functioning must have quantitative data such as this for both model construction and validation.

Study Site

The study area is in the Cesium 137 Forest Research Area, Oak Ridge National Laboratory, Oak Ridge, Tennessee. The site is a second growth, bottomland, mesic hardwood forest dominated by tulip poplar (78 percent of the above ground biomass) (Reichle, et al., 1973). The study area is in a karst depression in which an alluvial silt loam of the Emory series overlies dolomite bedrock. The study period was characterized by high humidity and dew deposition in the early morning with dew evaporation from leaf surfaces by late morning. 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. A more detailed description of the study site is found in a report by Reichle, et al. (1973).

Sampling Procedure

Data were collected in two phases, the first in July and August of 1973 and the second in May and June of 1974. The 1973 phase dealt with energy balance relationships while the 1974 phase dealt with stomatal dimensions versus leaf diffusion resistance measurements. Data were recorded during 1973 at three crown levels (top, middle, and bottom crown) at different times of the day. Individual leaves were sampled *in situ* with all data being recorded for each leaf before beginning the next sample. Data recorded for each sample leaf included: (1) time of day (eastern daylight saving time), (2) height of sample 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 (°C) and relative humidity were measured using a Bendix Psychron ventilated wet-dry bulb psychrometer equipped with mercury thermometers. The instrument was shaded and at the same height as the leaves sampled.

Leaf temperature (°C) was measured using a copper-constantan thermocouple constructed from 0.2 mm wire fused with a capacitive discharge system in a nitrogen

atmosphere. The junction was placed in contact with the lower leaf surface using a spring clip adapted for the purpose (Gale, Manes, and Poljakoff-Mayber, 1970). Once in place on the leaf, temperature measurement required less than 30 seconds. Between measurements the sensor was shaded to prevent heat build-up. Thermocouple output was measured with a Wescor Model MJ-55 Psychrometric Microvoltmeter.

A Weston Illumination Meter was used to measure incident light intensity (foot candles). The meter was oriented with and held next to the leaf for measurements. Resulting foot candle values were divided by 7000 to estimate the solar radiation intensity in cal cm^{-2} min^{-1} (Reifsnyder and Lull, 1965). Solar radiation intensity estimated in this way agreed well with values measured with a Kipp and Zonen solarimeter (0.3 to 3.0 μ wavelengths) (Figure 1).

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

Leaf dimensions were measured along the midvein (length) and at right angles to the midvein to the side lobe tips (width). A regression of the product of

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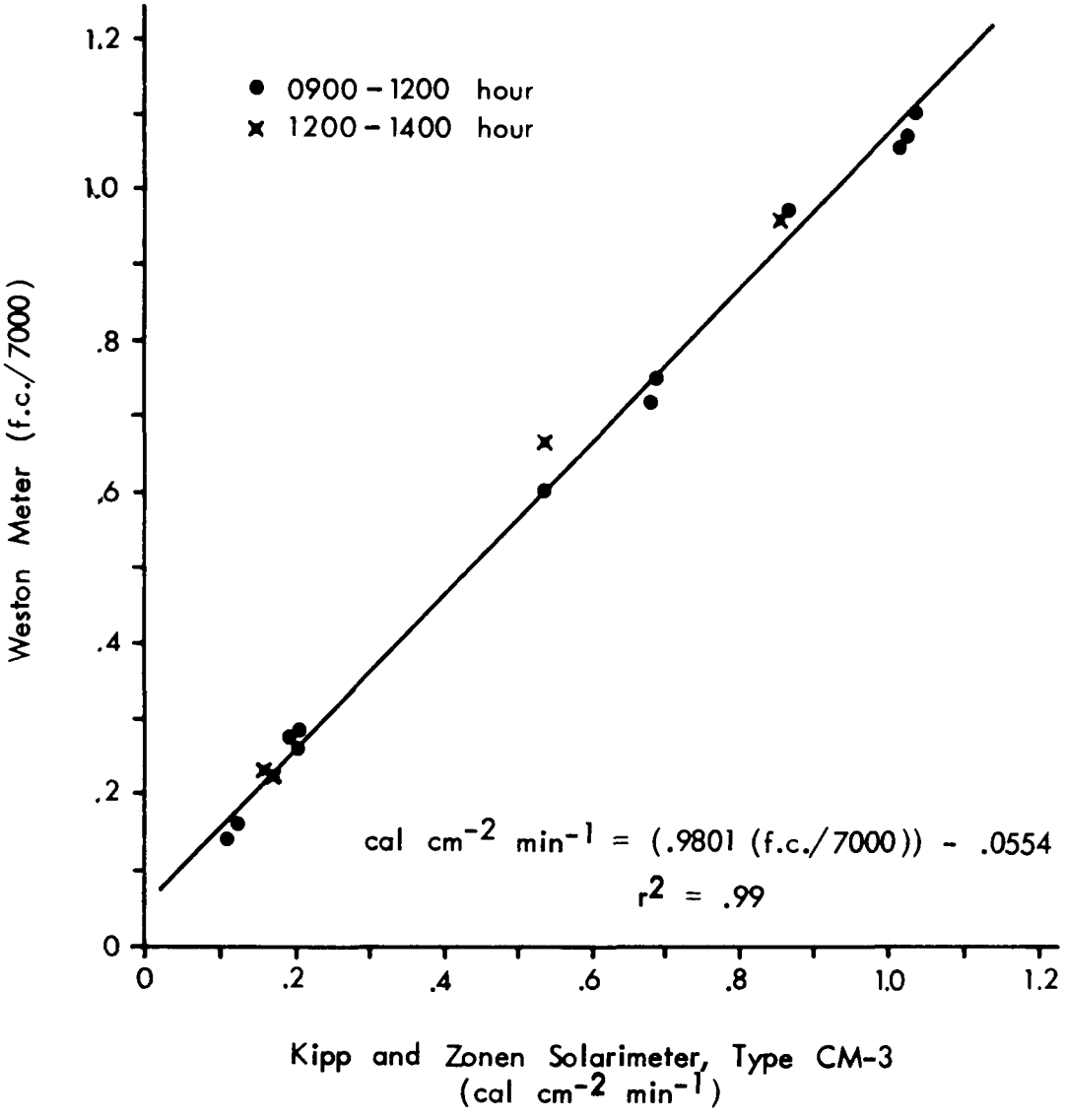

Figure 1. Comparison of light intensity measurements by a Weston Meter and a Kipp and Zonen Solarimeter.

length and width versus measured leaf area was developed and is given below:

$$A = 1.887 + 0.886\ (L_1 \times W_1) \qquad (1)$$

where A is the leaf area in cm^2, L_1 is leaf length in cm, and W_1 is leaf width in cm.

Wind speed (cm sec^{-1}) was measured with a sensitive 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.

A Scholander-type pressure bomb was used to measure leaf xylem water potential (-bars) (Scholander, et al., 1965). After all other measurements were completed the sample leaf was evaluated for xylem water potential within two minutes of excision. Water potential is defined as the difference in free energy or chemical potential between pure water and water in the leaf system. The potential of pure water is zero, therefore leaf xylem water potential is less than zero (negative) and is indicated by more negative values in bar units (Slatyer, 1967; Kramer, 1969). In this study leaf xylem water potential becoming more negative is defined as "increasing" and when becoming more positive is defined as "decreasing" water potential.

In 1974 epidermal leaf impressions were made on in situ leaves at the same three crown levels used in 1973. Leaf diffusion resistance measurements were made on each leaf before making the impression. Leaf area for these measurements was determined planimetrically from a tracing of the leaf outline.

Epidermal impression techniques have been described by Buscalioni and Pollacci (1901), Wenzl (1939), Long and Clements (1934), and Sampson (1961). The method I used was adapted from a technique suggested by K. Raschke (personal communication). A thin sheet of cellulose acetate was cut into 2 cm squares and attached to glass microscope slides. The surface of the acetate was softened with acetone then gently pressed against the lower leaf surface and allowed to dry. The impression was examined under a Nikon Model S-Ke light microscope using 400X and 1000X magnification. A calibrated ocular grid and micrometer scale were used to make measurements to the nearest ocular graduation, i.e., $\pm$ .27 μ at 400X magnification and $\pm$ .10 μ at 1000X magnification. Stomatal density counts were made at 400X and stomatal dimension measurements were made at 1000X. Leaves were divided into quadrants to assure that each major portion of the leaf was adequately sampled. Photographs were made using Panatomic-X 35-mm

film and a microflex photomicrographic attachment for the Nikon microscope. Kohler illumination was used to highlight detail in the impression.

Tulip poplar produces new leaves throughout the growing season, thus leaves of different ages existed at any time during sampling. Sample leaves were chosen at random to reflect the different age classes; those severely damaged by insect consumption were excluded from the sample.

The lack of independence for some of the variables measured does not permit the use of regression analysis procedures. A linear regression equation or straight line is only used to show the general trend of the data. The corresponding regression coefficient is presented only to indicate the dispersion of data about the line, or the "goodness of fit." Non-linear relationships were hand plotted from computer summarized data and thus represent trends in the data. Ranges of standard deviation (SD) about mean values used on graphs are shown using vertical range bars.

Measurement of diurnally fluctuating phenomena ideally requires a sampling scheme designed to obtain data instantaneously at all sampling locations. Unfortunately, manual sampling precluded instantaneous measurement, and the number of samples measured was

limited by the time needed for each measurement. Values measured at the top of the crown were not always comparable with measurements made later at the bottom of the crown. A large number of samples would be needed to adequately describe the energy balance phenomena by segregating the data by time, temperature ranges, height in the crown, etc. The data for this study could only be collected on Mondays due to access restrictions. Consequently, the results presented represent trends developed from all of the data collected.

Leaf Diffusion Resistance Calculations

The term "leaf diffusion resistance" is used to identify the resistance to vapor diffusion from the internal leaf cell walls to the atmosphere surrounding the leaf. Its component parts are: (1) resistance due to internal leaf geometry, (2) resistance of the stomatal pore, and (3) resistance to diffusive and turbulent vapor flux in the external air. These components form a variable system of successive diffusion resistances to passage of water vapor out of the leaf after the scheme presented by Brown and Escombe (1900). Discussions on the theory of stomatal dimensions and diffusion theory have been adequately discussed by Bange (1953), Meidner and Mansfield (1968), Jarvis, et al. (1967), Heath (1959), Parlange and Waggoner (1970), and

Penman and Schofield (1951). This analysis will use an equation developed after Meidner and Mansfield (1968) as follows:

$$R = \frac{1}{D_c} \left[L + \frac{.89(D')^{.46}}{V^{.56}} + \frac{A}{na} \left(1 + \frac{\pi d}{4} \right) \right] \quad (2)$$

$$D_c = .249 \left(\frac{T}{293} \right)^{1.75} \left(\frac{1013}{B} \right) \quad (3)$$

$$D^1 = \sqrt{A/.7854} \quad (4)$$

$$a = \pi \, dp \quad (5)$$

where R is the leaf diffusion resistance (sec cm^{-1}), D_c is the molecular diffusivity of water vapor in air (cm^2 min^{-1}), L is the length of diffusion path in the air space system of the internal leaf (cm), D' is the diameter of the whole leaf area (cm), V is the wind speed (cm sec^{-1}), A is the area of whole leaf surface (hypostomatous surface only) (cm^2), n is the number of stomata on the leaf surface, a is the cross-sectional area of one stoma (cm^2), 1 is the length or depth of the stomata tube (cm), d is the diameter of stomata tube (central aperture) (cm), T is the leaf temperature (°K), B is the barometric pressure equal to 986.6 mbars (approximate mean for the study area), and p is the stomata pore length (cm). This formula calculates leaf

diffusion from measurements of leaf size, stomatal dimensions, wind speed, and leaf temperature. It is based on both Fick's and Stefan's Laws that imply the rate of diffusion is a function of the geometry of the diffusion paths, and on Ohm's Law where resistance is the result of the driving force divided by the rate of flow. Resistances in series are summed to give the total resistance.

Energy Balance Theory

The coupling of the leaf to its environment occurs through the boundary layer at the leaf's surface. The energy exchange across this boundary is determined from physical theory. At any one instant under steady-state conditions, the total energy input to the leaf equals total energy loss. The individual energy fluxes involved in the leaf energy balance are shown in Figure 2.

The environmental factors most important to the leaf energy balance are: direct solar and diffuse short-wave radiation; infrared (thermal) radiation from the atmosphere, ground, and nearby objects; air temperature; wind; and water vapor concentration of the air (Gates, 1965a). Characteristics of the leaf involved in the energy exchange are: coefficients of mean absorptance, reflectance, thermal emittance, and convection; transpiration resistance; leaf geometry and orientation; and,

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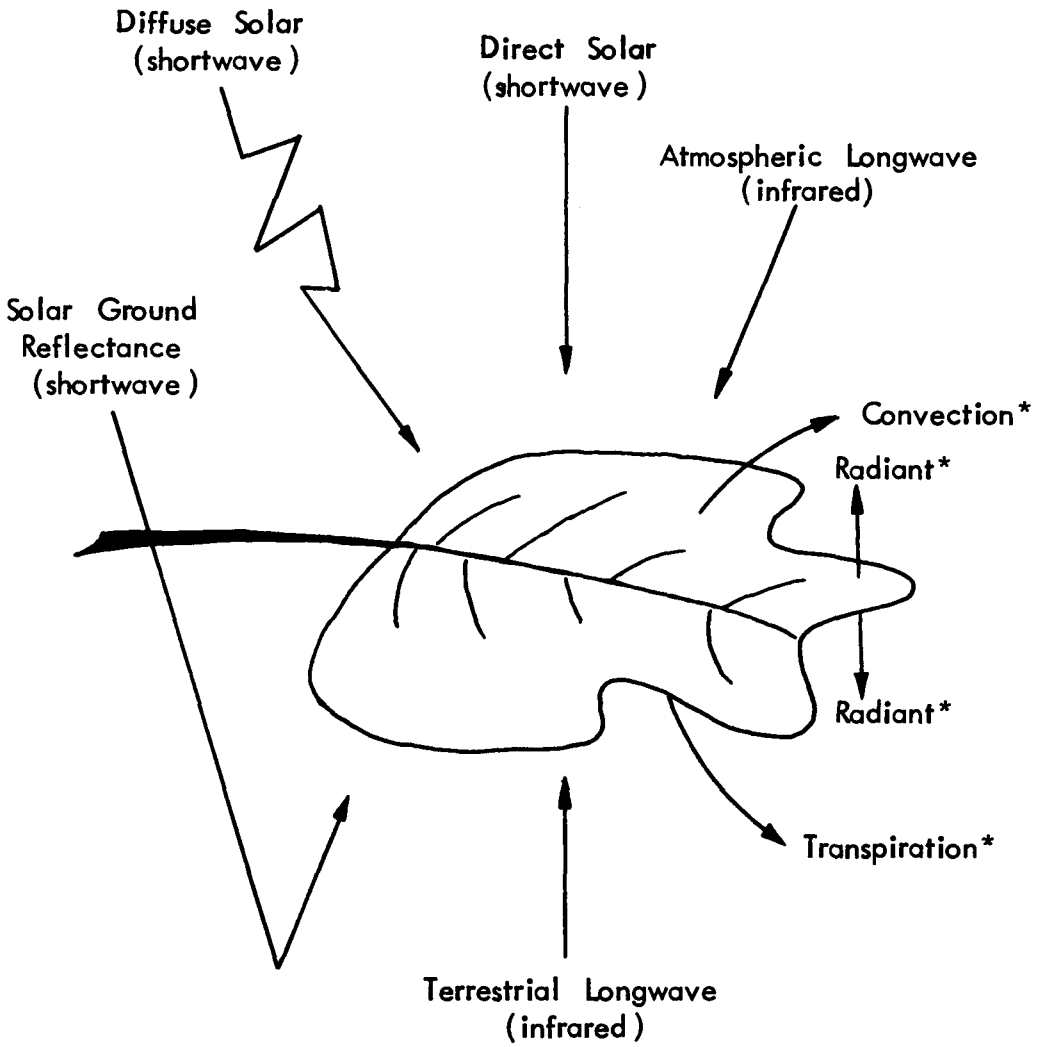

* energy loss terms

Figure 2. Components of the energy balance of a tulip poplar leaf.

leaf position in the crown. Empirical and theoretical formulations discussed below have been determined using these environmental and leaf factors to define the exchange of heat energy.

The energy exchange between the plant and its environment can be defined as follows:

$$\text{NETINPUT} = \text{TOTHEAT}$$

-or-

$$\text{NETINPUT} = IR \pm C + (L_e \times E) + P, \qquad (6)$$

where TOTHEAT is the total energy loss from the leaf in cal cm^{-2} min^{-1}, NETINPUT is the amount of radiation flux absorbed by the leaf surface in cal cm^{-2} min^{-1}, IR is the energy loss by emitted radiation in cal cm^{-2} min^{-1}, C is the energy gained or lost by convection in cal cm^{-2} min^{-1}, E is the transpiration rate in g H_2O cm^{-2} min^{-1}, L_e is the latent heat of evaporation of water (equal to 580 cal g^{-1} at 30° C), and (L_e x E) is the energy loss by transpiration in cal cm^{-2} min^{-1}. This formula only considers the steady-state energy flow between a leaf and its environment and not the short-term transient responses of warming and cooling. It assumes the leaf is a plane surface which does not move that is horizontal and parallel to the ground. The ground is specified only in terms of its over-all physical properties. The

upper leaf surface is assumed to be exposed only to the atmosphere and incident solar radiation.

The tree leaf is exposed to a radiation flux at all times. The leaf is coupled to this radiation flux by the absorptivity of its surface, which is wavelength dependent and may change with time. The amount of radiation absorbed by the leaf has been defined by Gates (1968) as follows:

$$2\ \text{NETINPUT} = \alpha_1(S + s) + \alpha_2\, r(S + s) + \alpha_3(IR_g + IR_a), \quad (7)$$

where S is the direct solar radiation in cal cm^{-2} min^{-1}, s is the diffuse skylight radiation in cal cm^{-2} min^{-1}, IR_a is the long-wave thermal radiation from the atmosphere in cal cm^{-2} $°K^{-1}$ min^{-1}, IR_g is the long-wave thermal radiation from the ground or underlying plants in cal cm^{-2} $°K^{-1}$ min^{-1}, α_1 is the absorptance to direct solar radiation and diffuse skylight, α_2 is the absorptance to sunlight and skylight reflected from the ground or underlying surfaces, r is the reflectance of underlying surface to direct sunlight and diffuse skylight, and α_3 is the absorptance to infrared thermal radiation from the surface of the ground, surrounding objects, or the atmosphere. A discussion of the theory and measurement of these terms can be found in Gates (1965b), Idle (1970), and Reifsynder and Lull (1965). The average absorptivity of a leaf to

radiation can be determined by multiplying the incident solar energy curve as a function of the frequency, or wavelength, by the spectral absorptivity values (Gates, 1962). The average absorptivity varies with changes in the spectral characteristics of sunlight that occur with time of day, sky conditions, season, and altitude. The spectral quality of sunlight in the field is not known and a mean absorptance value must be used. Gates (1965a) reported the mean absorptance of most deciduous plant leaves to incident sunlight and skylight to be between 0.45 and 0.60. He also reported absorption values of 0.50 to 0.60 for clear days and 0.60 to 0.70 for completely overcast conditions for some deciduous leaves. A mean absorptance of 0.60 will be used as a reasonable compromise value for α_1.

The absorptance of sunlight and skylight reflected from the ground or underlying surfaces is difficult to estimate. The amount of reflected light is small; thus, an error in estimating α_2 will not be too serious. The spectral quality of reflected light varies with the nature of the underlying surface. The amount of light reflected from an underlying vegetative surface will vary with incident light wavelength, species, leaf age, leaf position, leaf orientation, and season (Reifsynder and Lull, 1965). Values of

reflectance have been reported in a range from 0.08 to 0.30, and a reflectance of 0.30 will be used for tulip poplar (Birkebak and Birkebak, 1964; Gates, 1962). If the underlying reflective surface is vegetative, the reflected light will be rich in near infrared, which is poorly absorbed, resulting in a relatively low α_2 value of approximately 0.20 (Gates, 1968).

The leaf's absorptance to near infrared wavelengths is poor, but far infrared wavelengths are efficiently absorbed (Gates, 1965b). Gates and Tantraporn (1952) reported an α_3 value for plant leaves of 0.94 to 0.97. An α_3 value of 0.97 will be used for tulip poplar leaves.

The earth's atmosphere contains water vapor, carbon dioxide, and ozone, all of which absorb radiation and emit it according to Kirchhoff's Law (Geiger, 1965). The formulation of a value for long-wave thermal radiation from the atmosphere (IR_a), discussed by Gates (1962, 1965b), is complicated. Because water vapor is the primary source of IR_a, much of this radiant energy originates in the lower atmosphere and varies as its water vapor content varies. The radiation flux resulting from carbon dioxide and ozone is more or less constant since their atmospheric concentrations are rather stable. The Brunt formula given below will be used in determining

the IR_a component of equation 7 (Gates, 1962).

$$IR_a = \delta T_a^4 \ (0.44 + 0.08 \sqrt{AVP}), \qquad (8)$$

where δ is the Stefan-Boltzmann radiation constant, equal to 8.12×10^{-11} cal cm^{-2} $°K^{-4}$ min^{-1}, T_a is the air temperature (°K) at measuring height, and AVP is the vapor pressure of air at measuring height (millibars).

The value for the long-wave thermal radiation from underlying plants (IR_g) is computed on the assumption that the sample leaf will receive the IR_g energy component from the vegetation directly underneath. The underlying vegetation is assumed to be at the same temperature as the leaf being measured. These assumptions should be realistic except in the extreme lower crown where leaves will receive IR_g flux from understory vegetation or ground surfaces. The value of IR_g is computed using the Stefan-Boltzmann Law of radiation with emissivity being assumed equivalent to the absorptivity of leaves for infrared wavelengths greater than 2.5 μ (Geiger, 1965; Gates, 1965a), as follows:

$$IR_g = \delta \varepsilon T_l^4 \qquad (9)$$

where δ is the Stefan-Boltzmann radiation constant, equal to 8.12×10^{-11} cal $cm^{-2}°K^{-4}$ min^{-1}, ε is the emissivity, equal to 0.97, and T_l is the leaf temperature (°K).

The emission of radiant energy by the leaf is governed by two characteristics of the leaf: its temperature and its emissivity. According to Stefan's Law the quantity of energy emitted is a fourth power of the absolute temperature. The quality of radiation emitted, or color temperature, is calculated using Wien's Law. Objects at temperatures encountered in temperate terrestrial ecosystems radiate in the infrared wavelengths from 4 to 50 μ with a peak intensity at a wavelength of about 10 μ (Gates, 1965a). The radiation emitted by any natural body is always less than the ideal black-body radiation because the emissivity of the body is always less than one. Emitted radiant energy is defined by the Stefan-Boltzmann Law given below:

$$R = \delta \varepsilon T^4 \qquad (10)$$

where R is the energy lost by reradiation in cal cm^{-2} min^{-1}, ε is the surface emissivity equal to 0.97 (Gates, 1965b), δ is the Stefan-Boltzmann radiation constant equal to 8.12×10^{-11} cal $cm^{-2}°K^{-4}$ min^{-1}, and T is the surface temperature of leaf in °K. A corollary of Kirchhoff's Law states that for radiation of the same spectral distribution, an object's absorptivity will be the same as its emissivity (Reifsnyder and Lull, 1965).

Gates and Tantraporn (1952) have shown infrared absorptance, thus emissivity, beyond 3.0 μ wavelength to be between 0.94 and 0.97 for most plant leaves.

Latent heat flux, or transpiration, is a diffusion phenomena dependent on the random motion of atmospheric gases to transport molecules to or from the leaf surface. Transpiration is driven by the concentration gradient of water vapor between the sub-stomatal cavity and the free air beyond the boundary layer surrounding the leaf. The resistance of this diffusion pathway is the factor that couples the moisture loss of the leaf to the vapor pressure of the air. Diffusion resistance is subdivided into three components: mesophyll resistance; stomatal resistance; and boundary layer resistance. Of these, stomatal resistance and boundary layer resistance are the most variable, most easily measured, and probably account for most of the total resistance. Richardson, Dinger, and Harris (1973) found tulip poplar mesophyll resistance to be a small part of the total resistance, or a constant value.

The stomata typically control 90-95 percent of the water lost from a leaf, the remaining 5-10 percent being lost through the cuticle (Salisbury and Ross, 1969). Environmental factors regulating stomatal aperture are carbon dioxide, light, water stress,

temperature, and wind. These factors combine to form a complex system regulating water vapor loss through the stomata. Water evaporating from the leaf effectively regulates leaf temperature with 580 calories lost for each gram of water evaporated at 30° C. The interaction of the magnitude of the water vapor gradient, light, leaf geometry, wind, leaf temperature, air temperature, and diffusion resistance values result in a transpiration rate that is calculated by the equation reported by Gates (1965a) given below:

$$E = \frac{SVD_l - RH\ (SVD_a)}{R} \qquad (11)$$

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_l is the saturated water vapor density of air in substomatal cavity at leaf temperature (T_l) in g cm^{-3} (relative humidity of the sub-stomatal cavity is assumed to be 1.00), and R is the total resistance of diffusion pathway in min cm^{-1}.

The values for saturation water vapor density are best found directly from dew point measurements. For convenience, this study will use a derived equation from statements of Shaw (1930) presented by Idle (1970). The

equation below gives exact values at 20° C, a 1 percent negative error at 0° C, and a 5.3 percent positive error at 50° C (Idle, 1970).

$$SVD = 217/°K \times \exp\ [(5427 \times (0.00366 - 1/°K)) + 1.809]/1 \times 10^6 \quad (12)$$

where SVD is the saturated water vapor density in g cm^{-3}, and °K is the temperature of air or leaf in °K. The range of air and leaf temperature encountered in a tulip poplar stand will allow use of this equation with a small error involved.

The total resistance of the diffusion pathway (R) is composed of two components: stomatal diffusion resistance (r_s) and boundary layer resistance (r_a). Stomatal diffusion resistance was easily measured using a sensitive hygrometer, the Lambda diffusion resistance porometer, that was attached to the in situ leaf. Leaf boundary layer resistance is influenced by wind, leaf shape and size, and the difference between leaf and air temperature (Salisbury and Ross, 1969). The thickness of the boundary layer and the steepness of the water vapor gradient across the boundary layer are factors that control the rate of transpiration. A discussion on the computation of stomatal resistance can be found in Lee (1967), Lewis (1972), and Salisbury and Ross (1969).

The formulation of boundary layer resistance used for calculating tulip poplar transpiration rates (Gates, 1968) is given below:

$$r_a = k_1 \, (D^{0.35} \, W^{0.20} / \, V^{0.55}) \qquad (13)$$

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 14).

Wind influences transpiration by cooling the leaf and by disturbing the leaf's boundary layer. Generally, increased wind speed will result in a thinner boundary layer, a lower r_a, and an increased transpiration rate. Murphy and Knoerr (1972) calculated the wind speed profile through the plant canopy based on wind speed at the top of the canopy and a wind speed extinction coefficient using the equation presented below:

$$V = V_t \exp \, [k_2 \, (H_t - H)] \qquad (14)$$

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

The convection of sensible heat is the net transport of heat by the mixing action of the atmosphere. The movement of sensible heat is proportional to the heat gradient between the leaf and the atmosphere. Convective heat transport is accomplished through two modes of action: free convection and forced convection (Gates, 1962). Free convection occurs in still air where the temperature difference between the object and the surrounding medium creates a flow of air. There is usually some air movement in natural environments, thus still air is considered equivalent to a wind speed of 10 cm sec^{-1} (Gates, 1968). Forced convection, which considers heat transfer relationships with wind velocity, will be used for calculation of convective heat loss by leaves.

Some of the factors that determine the convective heat transfer along a temperature gradient can be summed into a convection coefficient term. The calculation of a convective coefficient to determine the influence of environmental and plant parameters on heat transfer discussed by Gates (1962); Parkhurst, et al. (1968); Knoerr and Gay (1965); and Murphy and Knoerr (1972) is complicated. The formula below, from Gates (1965b), calculates convective heat transfer for forced convection conditions as influenced by leaf size, leaf shape, wind

speed, and leaf orientation to the direction of the wind.

$$C = h_c \, (V/D)^{0.5} \, \Delta T \qquad (15)$$

where C is the convective heat transfer in cal cm^{-2} min^{-1}, h_c is the convective coefficient equal to 5.7 x 10^{-3}, V is the wind speed in cm sec^{-1}, D is the mean width of the leaf in cm, and ΔT is the difference between air and leaf temperature (T_1-T_2) in °C.

II. RESULTS

Stomatal Distribution and Density

Sampling was carried out to determine stomatal distribution and density on individual leaves, and the influence of crown position on these variables. Stomatal density was determined from tulip poplar leaf impressions which were taken from four leaf quadrants on foliage from each of three levels in the crown. Results presented in Table 1 show that stomatal density varied significantly ($P \leq 0.01$) with respect to position in the crown, but not between quadrants on individual leaves (Appendix, Table 11).

The number of stomata per leaf remained relatively constant throughout the tree crown (Table 2) with no significant differences being detected ($P \leq 0.10$) between the three crown levels (Appendix, Table 12). Small sun leaves in the upper crown had the greatest stomatal density, and large shade leaves lower in the crown had a lower stomatal density. The increase in stomatal density with increasing height was balanced by a coincident decrease in leaf size resulting in a relatively constant number of stomata per leaf.

Stomatal slit length, an indicator of stomatal size, did not differ significantly ($P \leq 0.10$) with leaf

Table 1. Tulip poplar stomatal density distribution for four leaf quadrants and three crown levels. Stomatal density measured at 400X magnification and expressed as stomata per cm^2 (± standard deviation).

Crown Level	Leaf Quadrant Number 1	2	3	4	Crown Level Means
Top	21,400 ±1,400	22,000 ±1,820	20,800 ± 980	20,700 ±1,260	21,200 ± 700
Middle	13,100 ±1,260	14,900 ±1,960	14,900 ±1,820	13,400 ±1,400	14,100 ± 840
Bottom	11,000 ± 700	11,600 ± 840	10,300 ± 420	12,100 ± 840	11,300 ± 280
Leaf Quadrant Means	15,200 ±5,300	16,200 ±6,500	15,300 ±5,800	15,400 ±5,000	15,500 ±5,700

Table 2. The number of stomata per leaf by crown level (± standard deviation).

Crown Level	Stomata Per Leaf
Top	2,180,000 ± 71,000
Middle	2,020,000 ± 125,000
Bottom	2,410,000 ± 62,000
Mean	2,220,000 ± 80,000

quadrant (Table 3; Appendix, Table 13). The middle and bottom crown mean slit lengths were not significantly different from each other, but both were significantly different ($P \leq 0.01$) from the top crown value (Appendix, Table 13). These results indicate a decrease in stoma size with increased stomatal density and with decreased leaf size.

Figure 3 is a microphotograph of a cellulose acetate epidermal impression of tulip poplar stomata. Stomatal density was easily determined, as were measurements of stomatal dimensions and epidermal features.

Table 3. Tulip poplar stoma slit length (μ) by crown level and leaf quadrant (± standard deviation).

Crown Level	Leaf Quadrant Number				Crown Level Means
	1	2	3	4	
Top	15.0 ± 2.7	13.0 ± 4.1	15.8 ± 2.3	16.4 ± 1.8	15.1 ± 3.0
Middle	19.2 ± 3.4	18.8 ± 3.6	19.9 ± 3.5	20.5 ± 3.7	19.6 ± 3.5
Bottom	18.4 ± 2.9	17.7 ± 3.4	17.8 ± 2.9	14.4 ± 2.1	18.1 ± 2.7
Leaf Quadrant Means	17.5 ± 3.5	16.5 ± 4.4	17.9 ± 3.3	18.4 ± 3.1	17.6 ± 3.6

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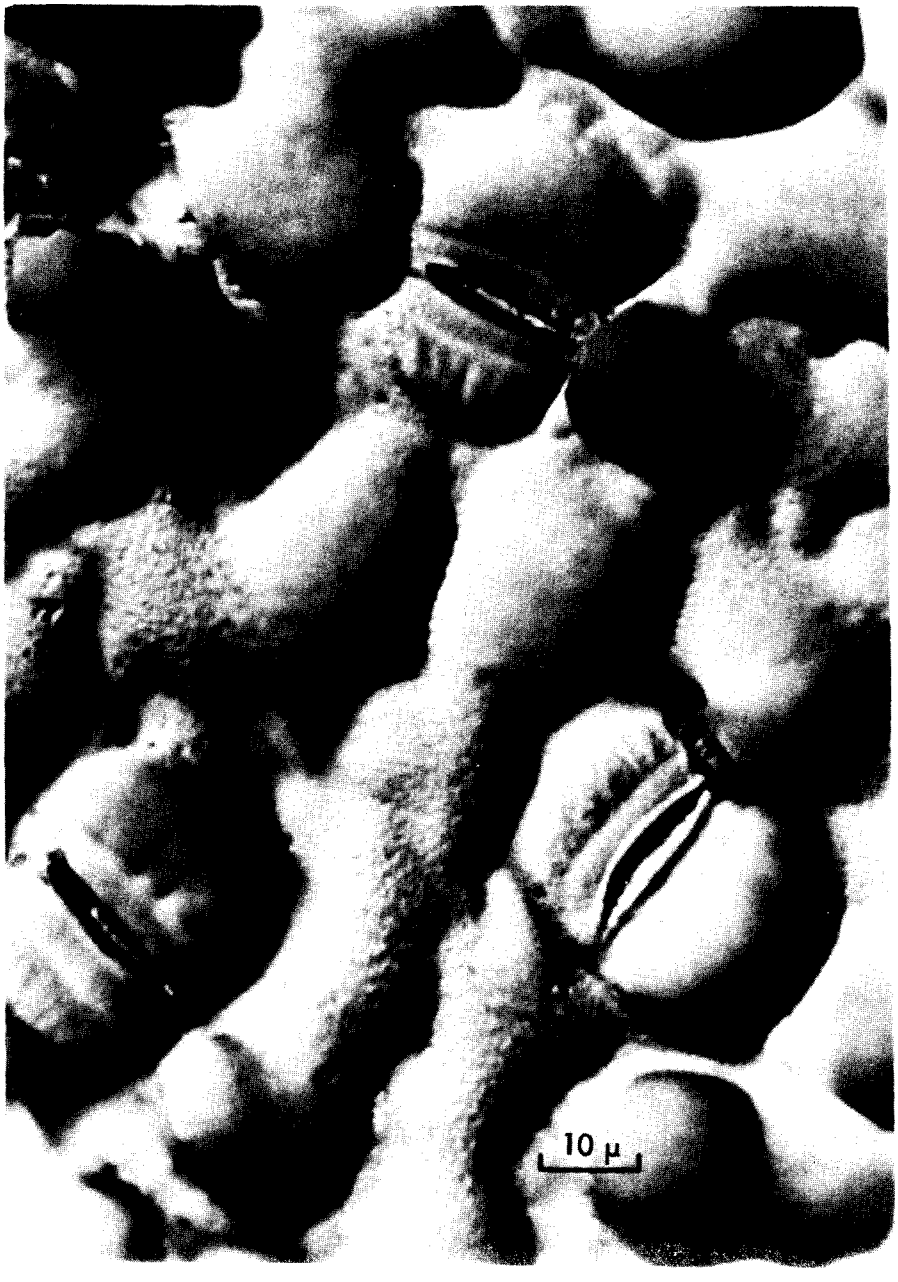

Figure 3. Photomicrograph of a tulip poplar leaf epidermal impression showing three stoma and other epidermal features.

It is doubtful that the impression allowed for measurement of the stoma's central aperture due to interference from the upper closing flaps.

Tulip Poplar Leaf Diffusion Resistance Calculated from Stomatal Dimension Measurements and Varying Environmental Parameters

Data gathered for tulip poplar leaf and stomatal dimensions are used with equations 2 through 5 to generate curves of changes in diffusion resistance values in response to changing environmental conditions. A mathematical simulation was run using the input data presented in Table 4. Measurements taken from upper crown leaves were used to estimate the range of values for pore depth and internal diffusion path length at the other two crown zones. Leaf area, stomatal numbers per leaf, and stomatal pore length values were obtained from actual measurements. The simulation used a computer program that varied stomatal width, wind speed, and leaf temperature over their naturally occurring range in a stepwise fashion to calculate leaf diffusion resistance for all combinations of these three variables at each level in the crown. All calculated leaf diffusion resistance values were used to plot graphs of the variables.

Calculated leaf diffusion resistance reaches its minimum value when stomatal width reached a value of

Table 4. Parameters used in simulation of tulip poplar leaf diffusion resistance.

Parameter	Crown Level		
	Top	Middle	Bottom
L	40 μ	34.8 μ	30 μ
A	101.7 cm^2	148.1 cm^2	220.7 cm^2
n	2,159,091	2,083,767	2,418,872
l	15 μ	12 μ	9 μ
p	14.8 μ	19.6 μ	18.1 μ
T	20-36 °C	20-36 °C	20-36 °C
d	0.1-6.0 μ	0.1-6.0 μ	0.1-6.0 μ
V	10-460 cm sec^{-1}	10-460 cm sec^{-1}	10-460 cm sec^{-1}

2 μ (Figure 4). Wind speeds at 10 cm sec^{-1} and above 60 cm sec^{-1} result in two separate bands of resistance values. The width of the bands (Figures 4 and 5) represents the range of calculated leaf diffusion resistance values resulting from differences in crown position and leaf temperature given in Table 4. Assuming still air conditions (10 cm sec^{-1} wind speed) occur infrequently in nature, the naturally occurring tulip poplar stomatal resistance would be located in the lower band. Figure 5 illustrates the effect of wind speed on leaf diffusion resistance. Values again fall in two bands, the upper band is for a stomatal width of 0.1 μ and the lower band for stomatal widths above 0.6 μ. Wind speeds above

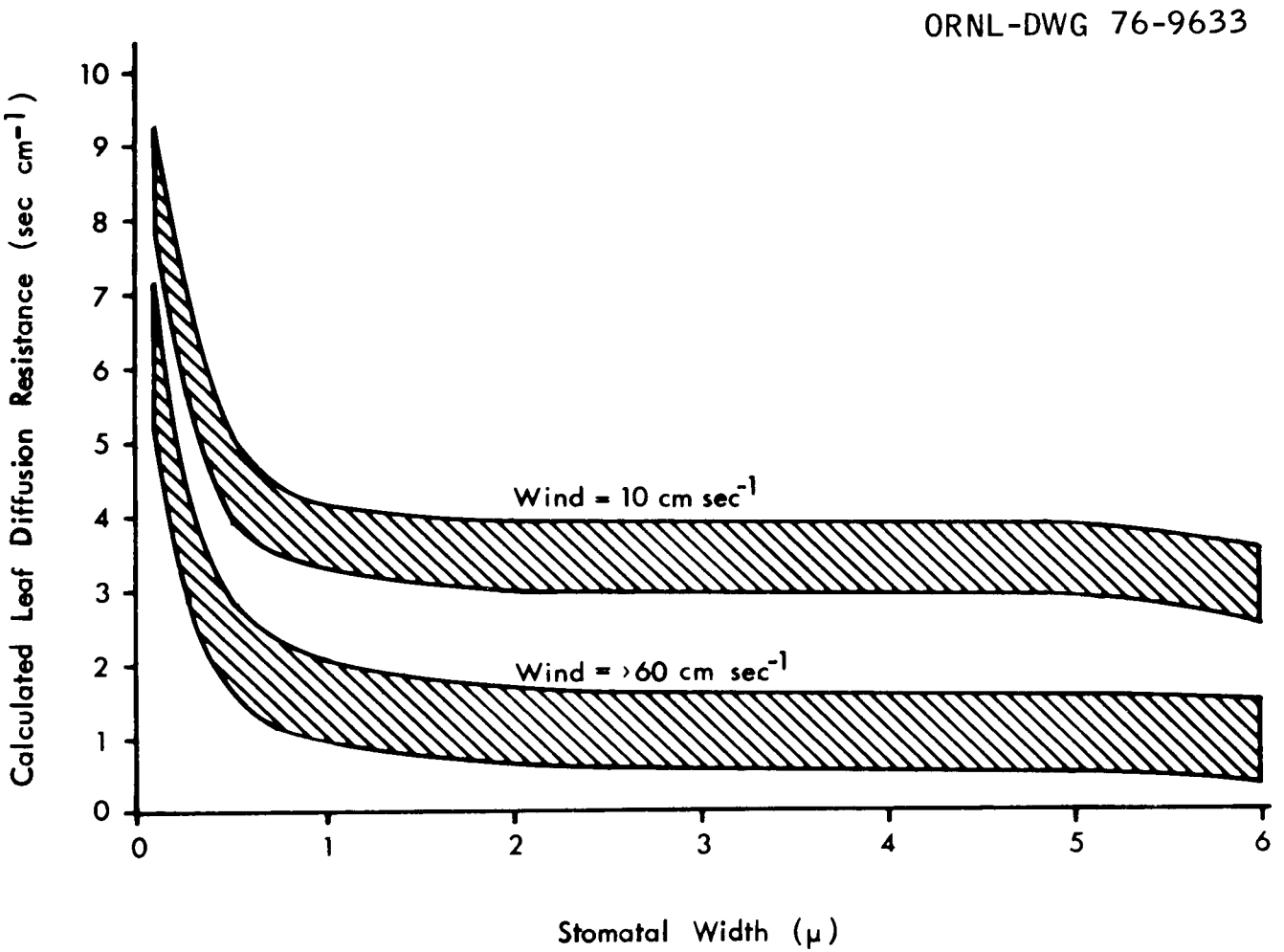

Figure 4. Variation of calculated leaf diffusion resistance with changing stomatal width and wind speed.

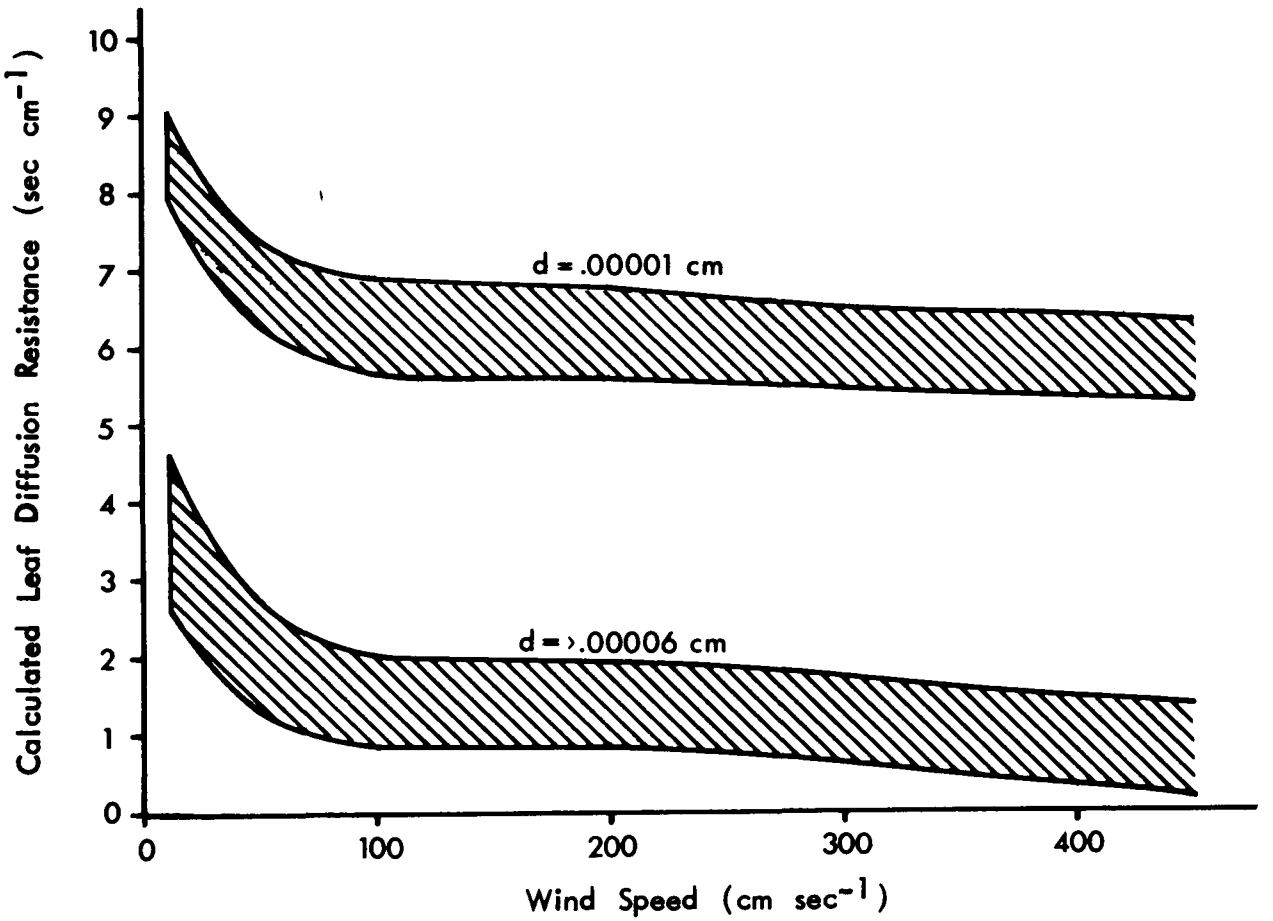

Figure 5. Variation of calculated leaf diffusion resistance with changing wind speed and stomatal width (d).

100 cm sec^{-1} do not continue to reduce diffusion resistance values. This suggests that stomatal widths greater than 0.6 μ may have little influence on leaf diffusion resistance in the natural environment. Widths smaller than 0.6 μ increase diffusion resistance values. As wind speeds increase from 0 to 100 cm sec^{-1}, there is a decrease in the boundary layer resistance; above 100 cm sec^{-1}, the decrease is relatively slow (Figure 6). The importance of the boundary layer resistance is indicated by the relationship summarized in Figure 7 where the cross hatched area represents the range of values for the ratio of boundary layer resistance to calculated leaf diffusion resistance. At low wind speeds leaf diffusion resistance is smaller than the boundary layer resistance. Values above one occurred at low wind speeds (< 60 cm sec^{-1}) when the stomata were open and leaf temperatures were high. Environmental parameters that influence the boundary layer resistance, especially at low wind speeds when the ratio value is greater than 1.0, could be the prime controllers of transpiration and carbon dioxide exchange through the stomata. Yet, since wind is usually above 50 cm sec^{-1} in the natural environment the ratio will normally be 1.0 or less.

Values of calculated leaf diffusion resistance and boundary layer resistance at 100 cm sec^{-1} wind speed

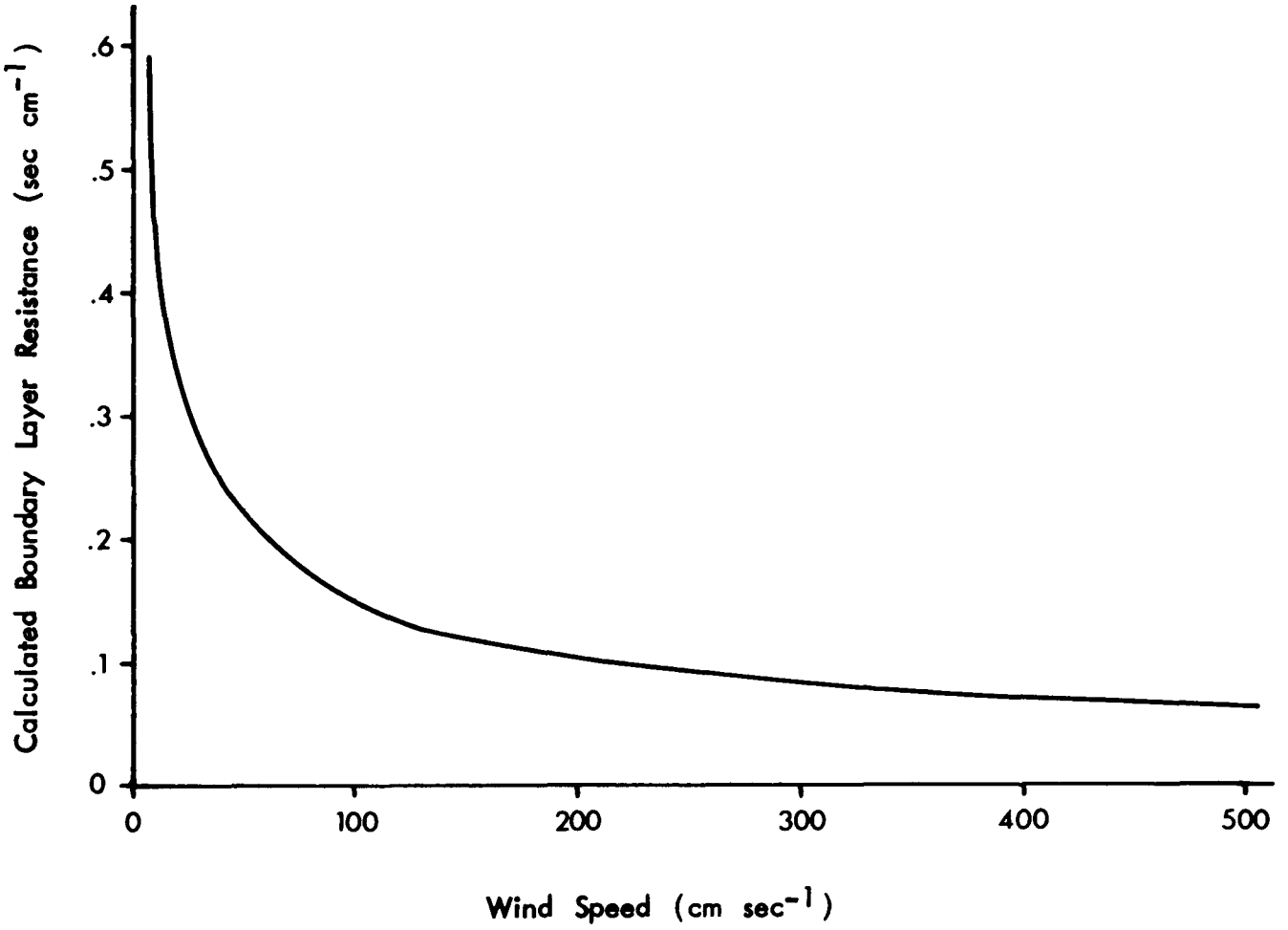

Figure 6. The influence of a range of wind speeds on calculated leaf boundary layer resistance.

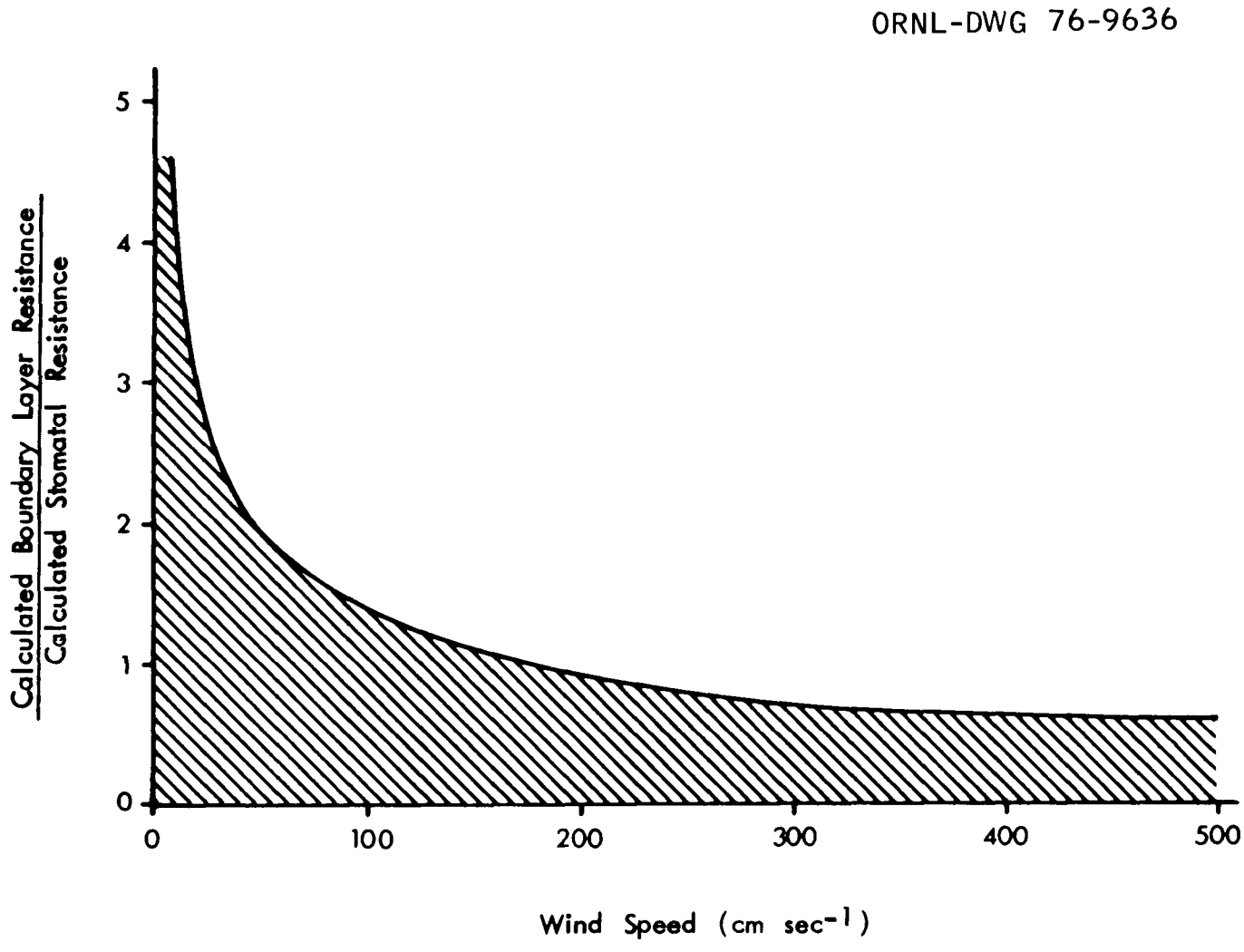

Figure 7. The influence of wind speed on the ratio of calculated boundary layer resistance to calculated stomatal resistance.

(Figures 5 and 6, pages 34 and 36, respectively) are approximately 1.4 sec cm^{-1} and 0.15 sec cm^{-1}, respectively. The sum, 1.55 sec cm^{-1}, compares favorably with minimum diffusion resistance values of 1.7 sec/cm measured for in situ tulip poplar leaves during the summer of 1973. The values simulated by the approach described above therefore seem to be a reasonable approximation of the physiological process.

Transpiration

Transpiration rates were calculated from measured stomatal diffusion resistance, calculated boundary layer resistance, saturated vapor deficit at air and leaf temperature, and relative humidity using equation 11. Transpiration rates during this study were in the range from 1.7 to 67.7 x 10^{-5} g cm^{-2} min^{-1} with the mean equal to 20 $\pm$ 16 x 10^{-5} g cm^{-2} min^{-1}. Transpiration is controlled by the interaction of environmental and plant variables, of which temperature and vapor pressure are important. Vapor pressure deficit (VPD), the gradient of vapor pressure from the leaf stomatal cavity to the atmosphere surrounding the leaf, was highly correlated with leaf temperature during this study (Figure 8).

As temperature increased, the difference between air and leaf temperature increased (Figure 9). Air and leaf temperature differences were greatest in the

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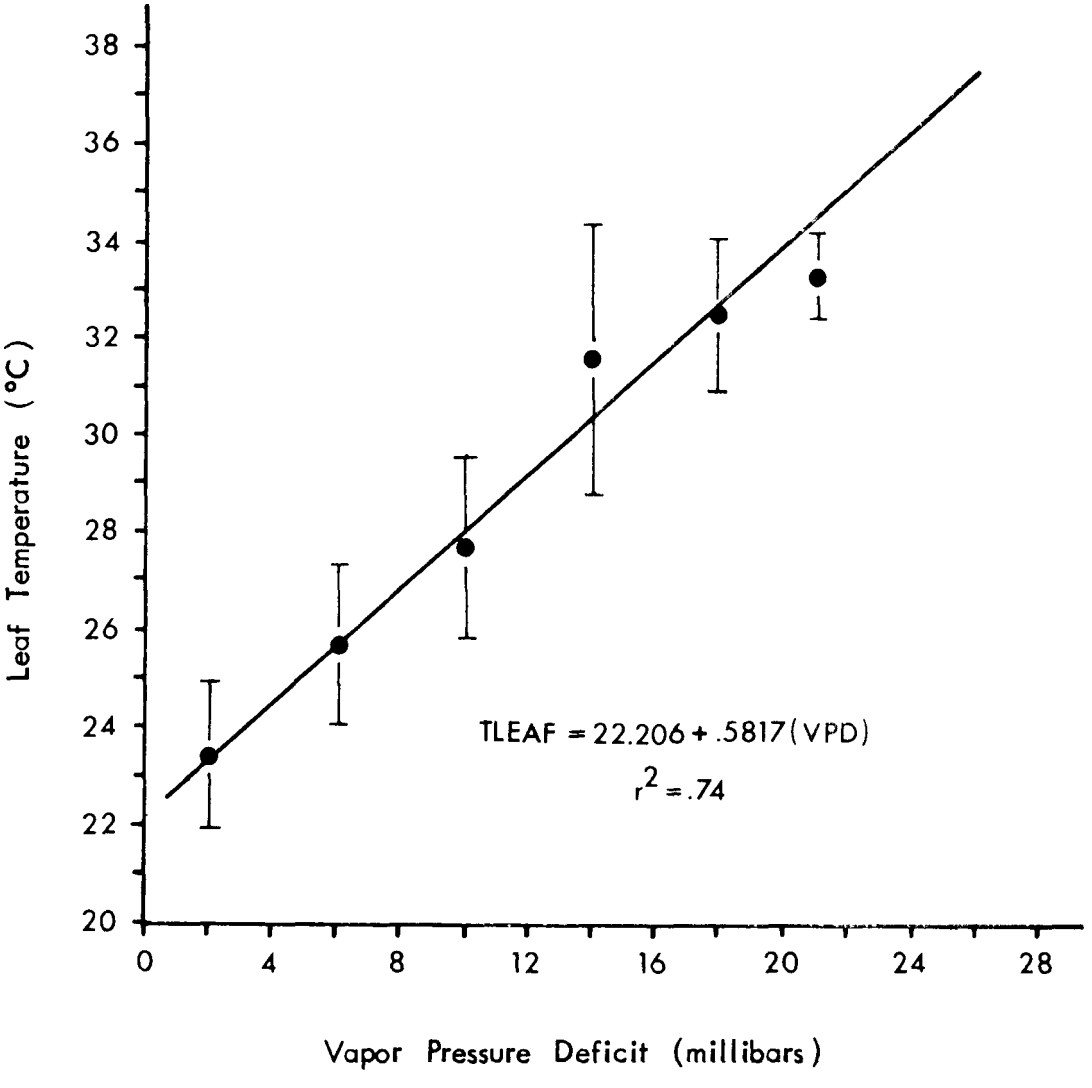

Figure 8. The relationship between vapor pressure deficit and leaf temperature (± SD) for <u>in situ</u> tulip poplar trees.

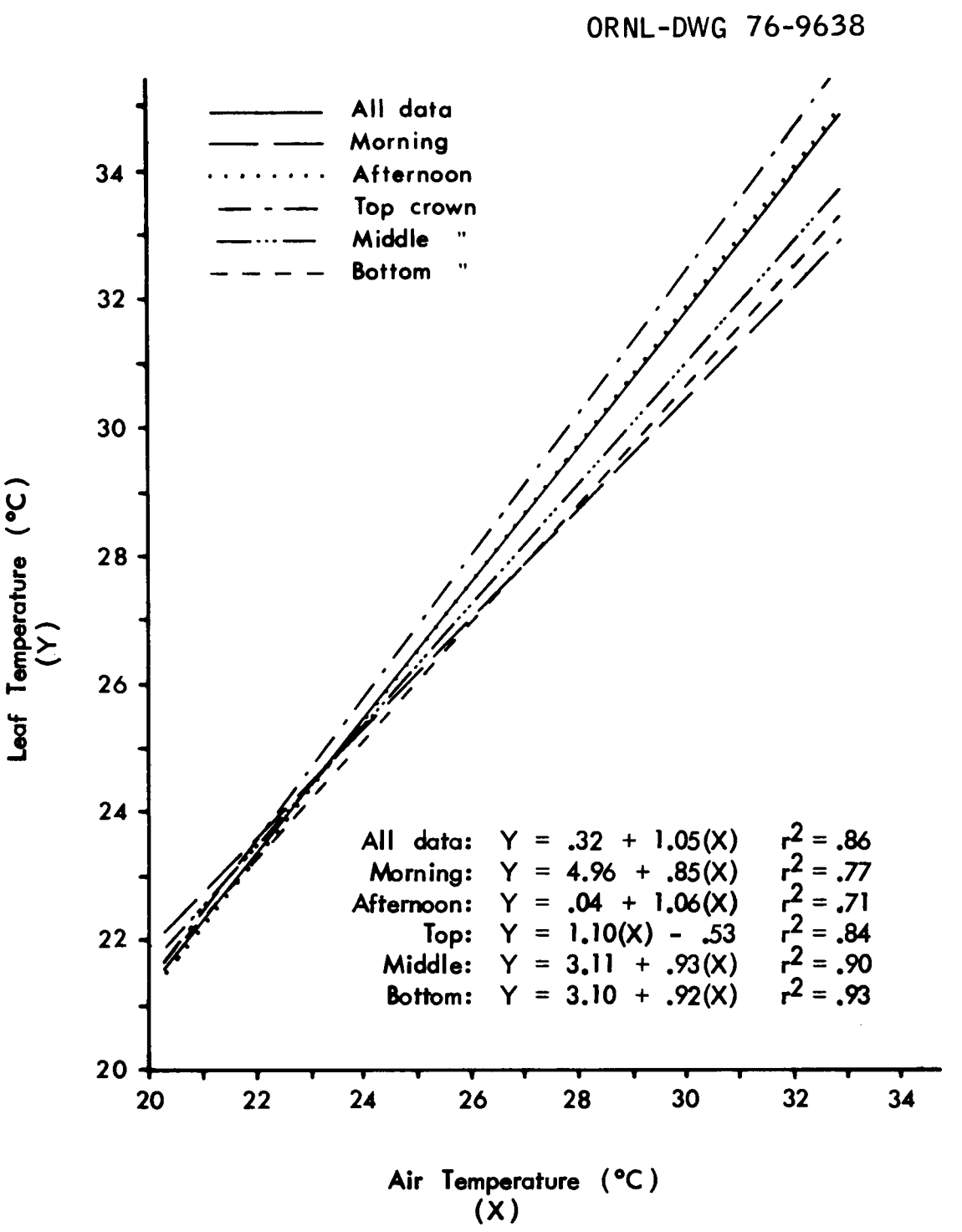

Figure 9. The relationship between air temperature and leaf temperature for tulip poplar leaves at three crown levels and two periods of the day (morning and afternoon).

afternoon and at the top of the tree crown, the time and crown position at which insolation was greatest. Air and leaf temperature difference is compared with total heat absorbed by the leaf in Figure 10 and shows an increase in temperature difference with increased heat energy input.

Leaf temperature decreased with decreasing crown height (Figure 9). This would result in decreasing VPD and leaf minus air temperature difference, and as a result transpiration rates would decrease with decreasing crown height as summarized in Table 5. The decreased transpiration rates were not due solely to VPD and leaf temperature changes, but also due to stomatal diffusion resistance and leaf structure changes with crown position, a relationship supported by Lewis (1972). The most linear relationship between transpiration rate and one of its driving variables was between transpiration rate and VPD (Figure 11). Transpiration rate steadily increases as stomatal diffusion resistance decreases as shown by the relationship in Figure 12.

Tulip poplar stomata reacted strongly to light (Figure 13). The minimum light intensity that initiated stomatal opening was around 0.04 cal cm^{-2} min^{-1} which is approximately equal to the carbon dioxide compensation point for tulip poplar (Dinger, 1972). Stomatal diffusion

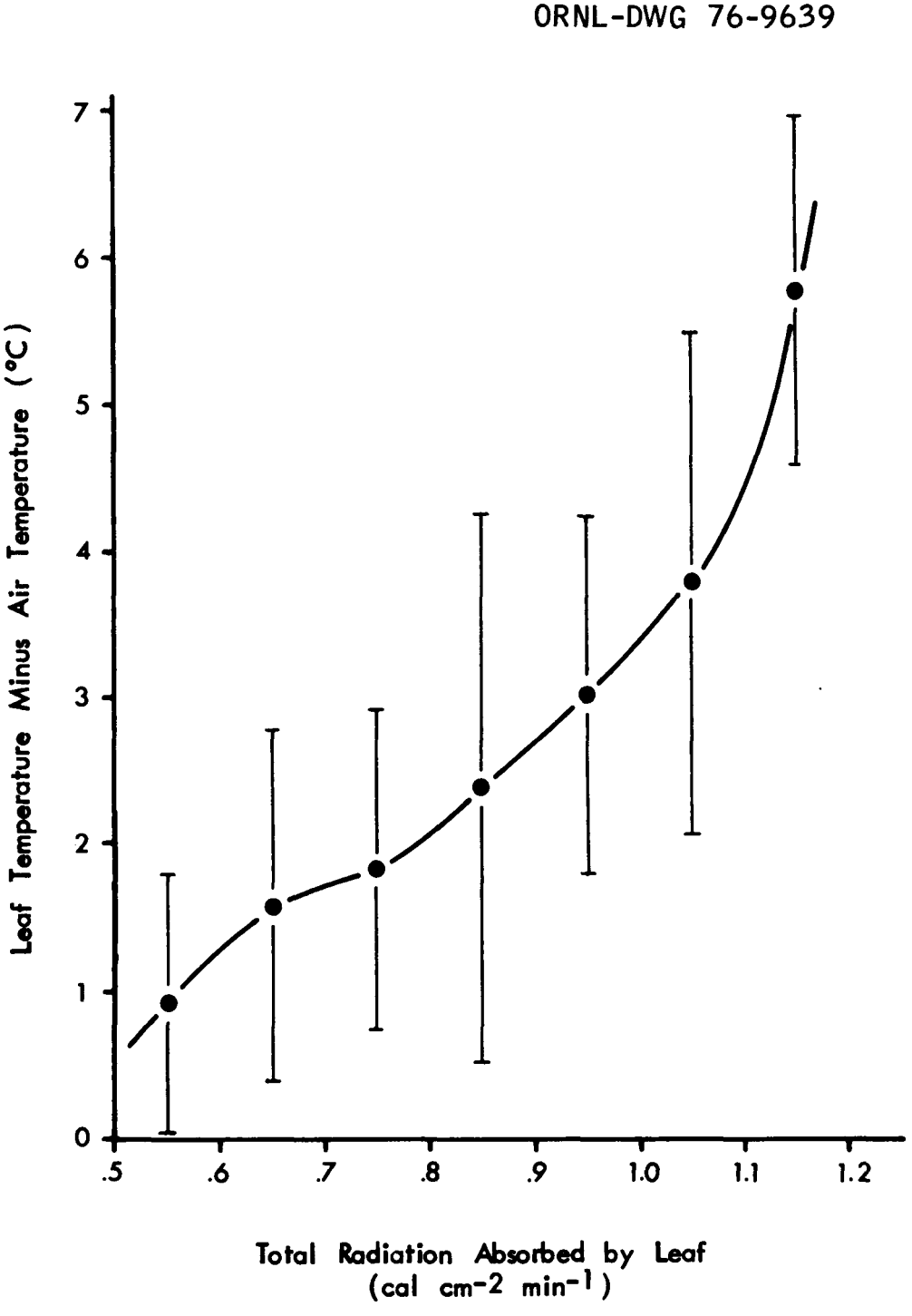

Figure 10. The relationship between leaf temperature minus air temperature (± SD) and total radiation absorbed by the leaf for in situ tulip poplar leaves.

Table 5. Calculated tulip poplar transpiration rate by crown level.

Crown Level	Mean Transpiration Rate ± SD
Top	$29.3 \pm 17.8 \times 10^{-5}$ g cm^{-2} min^{-1}
Middle	$14.3 \pm 7.7 \times 10^{-5}$ g cm^{-2} min^{-1}
Bottom	$8.1 \pm 6.5 \times 10^{-5}$ g cm^{-2} min^{-1}

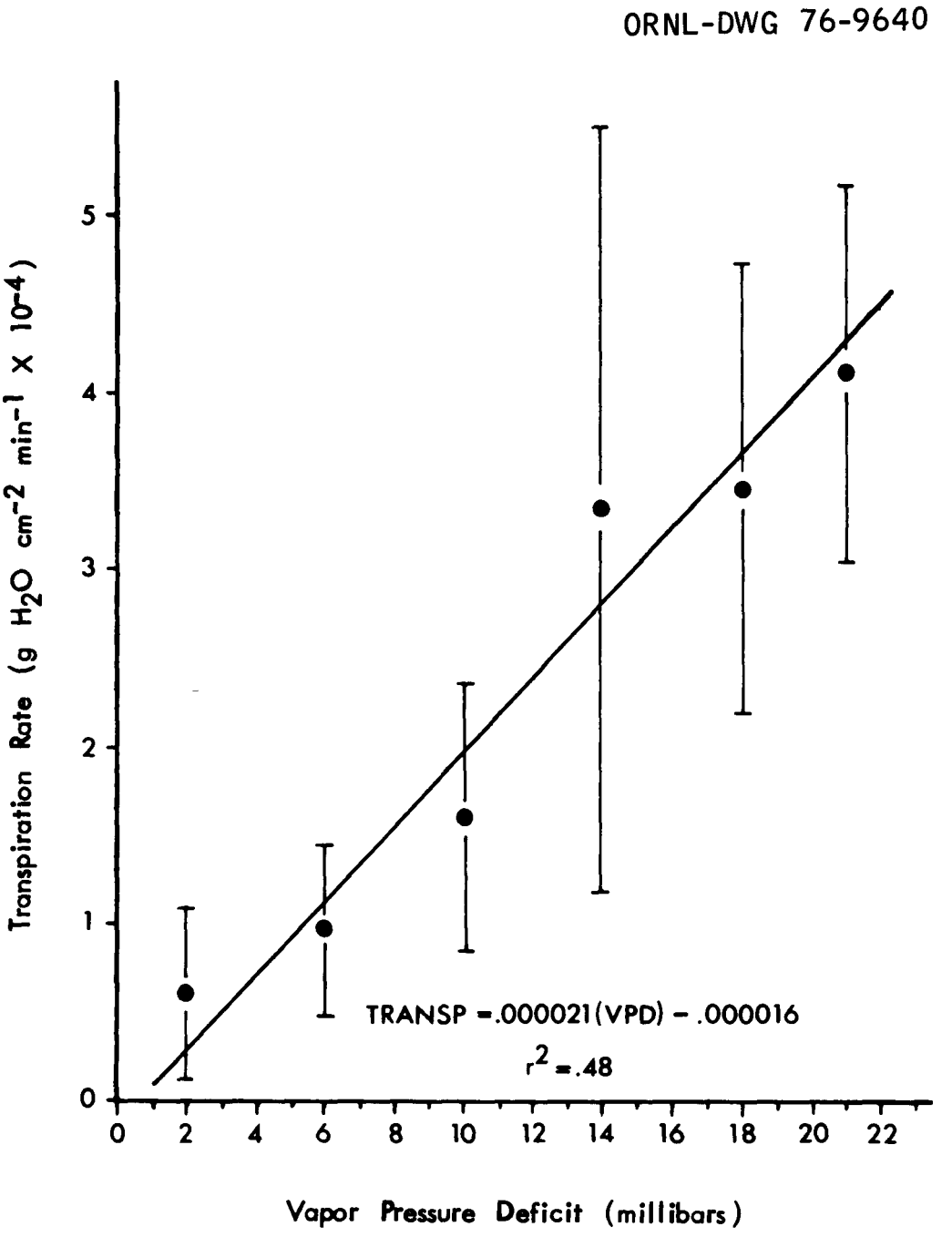

Figure 11. Calculated transpiration rate (± SD) versus vapor pressure deficit for in situ tulip poplar.

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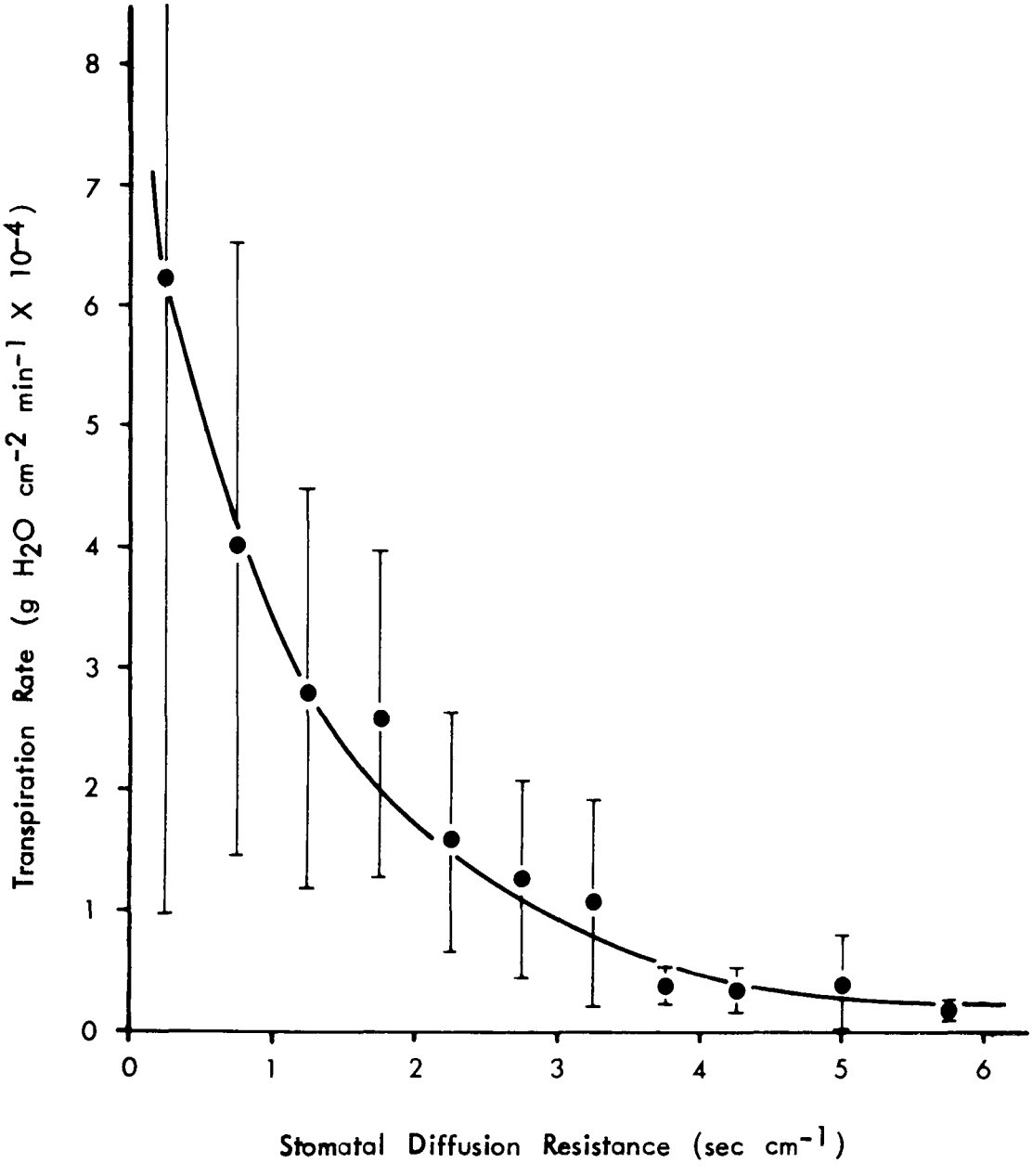

Figure 12. The relationship between calculated transpiration rate (± SD) and measured stomatal diffusion resistance for tulip poplar.

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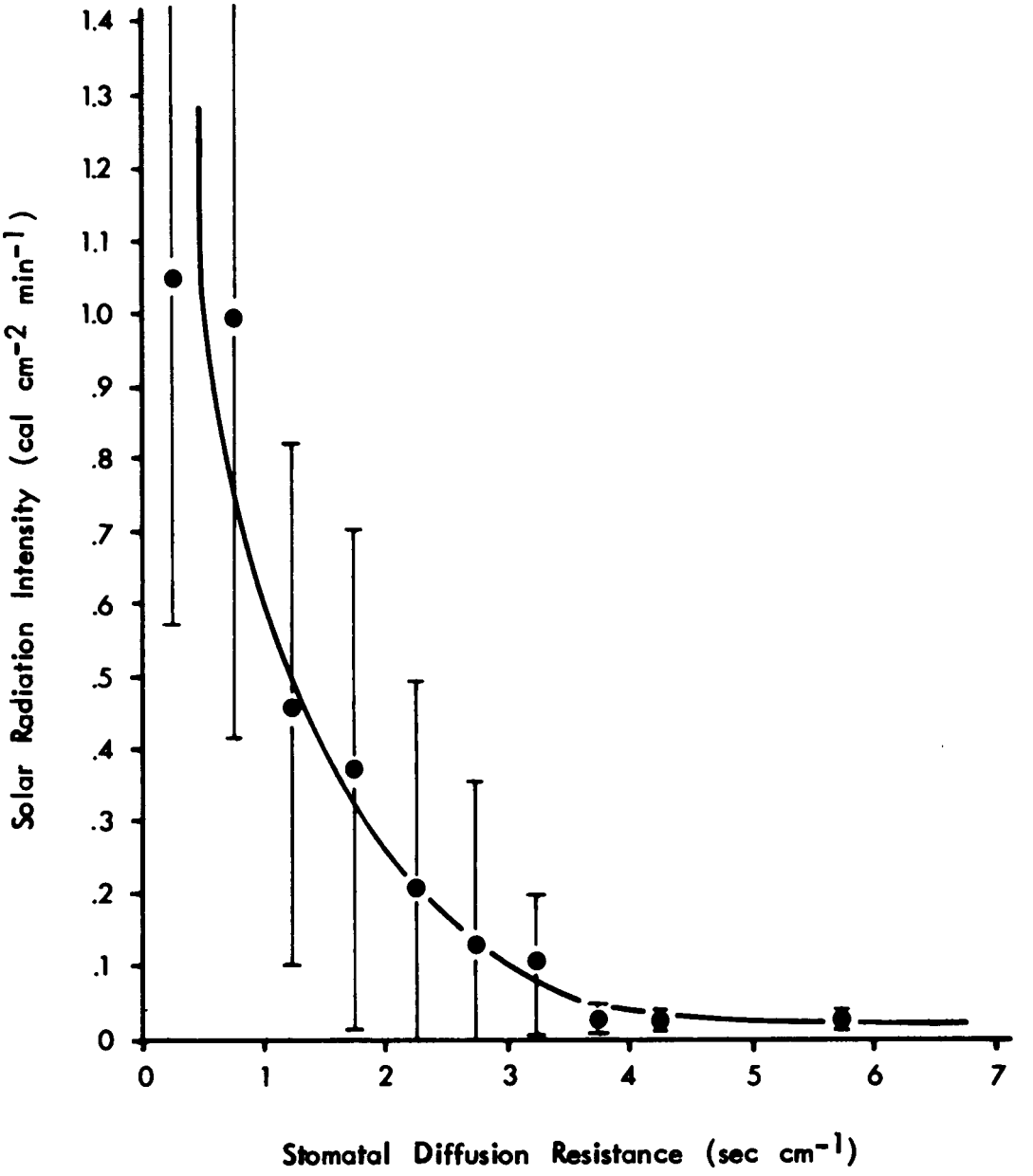

Figure 13. Measured stomatal diffusion resistance variation with changing solar radiation intensity (± SD).

resistance reached its minimum value at about 0.8 cal cm^{-2} min^{-1} and did not decrease significantly at higher light intensities. Stomata were not observed to close in response to changes in xylem water potential over a range from -3 to -14 bars (Figure 14). Leaf xylem potential values increased as stomatal resistance decreased and transpiration rates increased. The decrease in stomatal diffusion resistance occurred mainly in the morning when leaf xylem water potentials were increasing from the diurnal minimum. The rapid rise in xylem potential at 3.5 sec cm^{-1} stomatal diffusion resistance (Figure 14) corresponds to the 0.04 cal cm^{-2} min^{-1} inflection point where diffusion resistance begins to decrease with increasing light intensity. Leaf temperature did not have a significant effect on stomatal diffusion resistance (Figure 15). Any observed changes in stomatal diffusion resistance when compared with leaf xylem potential or leaf temperature appeared to be caused by diurnal cycles coupled to light intensity changes. The increase of stomatal diffusion resistance with decreasing crown height in Figure 16 was explained by the attenuation of light inside the tree canopy. Leaf xylem water potential also decreased in the lower crown (Figure 17) because increased stomatal diffusion resistance reduced transpiration rates. Leaf xylem water potential values

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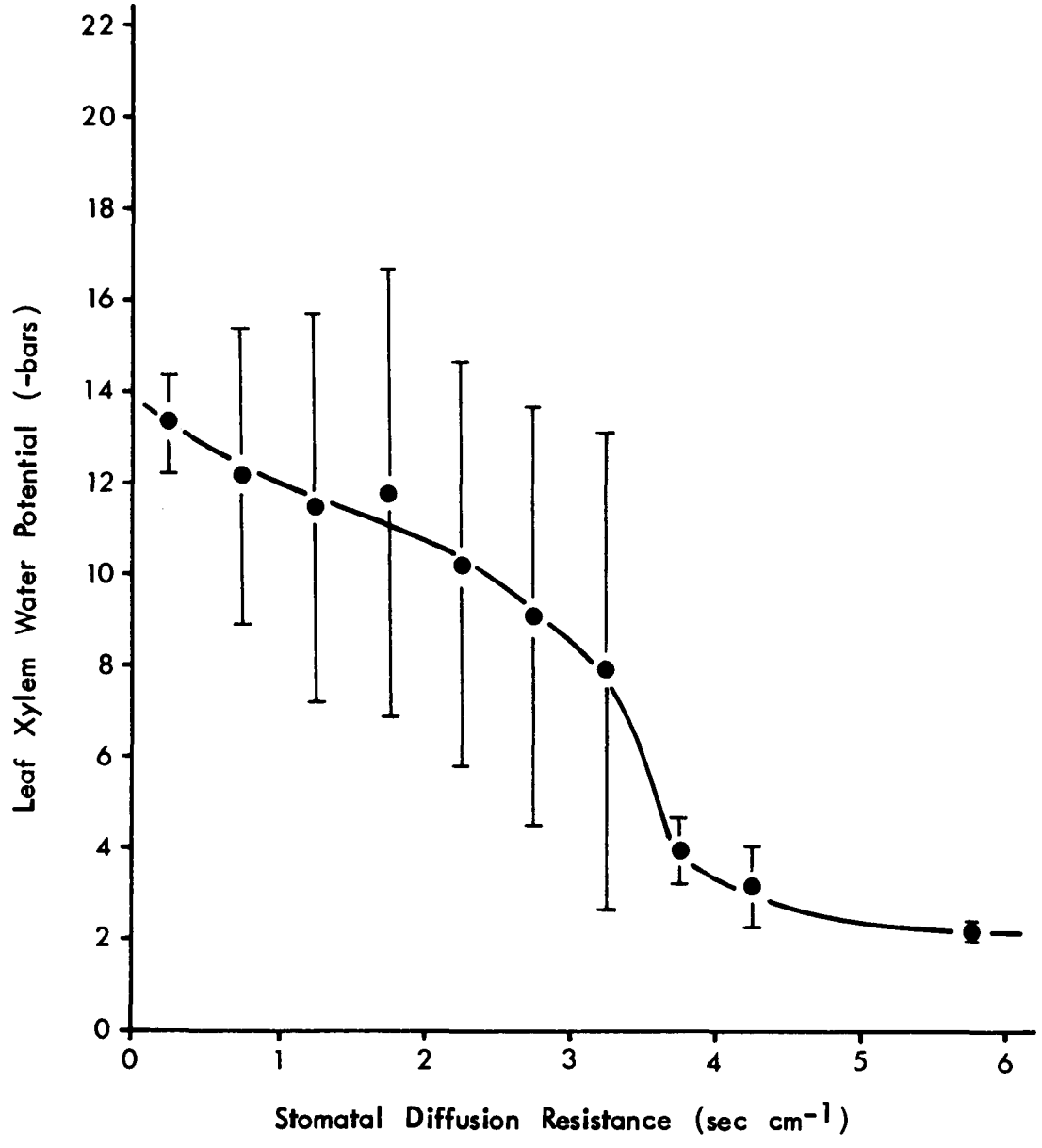

Figure 14. The relationship between tulip poplar stomatal diffusion resistance and leaf xylem water potential (± SD).

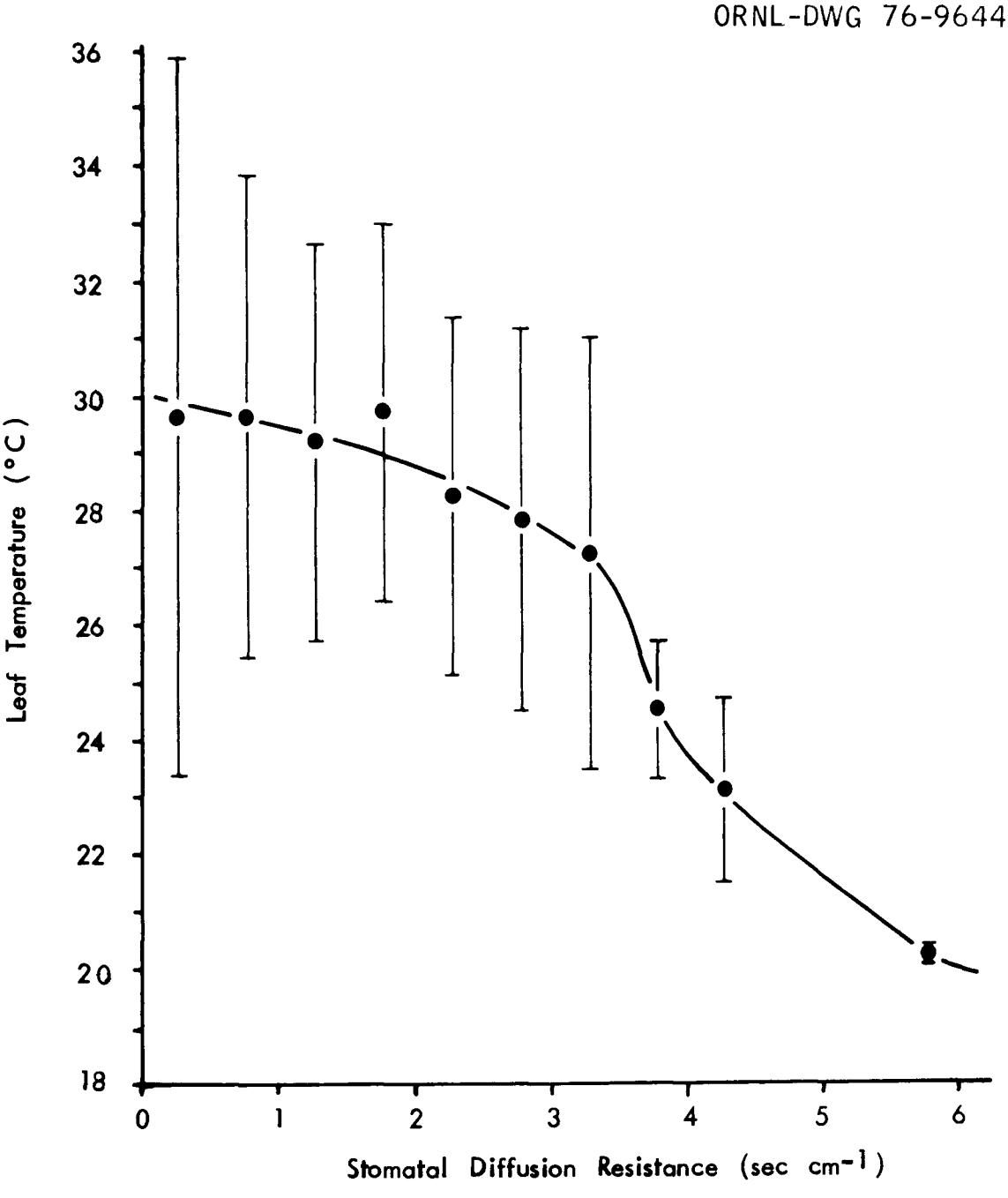

Figure 15. The relationship between tulip poplar stomatal diffusion resistance and leaf temperature (± SD).

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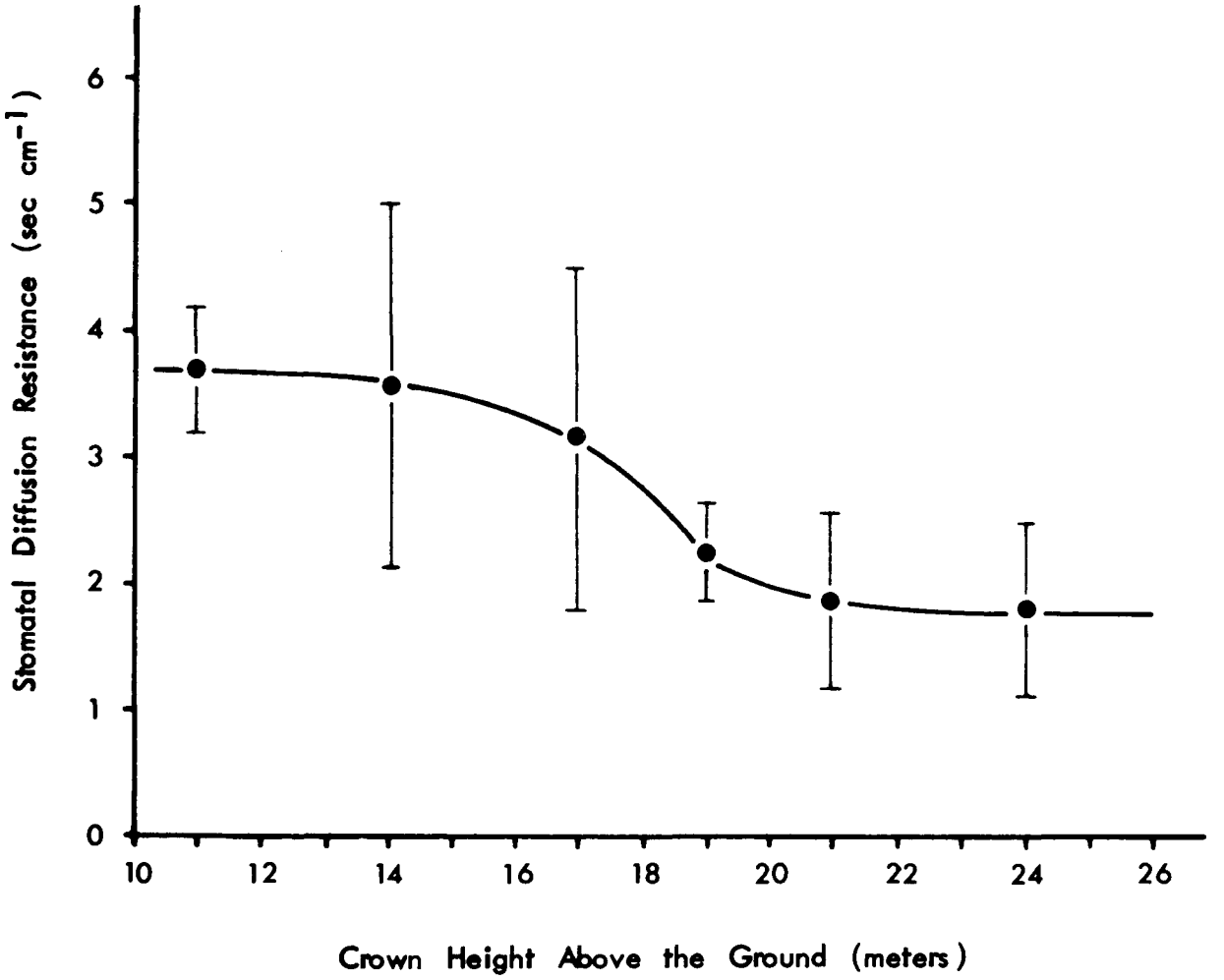

Figure 16. Tulip poplar stomatal diffusion resistance (± SD) variation with crown height above the ground.

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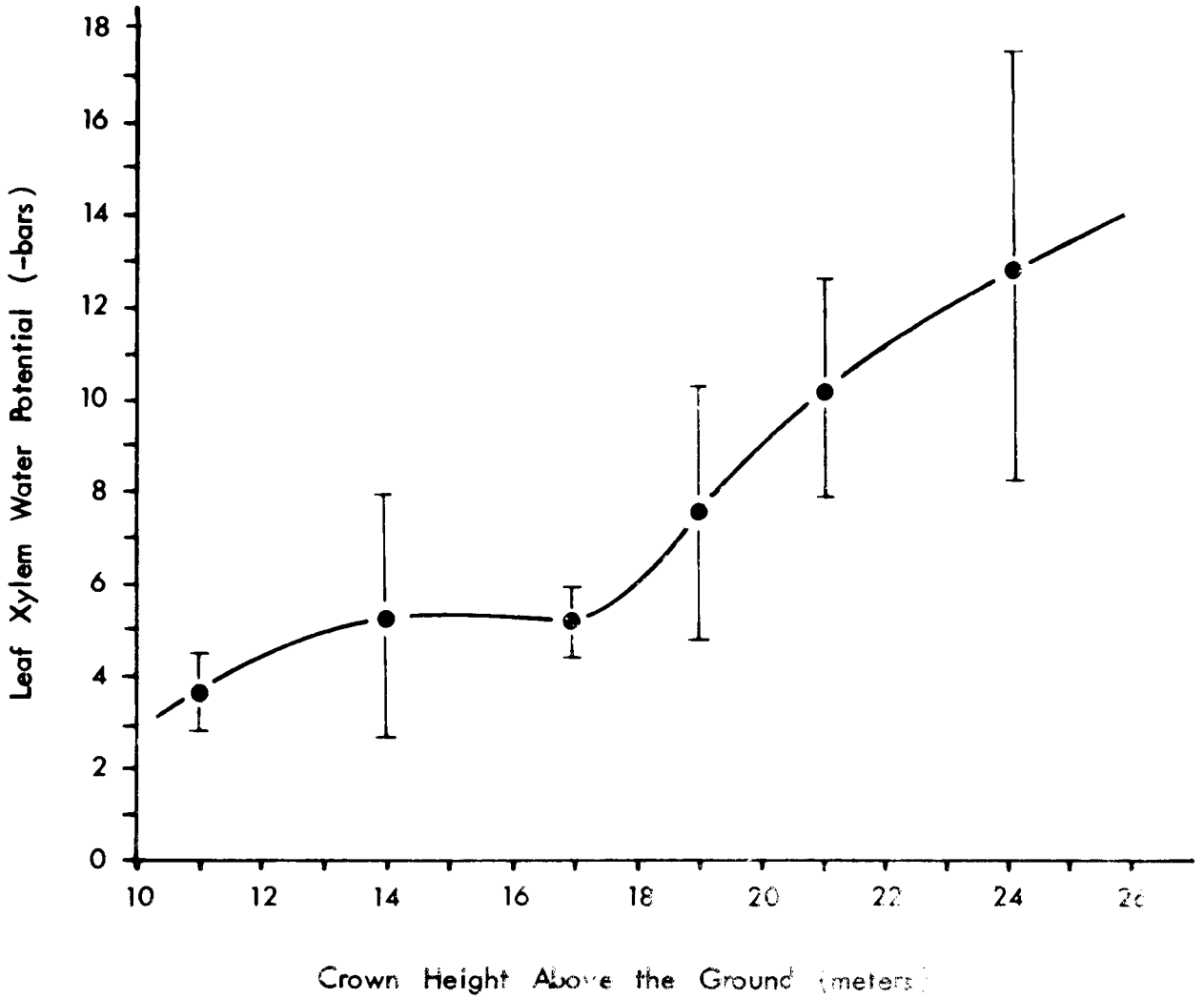

Figure 17. Tulip poplar leaf xylem water potential (± SD) variation with crown height above the ground.

increased with increasing transpiration rate (Figure 18); thus, the measured xylem potential values were the result of water losses exceeding water uptake. Transpiration rates above -22 bars xylem potential indicate the possible beginning of a decrease in transpiration in response to water stress.

Leaf Energy Balance Relationships

The exchange of energy at the leaf determines the magnitude of temperature and water vapor gradients between the leaf and the air. Gradients of temperature and water vapor are the pathways along which transpirational water losses occur, and gradient steepness determines the rate of water vapor losses. Therefore, understanding the component variables of the leaf's energy balance is important in understanding the process of transpiration.

Calculated values for radiative heat loss, evaporative heat loss, and convective heat loss are summed to give total heat loss. Total heat loss is theoretically equal to the calculated total radiation absorbed by the leaf.

Total heat loss values are compared with solar radiation values collected by the National Oceanic and Atmospheric Administration (NOAA) at Oak Ridge, Tennessee, approximately 16 kilometers from the research site.

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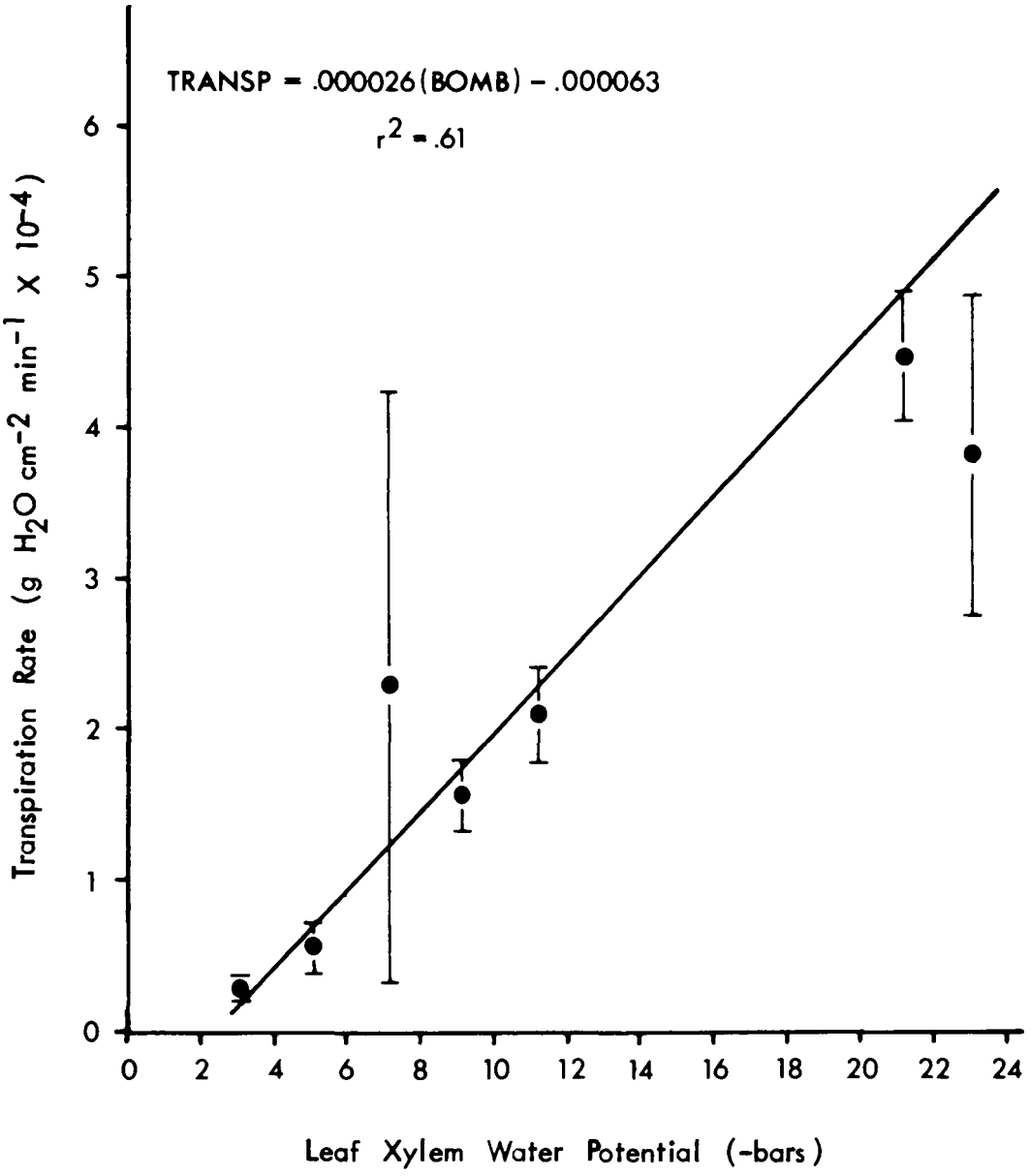

Figure 18. The variation of calculated transpiration rate (± SD) with tulip poplar leaf xylem water potential.

Solar radiation wavelengths measured by NOAA were from 0.3 to 3.0 μ using an Epply pyranometer. Hourly mean NOAA values and corresponding hourly mean total heat loss values for sun leaves in the upper crown are summarized in Figure 19. The Epply pyranometer did not sense either atmospheric or ground thermal infrared radiation (> 3 μ wavelength), but this radiation input was included in the total heat loss value which exceeded solar radiation (Figure 19) when thermal infrared radiation was a large percentage of the total absorbed radiation. The percentage of thermal infrared radiation absorbed by the leaf changed as the total radiation absorbed by the leaf increased (Figure 20). Thermal infrared radiation was at least 50 percent of the calculated total radiation absorbed by the leaf. The diurnal trend illustrated in Figure 19 shows solar radiation became larger than total heat loss from 12:00 A.M. to 2:00 P.M., the period of maximum solar radiation input. Early morning values are clustered around the 1:1 line. As the day progressed, branches and leaves warmed and emitted more thermal radiation. In the late afternoon as solar radiation decreased, heat stored by objects surrounding the leaf was radiated as thermal infrared radiation causing total heat loss to be larger than the NOAA solar radiation value. During the day the forest

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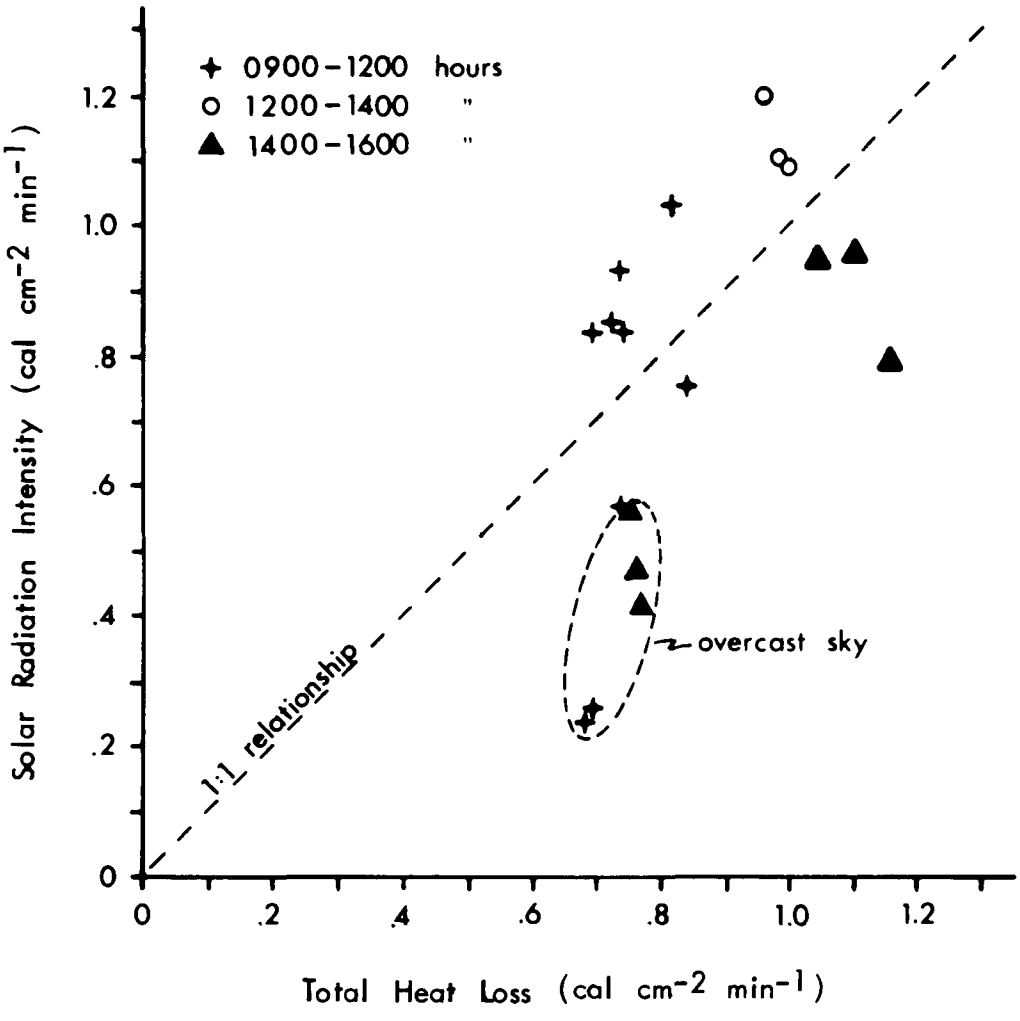

Figure 19. Mean daily values of calculated total heat loss from a tulip poplar leaf compared with measured direct beam solar radiation intensity of 0.3 to 3.0 μ wavelength.

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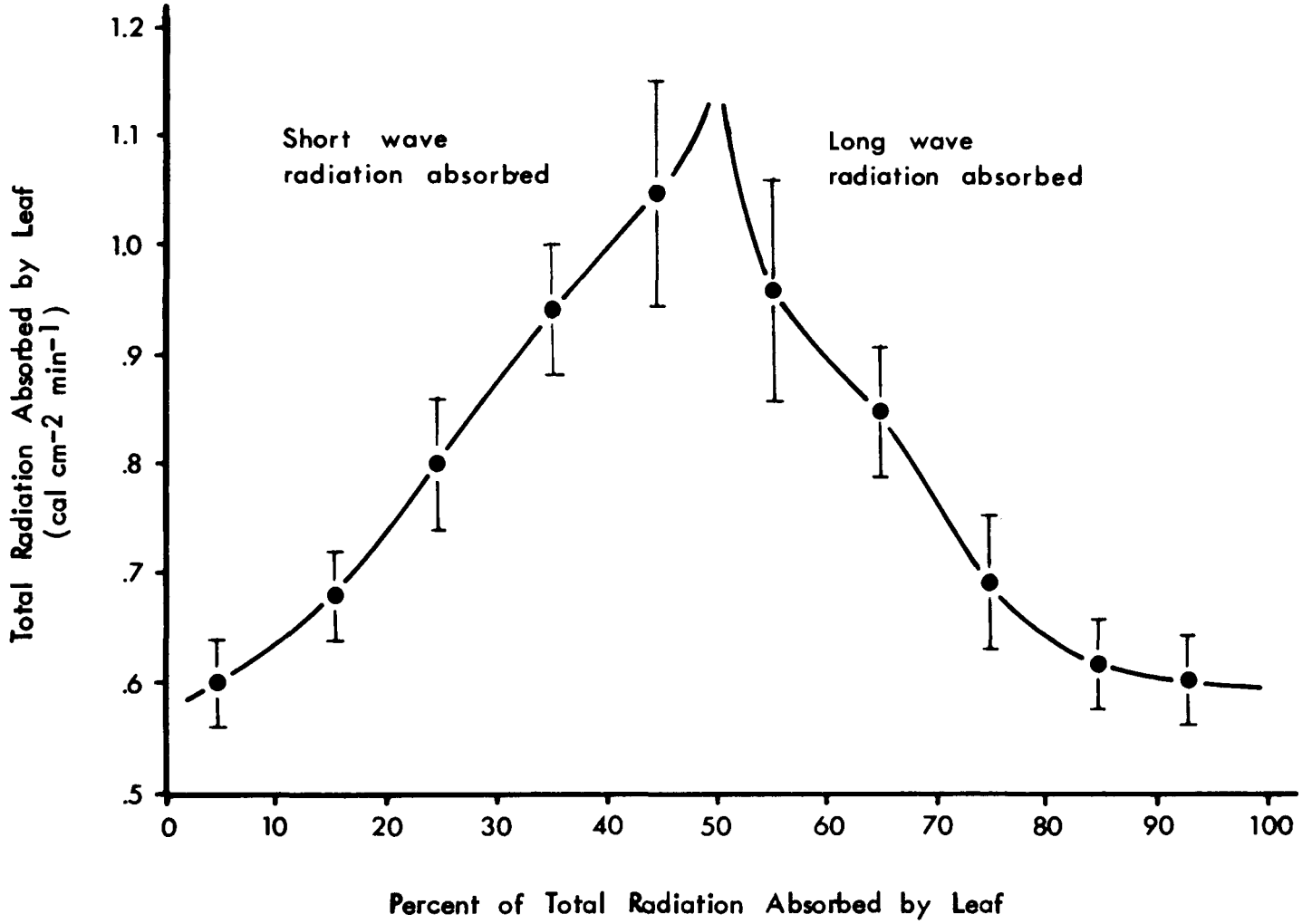

Figure 20. The percent of calculated short-wave and long-wave radiation absorbed by a tulip poplar leaf compared with the calculated total radiation absorbed (± SD).

would be expected to act as a heat sink with thermal infrared radiation being released in the late afternoon and evening. Overcast conditions should also result in a high percentage of thermal infrared radiation in the total radiation input. Thus, thermal infrared radiation was an important influence on the diurnal leaf energy balance.

Total heat loss values were representative of the amount of incoming solar radiation absorbed by the leaf as shown by the agreement between total heat loss and solar radiation values summarized in Figure 19, page 55. Calculated total radiation absorbed by the leaf and total heat loss are compared in Figure 21. The regression analysis shows total heat loss to be 5 percent higher at high radiation values than would be expected if an ideal relationship existed, and 20 percent higher at low radiation values. This discrepancy is probably a result of underestimating atmospheric and ground thermal infrared radiation values in calculating total radiation absorbed by the leaf. More detailed radiation measurements would be needed before this relationship between total heat loss and total radiation absorbed by the leaf could be adjusted or verified.

The energy budget derived from all the collected data is shown in Figure 22. Data for radiative heat loss,

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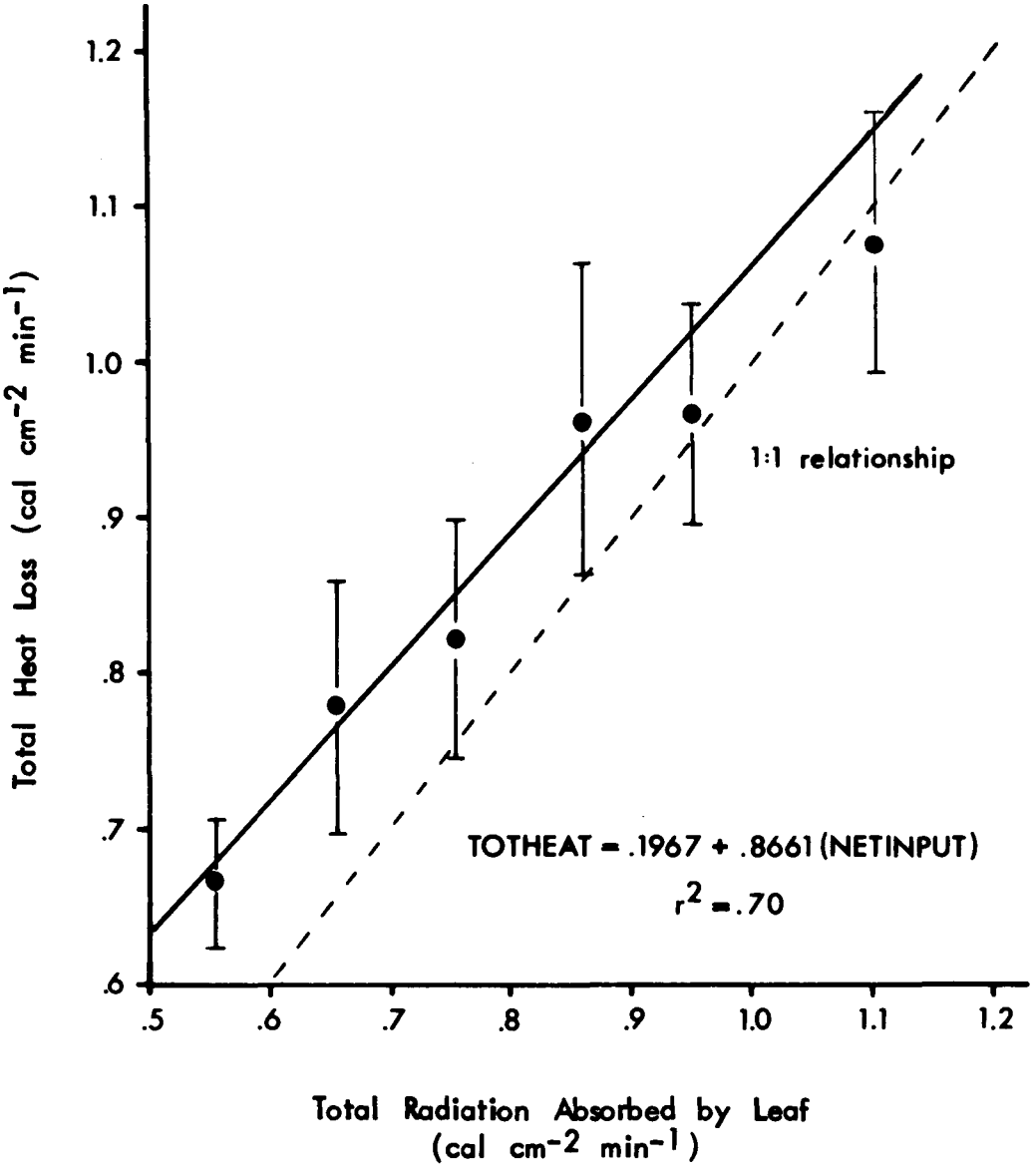

Figure 21. The comparison of calculated total radiation absorbed and calculated total heat lost (± SD) from tulip poplar leaves.

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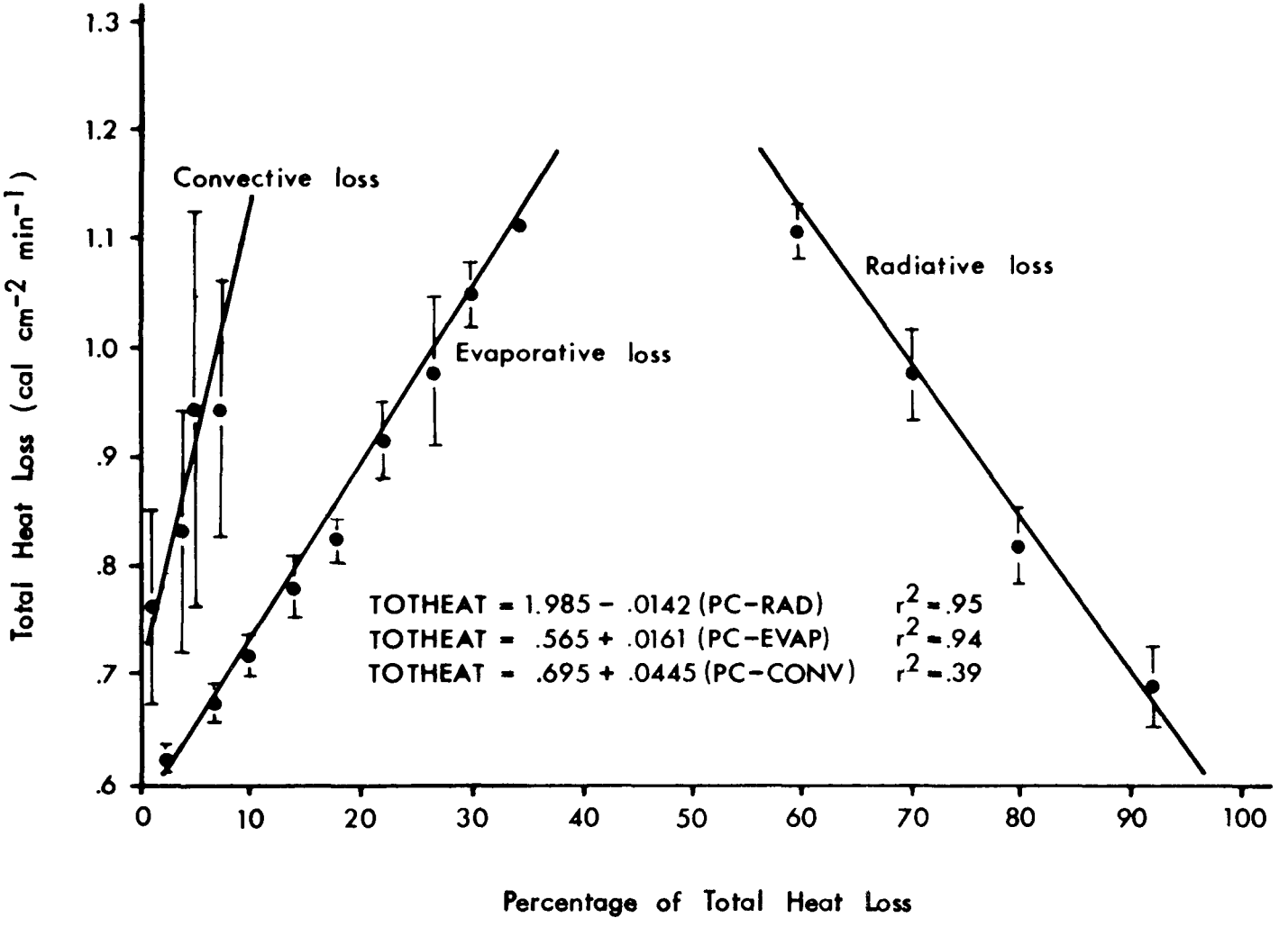

Figure 22. Percent heat loss by convection, evaporation, and radiation compared with calculated total heat loss (± SD) from tulip poplar leaves.

as a percent of total heat loss, and evaporative heat loss, as a percent of total heat loss, have high regression coefficient values and are well described by their respective regression line. Convective heat loss valves, as a percent of total heat loss, are scattered due to inaccuracies of the calculated wind speed in the canopy; thus, the low regression coefficient value.

The partitioning of total heat loss terms with height in the crown is summarized in Figure 23. The larger total radiation absorbed by the leaf, leaf and air temperature difference, VPD, and wind speed values found in the upper crown result in greater heat loss by evaporation and convection than lower in the crown. In the middle and bottom crown levels the environmental variables that drive evaporative and convective heat losses were smaller, and radiative loss accounted for most of the heat loss. Tulip poplar leaves in the top crown level were observed to be more vertically oriented than those of lower levels. This reduced the amount of solar radiation absorbed by the leaf.

Diurnal Trends

Diurnal trends were driven by incoming solar radiation. The leaf stomata opened in response to increasing light intensity (Figure 13, page 46). Radiation absorbed by the leaf (Figure 24) and air brought about heating that increased the steepness of the VPD

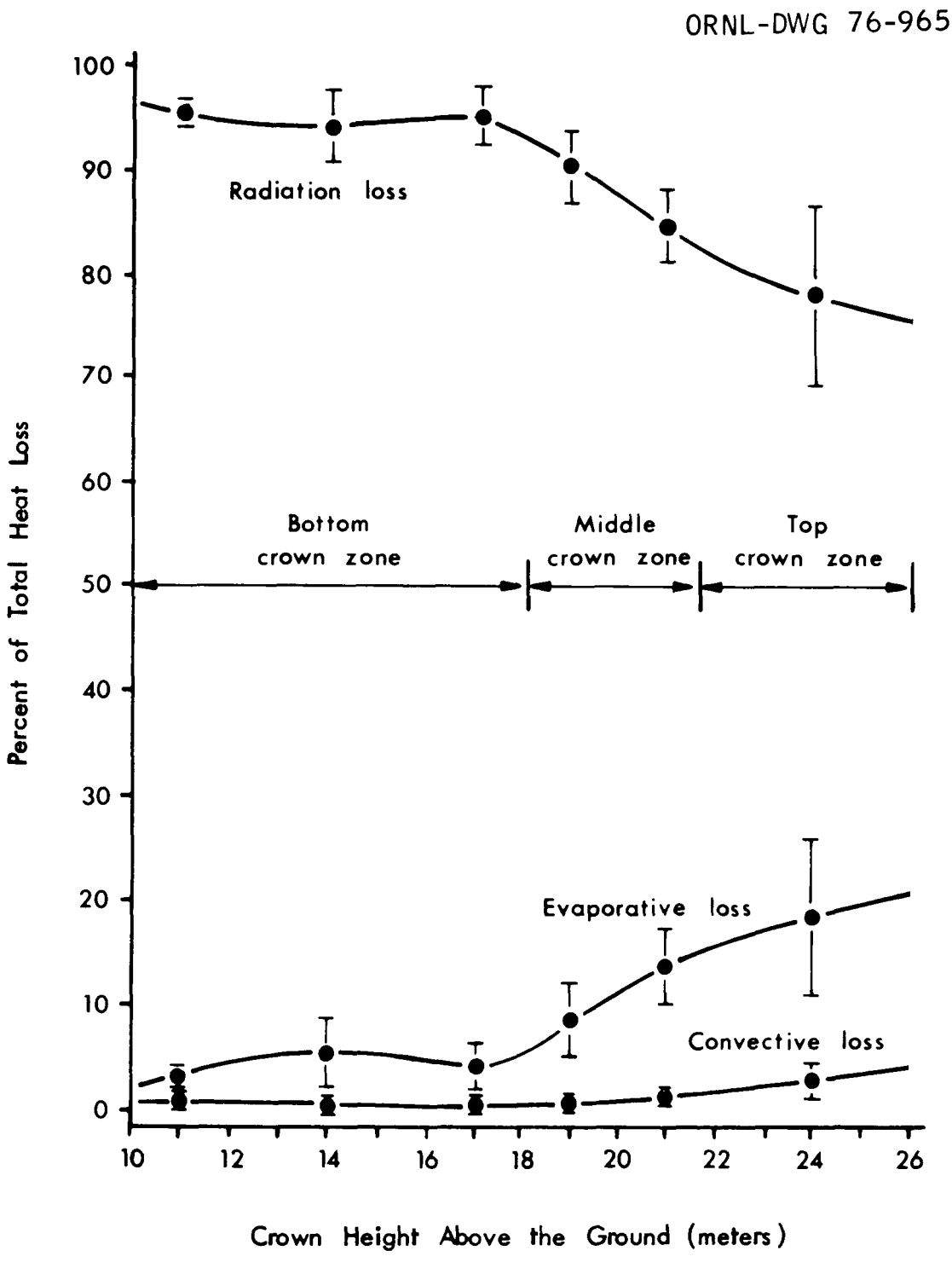

Figure 23. Radiative, evaporative, and convective heat losses as a percent of calculated total heat loss (± SD) from tulip poplar leaves at different heights in the tree crown.

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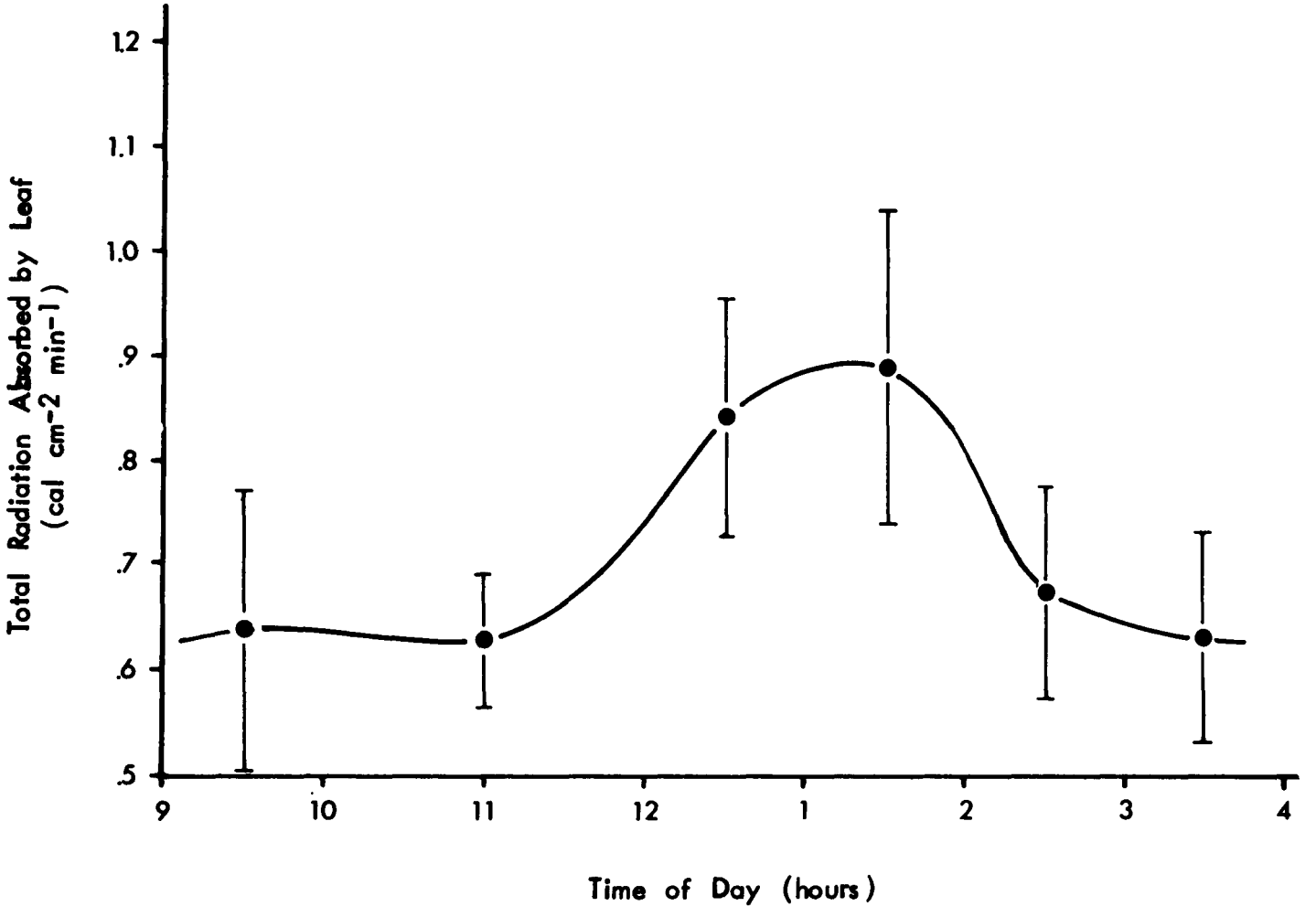

Figure 24. The diurnal variation of calculated total radiation absorbed (± SD) by tulip poplar leaves.

and temperature gradients across the leaf boundary layer. Transpiration rates, represented by evaporation loss (Figure 25), increased resulting in cooling of the leaf and a rise in water deficits. Leaf temperature increased resulting in an increase between leaf and air temperature. The larger leaf minus air temperature difference along with increased wind in the afternoon resulted in greater convective cooling. As radiation absorbed by the leaf decreased in the afternoon, the other variables also decreased. Stomatal diffusion resistance values began to increase in response to reduced light after 2:00 P.M. Transpiration was reduced as diffusion resistances increased and VPD and temperature gradients lessened.

The diurnal trends of the variables discussed above are illustrated in Figures 24-29 based on data collected during July and August, 1973. Stomatal diffusion resistance values reached a minimum and then began increasing after about 1:30 P.M. The increase in stomatal diffusion resistance corresponded with the decline in values of other environmental variables. Sampling procedures may explain the steep afternoon decline of total radiation absorbed by the leaf (Figure 24) since measurements were made on the shaded side of the tree in the afternoon. Heavy dew was common on the

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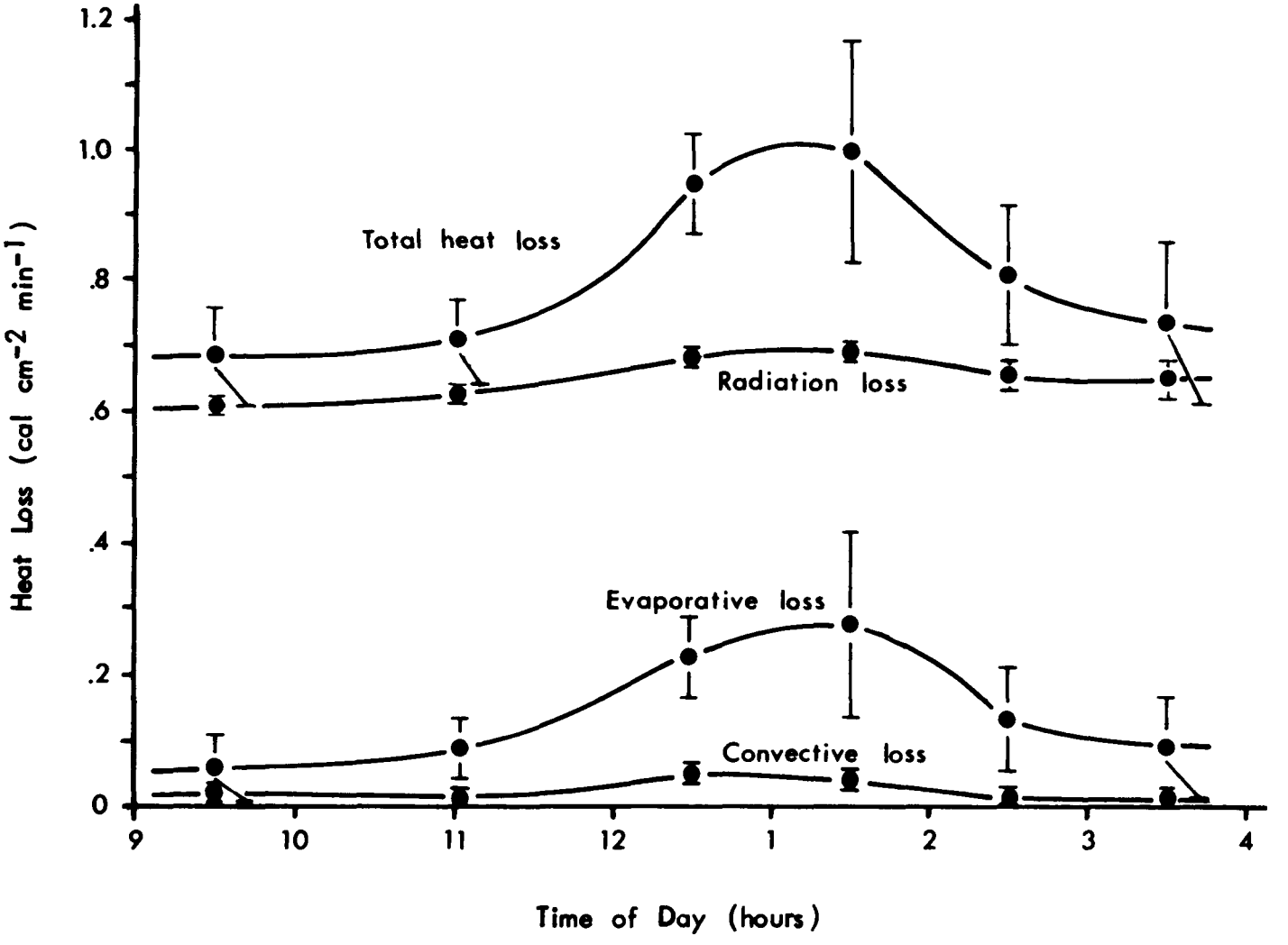

Figure 25. The diurnal variation of calculated total radiation, evaporation, and convection heat losses for tulip poplar leaves (± SD).

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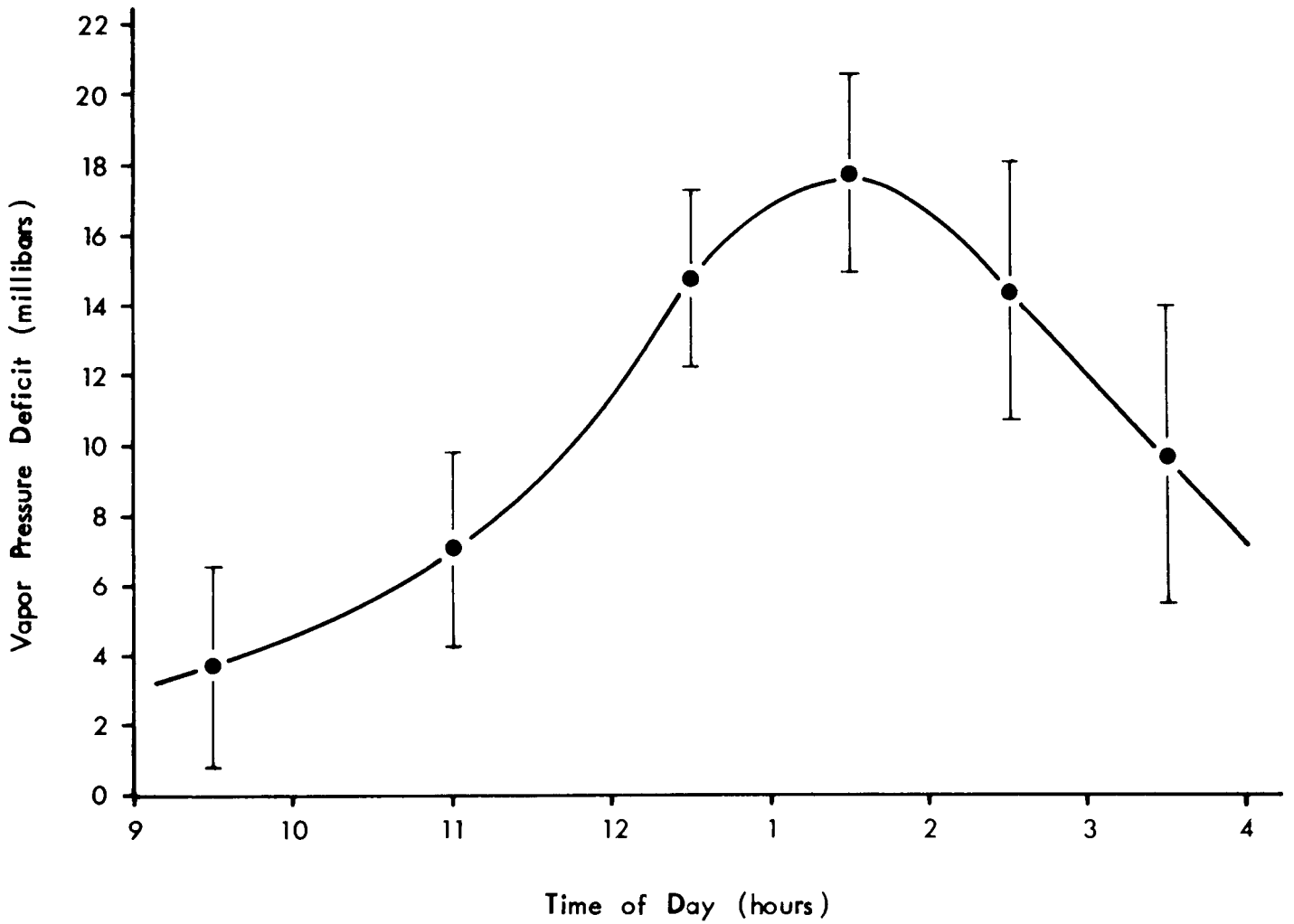

Figure 26. The diurnal variation of vapor pressure deficit (± SD).

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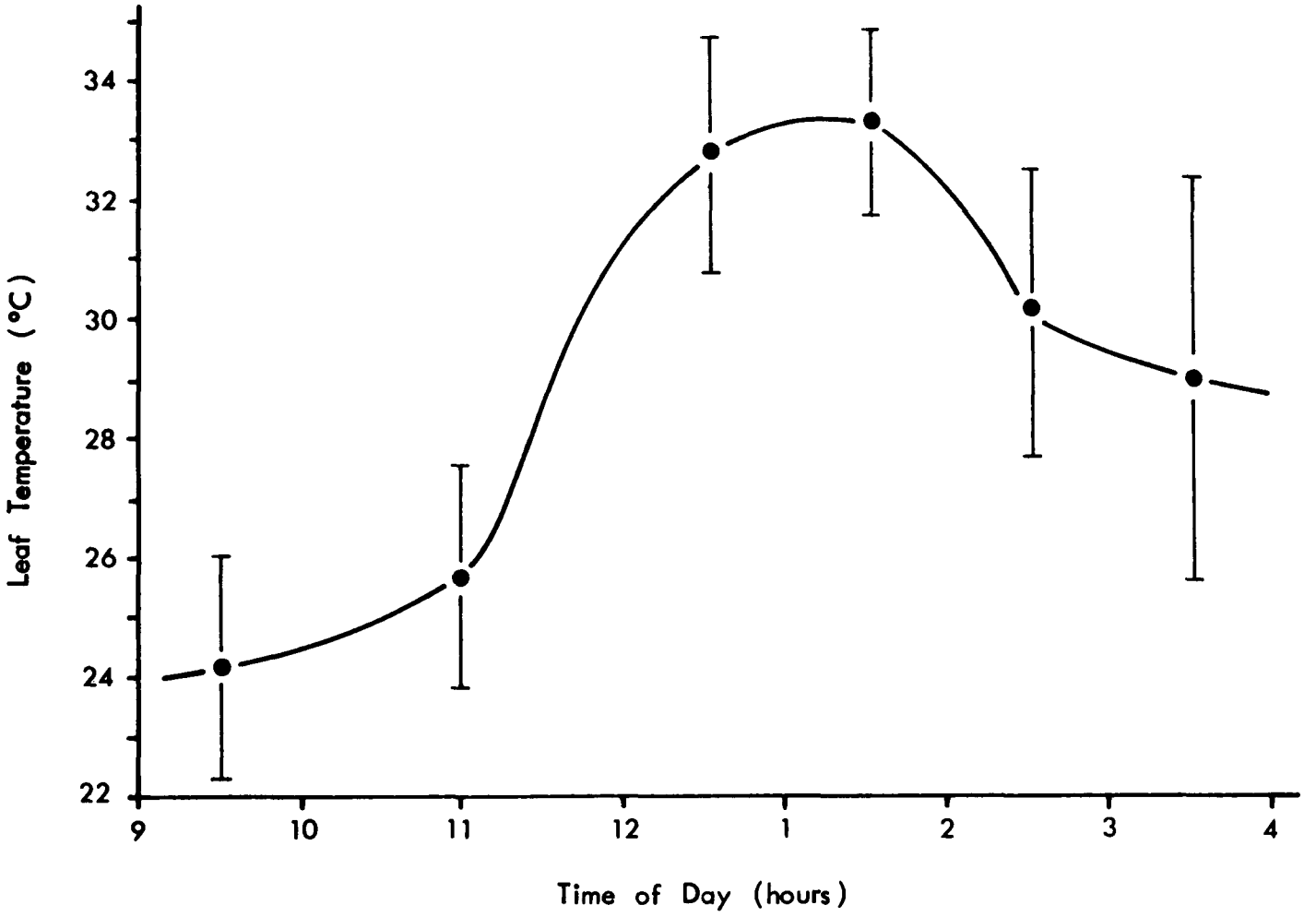

Figure 27. The diurnal variation of tulip poplar leaf temperature (± SD).

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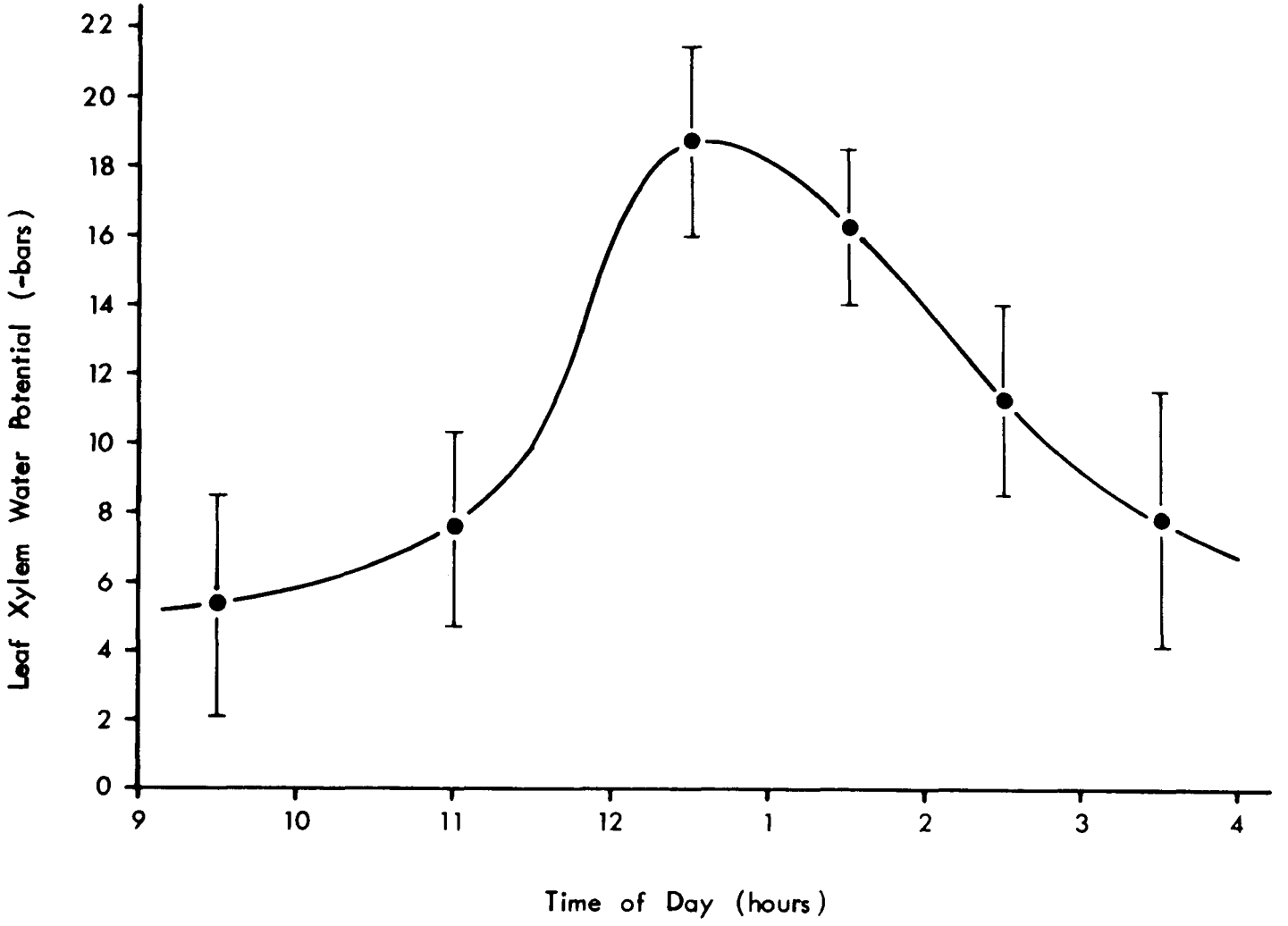

Figure 28. The diurnal variation of tulip poplar leaf xylem water potential (± SD).

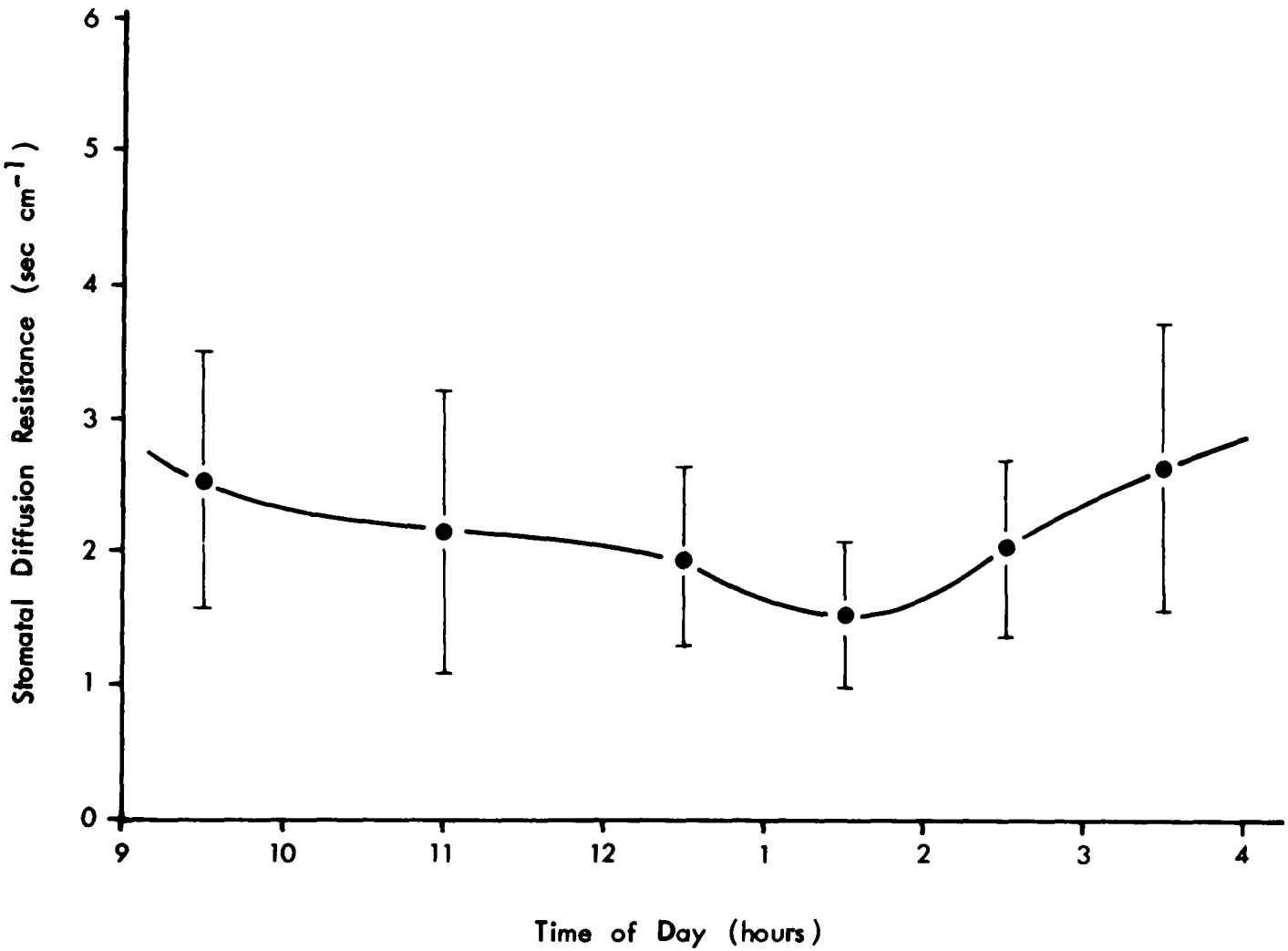

Figure 29. The diurnal variation of tulip poplar leaf stomatal diffusion resistance (± SD).

leaves in the morning. Dew evaporation would tend to cool the leaves and form a sink for heat absorbed early in the day. This would explain the gradual change of water potential, stomatal resistance, and leaf temperature during the early morning hours. Dew was usually gone by 10:00 or 11:00 A.M. Transpiration, represented by evaporative heat loss on Figure 25, page 64, showed a more rapid increase after about 11:00 A.M. in response to the disappearance of the dew on the leaves. The peak value of xylem potential occurred about one hour prior to the maximum diurnal values of VPD and transpiration. Thus, diurnal transpiration rates were determined by saturated vapor deficits and stomatal resistance which varied with changing light intensity. Diurnal transpiration rates were not observed to be limited by measured leaf xylem water potential.

III. DISCUSSION

Stomatal Size and Distribution

The stomatal impression technique proved to be an efficient method for obtaining leaf impressions in the field. Counting individual stomata for density determinations was easily accomplished, as were measurements of the guard cell dimensions and epidermal surface features. Stomatal density and slit length measurements are consistent with values and variations reported for other species by Meidner and Mansfield (1968). Accurate measurement of the stomatal opening was more difficult, since the narrowest part of the stomatal aperture must be observed to adequately measure the controlling aperture (Gloser, 1967). Although detailed views of a transverse section of a tulip poplar stoma were not observed, Figure 30 is believed to represent this structure.

The stomatal impression must reproduce the central aperture to adequately reflect the stomatal width controlling diffusion. Gloser (1967) found when the eisodial aperture was small, about 1-3 μ, impressions would not show the central aperture. Thus, the upper closing flaps are an obstacle to obtaining impressions of the central aperture. Wenzl (1939) studied the applicability of epidermal impressions to studies of the stomatal aperture.

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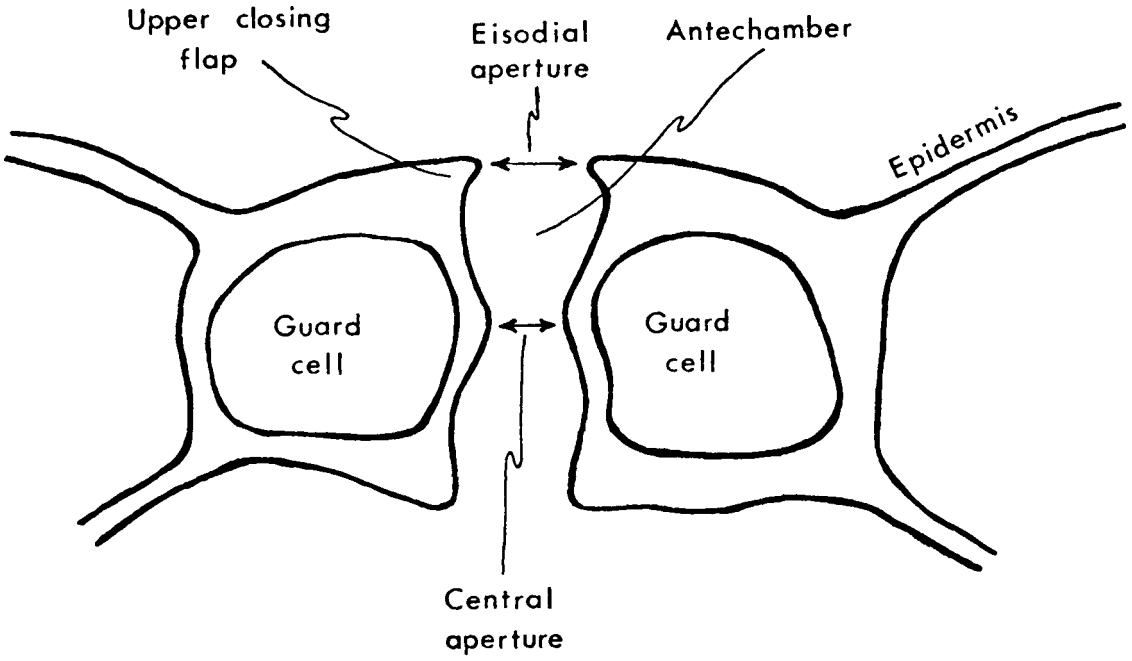

Figure 30. Representation of a stoma transverse section showing the relative position of the eisodial and central apertures.

He concluded this method was applicable only when stomatal closing was achieved by the upper closing flaps, or when the movement of the flaps corresponded to changes in the central aperture. Meidner and Mansfield (1968) reported that the upper closing flaps and the central aperture did not always move in unison, thus the antechamber may remain unaltered while the central aperture changes in dimensions, or vice versa. Figure 3, page 30, shows the upper closing flaps of the stomata and suggests the impression does reach into the antechamber, but it is doubtful if the impression technique used in this study

allowed measurement of the central aperture.

Stomatal density and slit length values were uniform over the leaf, although microscopic observation revealed a density gradient that appeared to decrease with distance from major leaf veins. This gradient, although not measured, must have been uniform over the leaf surface to result in equal stomatal density between leaf quadrants. Tulip poplar stomatal density and size varied significantly with respect to height in the crown. Yet, the inverse relationship between stomatal density and leaf size with height resulted in a relatively equal number of stomata per leaf in all three crown levels.

The importance of stomatal density, stomatal size, and leaf size variations with crown level must be evaluated in terms of their importance to physiological processes. These variables must interact to optimize diffusion of both carbon dioxide and water vapor through the stomata per unit of leaf surface area. One index of the interaction of these variables could be the distance between neighboring stomata corrected for stomatal size. This concept was used by Bange (1953) to test for transpiration interference between stomatal pores. Parlange and Waggoner (1970) found when the interstomatal spacing was three times the longer dimension of a stoma the interference between pores was minimal, and that for the

stomatal spacing normally found in nature interference is negligible. Still, stomatal spacing must be suited to a particular environment. A ratio of the mean inter-stomatal spacing over the mean stomatal slit length for the three crown levels is presented in Table 6. The ratio is similar at all three crown levels; thus, the variation in leaf size, stomatal density, and slit length combined to produce the same relative spacing for all positions in the crown.

Stomatal and Boundary Layer Resistances

The boundary layer resistance was not greatly influenced by stomatal size or distribution since it

Table 6. Tulip poplar interstomatal spacing by crown level.

Crown Level	Mean Pore Area (cm^2)	Interstomatal Spacing (μ)	Mean Slit Length (μ)	Ratio
Top	4.65×10^{-5}	76.98	15.05	5.11
Middle	7.34×10^{-5}	96.70	19.60	4.93
Bottom	9.16×10^{-5}	107.98	18.10	5.97
Mean	6.67×10^{-5}	92.18	17.58	5.24

depended on atmospheric conditions, leaf shape, and the presence of other leaves. Bange (1953) calculated the diffusion rate (i) from stomatal resistance (r_s) and boundary layer resistance (r_a) using equation 16:

$$i = (C_s - C_a)/r_s + r_a \qquad (16)$$

where C_s is the water vapor concentration in the substomatal space and C_a is the water vapor concentration in the surrounding air. When r_s was larger than r_a, r_s would practically determine the transpiration rate, thus transpiration would be proportional to the stomatal aperture. As the stomatal aperture increased, r_a became more important and may have constituted the main limiting factor to transpiration. The relationship of leaf diffusion resistance, or transpiration rate, to wind speed was presented in Figure 5, page 34. Wind speeds able to remove all external boundary resistances would result in transpiration rates being directly proportional to stomatal aperture. Bange (1953) presented data by Stålfelt (1932) showing a 10 cm sec^{-1} wind speed increased transpiration by 90 percent and a 60 cm sec^{-1} wind speed increased transpiration by 140 percent over still air conditions. These increases in transpiration can be assumed equivalent to decreases in diffusion resistance. In Figure 4, page 33, the lowest wind speed was 10 cm

sec^{-1} and the next increment of wind speed was 60 cm sec^{-1}. The difference of 50 percentage units between a 90 and 140 percent decrease in total diffusion resistance due to wind speed would result in the two bands of calculated diffusion resistance in Figure 4, page 33. Bange (1953) also presented data showing removal of the boundary layer resistance by wind resulted in lower total diffusion resistances over a range of stomatal aperatures to give the same relationship presented in Figure 4. Wind speed increasing from 10 cm sec^{-1} to 60 cm sec^{-1} on Figure 4 decreased calculated leaf diffusion resistance 56 to 41 percent as stomatal width increased from 0.6 μ to 3.0 μ, respectively.

Leaf boundary layer resistance and stomatal resistance combine to control transpiration. Stomatal resistance was found to be controlling at small apertures and the boundary layer resistance was dominant at larger stomatal apertures at low wind speeds (Figure 7, page 37). Wind speeds above about 60 cm/sec had no major influence in reducing total leaf resistance, with stomatal resistance being dominate.

Transpiration

The mean rate of transpiration calculated for this study was $20 \pm 16 \times 10^{-5}$ g cm^{-2} min^{-1}. Harris, Witherspoon, and Olson (1970) reported a transpiration rate of 5×10^{-5} g cm^{-2} min^{-1} for excised tulip poplar

seedling leaves. The values in Table 7 were published by Kramer and Kozlowski (1960) as daily average rates during August. These values were recomputed assuming a 10-hour day during which most transpiration occurred, and the resulting values closely approximate the mean transpiration rate measured for this study.

The best linear correlations were between transpiration and its driving variables, VPD, wind speed, and the difference between leaf and air temperature. Transpiration values decreased with decreasing height in the crown in response to decreasing radiation inputs, and the concomitant decreases in the driving gradients. Leaf xylem water potential became less negative with height along with decreasing transpiration rates. Stomatal diffusion resistance responded strongly to light intensity with stomatal opening beginning at 0.04 cal cm^{-2}

Table 7. Published transpiration rates for tulip poplar during August.

Location	Published Rate	Recomputed Rate
Columbus, Ohio	10.11 g dm^{-2} day^{-1}	17 x 10^{-5} g cm^{-2} min^{-1}
Durham, N. C.	11.78 g dm^{-2} day^{-1}	20 x 10^{-5} g cm^{-2} min^{-1}
Durham, N. C.	9.76 g dm^{-2} day^{-1}	16 x 10^{-5} g cm^{-2} min^{-1}

min^{-1}, a value that corresponds to the carbon dioxide compensation point for tulip poplar. Transpiration rates increased as xylem water potential values became more negative, and increasing water stress did not cause stomatal closure. Stomatal diffusion resistances were not substantially affected by any variables other than light intensity. Transpiration water losses increased water deficits in the leaves and also provided evaporative cooling to maintain relatively low differences between leaf and air temperature.

Opening and closing of stomata is controlled by light, leaf water content, and temperature (Kramer and Kozlowski, 1960). Low partial pressures of carbon dioxide, or other environmental factors acting indirectly through internal carbon dioxide partial pressures, are thought to influence stomatal actions (Salisbury and Ross, 1969). Other chemical mechanisms have also been suggested as acting indirectly from the effect of light (Raschke, 1975).

Comparing diffusion resistance versus light intensity shows that the abrupt decrease of stomatal diffusion resistance, or stomatal opening, at a value of 3.75 sec cm^{-1} occurs at a point that corresponds to the carbon dioxide compensation point light intensity for tulip poplar. Xylem potential rapidly becomes more

negative as diffusion resistance decreases below the 3.75 sec cm^{-1} value. The mean diffusion resistance value for leaves at the base of the crown was 3.75 sec cm^{-1} (Figure 16, page 50). This trend suggests diffusion resistance values below 3.75 sec cm^{-1} represent stomatal openings that influence physiological functions, and that leaves at the base of the crown may be photosynthesizing near the carbon dioxide compensation point. Data shown on Figure 31 were collected on small, open-grown tulip poplar saplings during April and May (Shimshi, unpublished). Diffusion resistances below 3.75 sec cm^{-1} resulted in an increase in photosynthetic rate. The diffusion resistance, light, and photosynthesis relationships for these saplings would be different than for the tree sampled in this study. Thus, for larger trees later in the season a 3.75 sec cm^{-1} diffusion resistance value may be a threshold value for physiological functions.

Increases in leaf water potential over a narrow range have been shown to cause a large change in diffusion resistance (Boyer, 1970; Jordan and Ritchie, 1971; and Miller, Gardner and Goltz, 1971). The contrasting data gathered on tulip poplar seedlings by Richardson, Dinger, and Harris (1973) showed xylem potentials more negative than -18 bars to cause stomatal closure (stomatal resistance values in excess of 45 sec cm^{-1}). These

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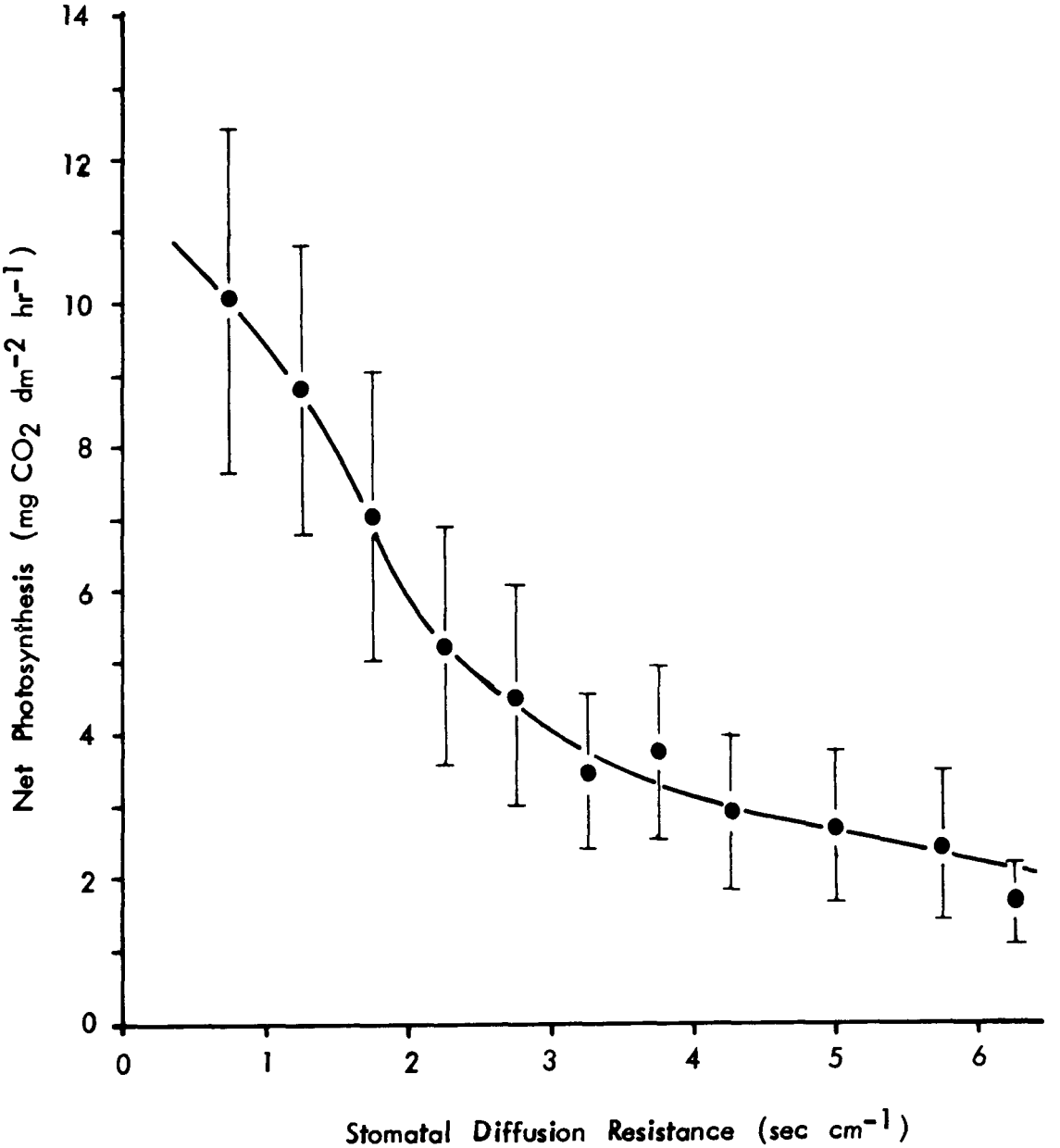

Figure 31. Tulip poplar net photosynthetic rate (± SD) as a function of leaf stomatal diffusion resistance.

seedlings were allowed to experience cumulative increases in xylem potential from day to day, or high morning xylem potentials of -15 bars. The effect of cumulative water stress may be the factor responsible for the seedlings showing stomatal closure and forest trees not exhibiting closure. The *in situ* forest tree used for this study was growing in moist soil that rarely exceeded -5 bars water potential, and the leaves routinely exhibited a low morning leaf xylem potential between -4 and -7 bars (Burgess and O'Neill, 1975). Thus, the tree was able to recover overnight from afternoon water deficits and did not experience high cumulative water deficits and stomatal closure. Other researchers have reported stomatal closure at a threshold level of water stress ranging from -7 to -18 bars depending on the plant species (Hsiao, 1973). Further study has shown this threshold value to respond to the growing environment with greenhouse grown plants closing stomata at water potentials of -16 bars, and field grown plants of the same species closing at potentials of -27 bars (Hsiao, 1973). Thus, a more negative threshold water potential for stomatal closing in field grown plants versus greenhouse grown plants is not unique to tulip poplar. The threshold xylem potential value for stomatal closing was not reached during this study on forest grown *in situ*

tulip poplar leaves, although there was a possible decrease in transpiration rate at leaf xylem water potentials more negative than -22 bars (Figure 18, page 53).

The tulip poplar canopy microclimate is essentially "light dependent," in that changes in temperature, relative humidity, and ambient CO_2 occur in direct proportion to fluctuations in radiant intensity (Dinger, 1972; Burgess and O'Neill, 1975). Tulip poplar stomata react primarily to light intensity. Thus, plant water status, which is correlated with stomatal resistance, is also related to radiant intensity. Stomatal resistance was not increased by xylem potentials resulting from transpiration water losses, thus moisture stress does not become limiting to stomatal diffusion. These findings indicate characterization of the broad features of tulip poplar photosynthetic response can be a function of light and temperature (Burgess and O'Neill, 1975). Such an approach was used in a terrestrial ecosystem energy transfer model (Shugart, et al., 1974), the simulation results of which were very much in line with projections based on field studies. Figures 13 and 31, pages 46 and 79, respectively, show the similarity in the shape of the curves of light and photosynthesis rate versus leaf diffusion resistance. Leaf xylem potential did not increase stomatal diffusion resistance or decrease

photosynthesis over the range of values measured in the field.

Leaf Energy Balance

Energy balance values developed in this study compare favorably with similar values reported in Salisbury and Ross (1969) for a cocklebur leaf (Table 8). The cocklebur values are theoretical calculations representing temperate zone conditions for a bright, warm day with high humidity. These same conditions were normal for the tulip poplar study area.

Table 8. Energy budget for a cocklebur leaf and a tulip poplar leaf.

Energy Balance Components	Cocklebur Leaf[a]	Tulip Poplar Leaf[b]
Radiant energy absorbed or lost (cal cm^{-2} min^{-1})	1.04	1.04
Transpiration energy	17%	28%
Convective energy	12%	8%
Energy reradiated from the leaf	71%	66%

[a]Cal cm^{-2} min^{-1} as a percent of energy absorbed.

[b]Cal cm^{-2} min^{-1} as a percent of energy loss.

Knoerr and Gay (1965) exposed detached black oak (Quercus velutina Lam.) leaves to high radiation intensities and a range of wind velocities. They computed convection values as a residual in the energy balance equation, with the other components being measured. A comparison of their data with similar data from this study is presented in Table 9. Their leaf temperatures were higher than those measured in this study. Considering the difference in species and experimental conditions, the agreement between the tulip poplar and black oak leaf values are reasonable.

Energy exchange relationships developed during the course of this study are comparable to those of the cocklebur and black oak leaf. The method used to calculate total heat loss from a tulip poplar leaf resulted in values of total heat loss that closely approximated measured solar radiation fluxes. Calculated values of total radiation absorbed by the leaf were within 5 percent of total heat loss values at high leaf insolation values and within 20 percent at low leaf insolation values. Long-wave thermal heat loss accounted for most of the heat lost from the leaf and its value was relatively constant, about 0.6 cal cm^{-2} min^{-1}, from 9:30 A.M. until 3:30 P.M. Evaporative and convective heat losses responded mainly to changing leaf temperature,

Table 9. Energy balance for detached black oak (Quercus velutina Lam.) leaves with free and forced convection, and in situ tulip poplar (Liriodendron tulipifera) leaves.

Species and Convection Mechanism	Energy Input[b]	Heat Loss Components[c]			Leaf Temperature[d]
		Radiation Heat Loss in Percent	Evaporation Heat Loss in Percent	Convection Heat Loss in Percent	
Black oak					
Forced convection ($V = 50$ cm sec^{-1})[a]	1.10	69	14	16	41
Forced convection ($V = 425$ cm sec^{-1})	1.10	67	14	19	38
Free convection ($V = \sim 10$ cm sec^{-1})	1.19	72	22	6	50
Tulip poplar (this study)					
Forced convection ($V = \sim 60$ cm sec^{-1})	1.15	68	25	7	36

[a]V is wind speed in cm sec^{-1}.

[b]Energy input is energy absorbed by the leaf in cal cm^{-2} min^{-1}.

[c]Radiation, evaporation, and convection heat losses as a percent of Energy Input.

[d]Leaf temperature in °C.

vapor pressure deficit, differences between leaf and air temperature, and light intensity. Wind was not adequately measured to assess its impact on these loss terms, but available wind data were used to calculate a theoretical wind profile with height. Evaporative heat loss was roughly four times convective heat loss at the highest value of total heat loss. At low values of total heat loss, 95 percent of the heat loss was attributed to radiative heat losses.

The position of the leaf in the crown, as well as its size and its orientation from horizontal, influenced its energy balance strategy. Parkhurst and Loucks (1972) developed a model describing leaf size variations with environment. They concluded that the plant, in adapting to its environment, evolved a leaf size that increased the efficiency of water utilization. Tulip poplar leaf size changed with crown height (Table 10). Small upper crown leaves efficiently lost heat by evaporation and convection, since boundary layer thickness is directly proportional to leaf size. The smaller leaves in the upper crown were also more vertically oriented than those of the lower crown. Vertical orientation reduced the absorption of solar radiation helping minimize the difference between leaf and air temperature. For example, Konis (1950) measured a 5.2 °C leaf

Table 10. Measured tulip poplar leaf size by crown level.

Crown Level	Leaf Length	Leaf Width	Leaf Area[a]
Top	8.17 cm	10.96 cm	81.22 cm^2
Middle	9.30 cm	13.96 cm	112.30 cm^2
Bottom	9.40 cm	12.80 cm	108.49 cm^2
Mean	9.04 cm	12.56 cm	102.49 cm^2

[a]Leaf area calculated using equation 1.

temperature difference between horizontal and vertically oriented Quercus caliprinos L. leaves. This study indicates leaves of the upper crown have adapted to reduce radiation absorption and minimize resistance to convection and evaporation.

Leaf position with respect to height in the crown influenced the mechanism by which heat was lost. Heat was lost in the lower crown by reradiation, with evaporative and convective heat loss as a percent of total heat loss becoming greater with increasing height (Figure 23, page 61). Leaf temperature, leaf and air temperature difference, VPD, wind speed, and light intensity values all decreased with decreasing height, thus the gradients that drive transpiration also

decreased in magnitude. These factors, along with increased stomatal diffusion resistance, reduced the transpiration rate in the lower crown. The data indicate the importance of certain variables in controlling transpiration changes between the top and bottom levels. For example, VPD seemed to exert more control over transpiration in the bottom than in the top of the crown. Stomatal resistance values increased with a decrease in height. This may be a reaction to decreased light levels lower in the canopy. Less negative leaf xylem water potential reflected the lower transpirational water losses lower in the crown, and perhaps the better balance between water loss and water supply at the leaf.

The diurnal trend of energy balance data and transpiration showed a single peak for all variables at around 1:00 P.M. Variables followed the daily changes in calculated total radiation absorbed by the leaf. The peak value for xylem water potential occurred about one hour prior to the maximum diurnal values of VPD and transpiration, and diurnal minimum diffusion resistance. Xylem water potential became less negative while transpiration peaked and diffusion resistance reached its minimum value. This suggests the possibility of osmotic solute regulation in the leaf cells. This would maintain cell turgor to decrease diffusion resistance while causing

a less negative measured xylem water potential (Hsiao, 1973).

Early morning dew deposition, especially on top and middle crown level leaves, was very common during the period of the study. The dew delayed increases in VPD, leaf temperature, transpiration, and xylem water potential. The valley location of the research site delayed direct solar radiation input until the sun rose above the surrounding ridge tops. As a result dew was not evaporated until around 10:00 or 11:00 A.M. The effect of this process is seen in the rapid increases of the variables listed above after 11:00 A.M. (Figures 24 through 29, pages 62 and 64 through 68, respectively). This phenomena may also be partially responsible for the rapid increase seen on Figures 14 and 15, pages 48 and 49, respectively.

Segregating data by time of day or sampling position resulted in better correlation between measured variables. Morning data gathered during this study gave higher correlation coefficients than afternoon values. Data segregated by crown level, especially in the lower crown, had higher correlation coefficients than the combined data. Reifsnyder and Lull (1965) reported that transpiration was strongly correlated to solar radiation and that air temperature was unsuitable for making

transpiration predictions since cloudiness can reduce transpiration rates without changing air temperature. Khashes and Bobro (1972) reported coefficients of correlation between transpiration and meteorological factors that became weaker in the second half of the day. Their correlation coefficients for transpiration versus saturation density dropped from a morning value ranging between .60 and .80 to negative values in the afternoon for Salix alba and Populus berolineusi.

Seasonal Water Stress Effects

The effect of water stress on growth is related to the tree's phenology. Tulip poplar branches are capable of forming primordia and continuing extension growth throughout the growing season; thus, growth is dependent on current photosynthesis and is affected by late season water deficits. Tyron, Cantrell, and Carvell (1957) found no effect of previous years' drought history on tulip poplar height increment, but current year May-June rainfall was positively related to current growth. Figure 32 shows the typical seasonal trend for leaf xylem potential, soil water potential, and rainfall at the study site (Burgess and O'Neill, 1975). Leaf water potentials correlated well with changing soil moisture conditions, with both of these parameters being inversely related to precipitation. Extrapolation of one year's

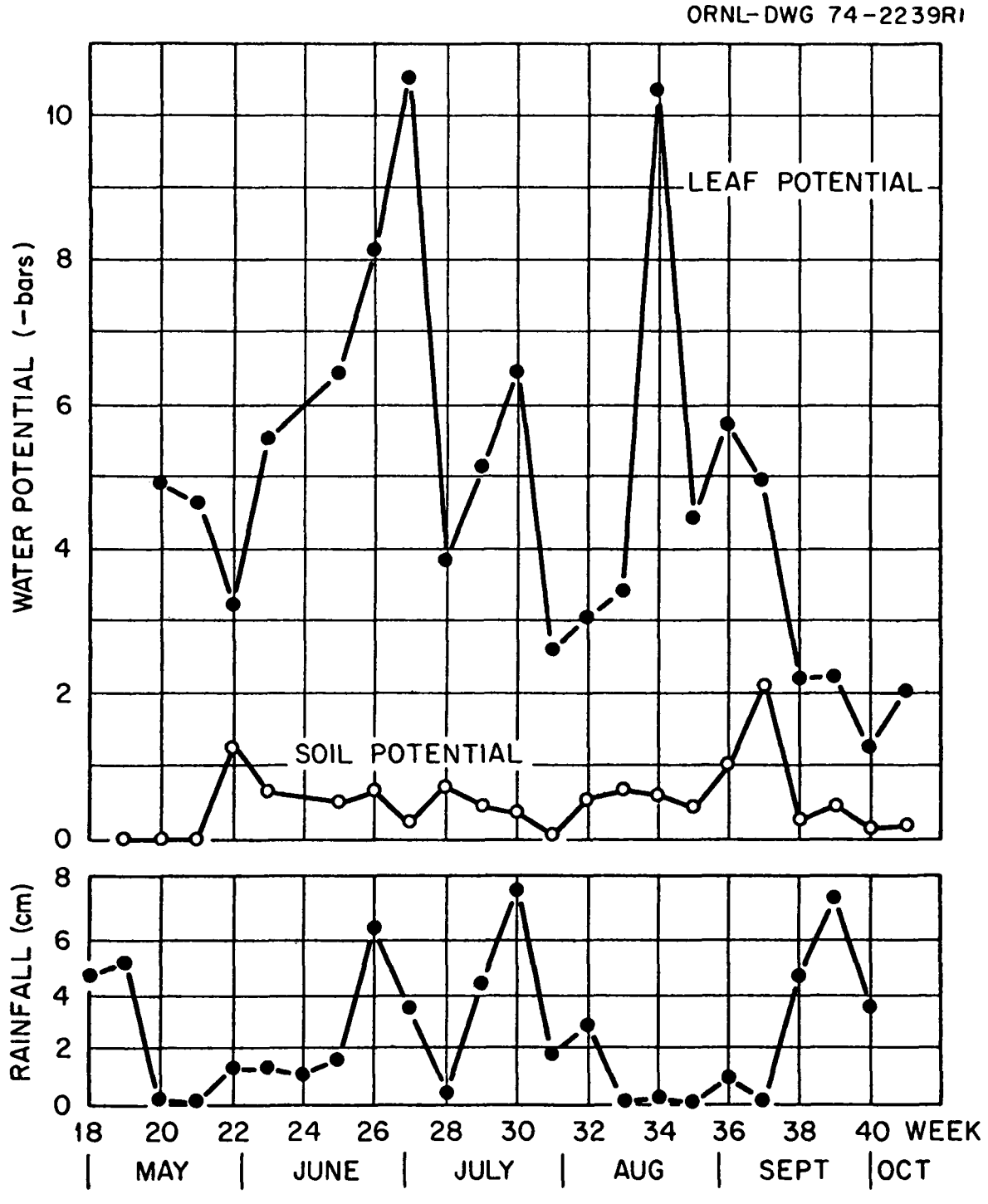

Figure 32. Weekly mean leaf xylem water potential (8:00 - 10:00 A.M.), weekly mean soil moisture potential (30 cm depth), and weekly precipitation totals during the 1972 growing season.

data to another year may be tenuous since Hinckley, et al. (1975) found inconsistent relationships between leaf diffusion resistance and xylem water potential afternoon values from summer to summer for white oak. They associated the differences with varying drought stress history from year to year, leaf age variations, and shifts in guard cell osmotic potential.

Leaf surface area measurements during the summer of 1972 show the probable effect of increasing water deficits on leaf growth (Figure 33). Leaf primordia continue to produce new leaves throughout the season, thus high water stress during the season would influence leaf size. Cell expansion has been found to be one of the most sensitive plant processes to water stress, and can be inhibited by long exposure to mild water stress (Hsiao, 1973). Hsiao (1973) also pointed out that stresses not severe enough to cause stomatal closing or reduce photosynthesis are still capable of reducing growth, or leaf surface area. Comparing Figures 32 and 33, the high water stress in late June and August resulted in a decrease in leaf area during July and September, respectively. Conversely, low water stress during early June and late July resulted in increased leaf size during June and August, respectively (Figures 32 and 33). The effect of the higher water

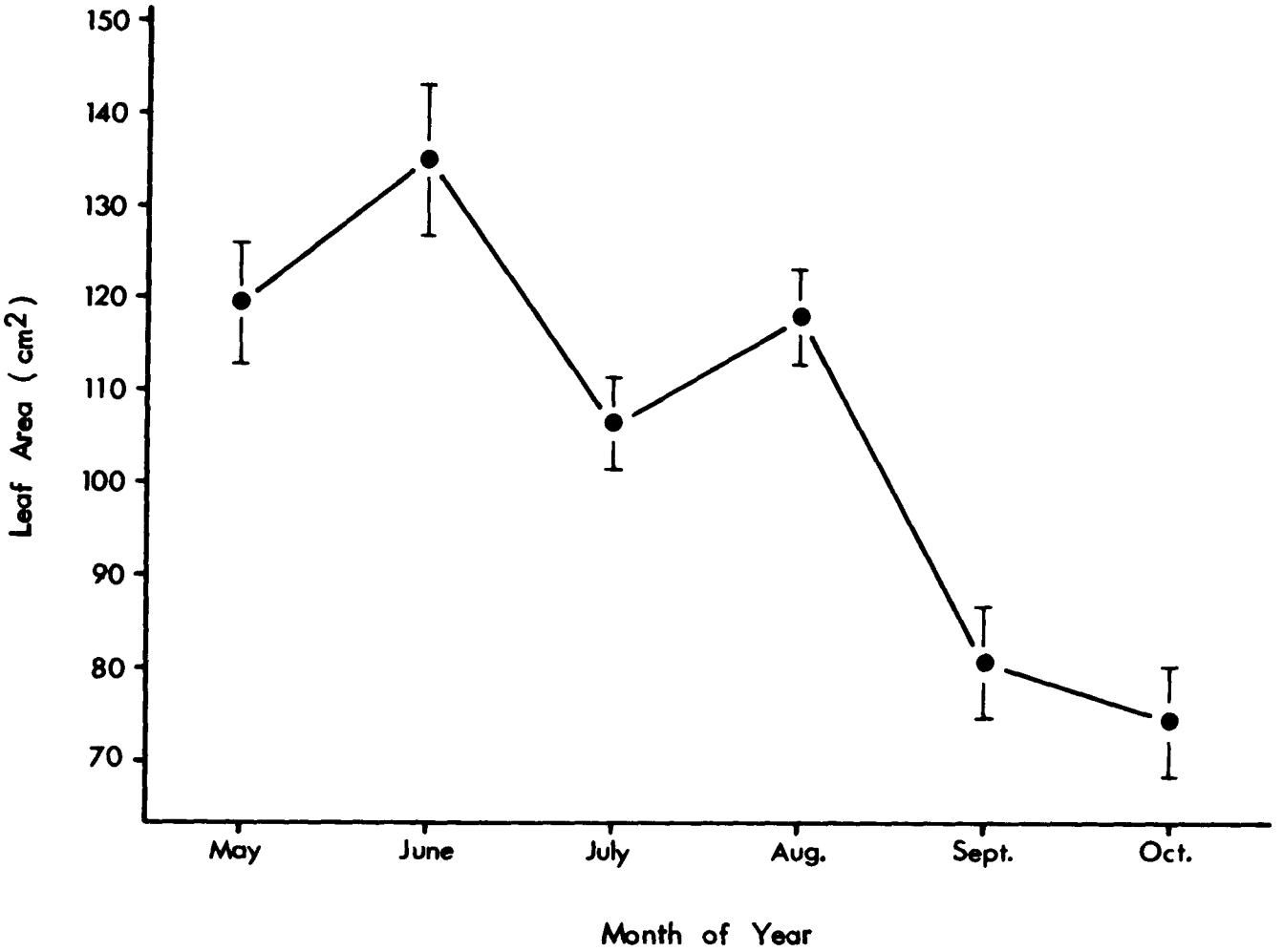

Figure 33. The 1972 seasonal change in monthly mean tulip poplar leaf area (± SE) computed from all crown levels. Seasonal mean leaf area equaled 106.5 ± 9.4 cm^2.

stress on developing leaf primordia resulted in decreased leaf size several weeks later.

IV. CONCLUSIONS

Results of this study relate to the function of forest-grown tulip poplar trees as they react to their forest environment. An examination of stomatal dimensions and density of single leaves showed that stomatal density per unit of surface area increased as leaf size decreased, and that stomata became smaller as their density increased. As a result, the numbers of stomata per leaf remained constant throughout the crown, even though leaves became progressively smaller with increasing height. The stomatal impression technique yielded stomatal density and dimension measurements, but did not allow accurate measurement of the stomatal central aperture.

Calculation of diffusion resistance from stomatal dimensions and environmental variables showed that the minimum value of leaf diffusion resistance occurred at stomatal widths between 2 and 6 μ. Wind speeds between 100 and 500 cm sec^{-1} did not further reduce calculated diffusion resistance values or calculated boundary layer resistance values. Under normal environmental conditions stomatal resistance was larger than boundary layer resistance, and thus had more control over transpiration.

Transpiration was most closely related to VPD,

wind speed, and the difference between air and leaf temperature. Stomatal diffusion resistance varied inversely with transpiration. The decrease of stomatal resistance values from 3.75 to 0.30 sec cm^{-1} was accompanied by a rapid increase in transpiration rates. Stomatal opening was controlled by light intensity. Stomatal diffusion resistance of 3.75 sec cm^{-1} corresponded to the light intensity associated with the carbon dioxide compensation point. Xylem water potential measured during this study at a mesic site was never negative enough to result in stomatal closure or increased stomatal diffusion resistance. Leaf xylem water potentials became more negative with increasing transpiration.

Transpiration rates decreased with decreasing crown height in response to a reduction in VPD, leaf temperature, stomatal diffusion resistance, and wind speed. Stomatal diffusion resistance increased with decreasing crown height, and the lower crown diffusion resistance corresponded to the value equated with the carbon dioxide compensation point. Xylem water potential was less negative at lower crown heights as a result of smaller transpiration water losses.

Research on tulip poplar seedlings elsewhere has demonstrated stomatal closure at water stresses more

negative than -18 bars. Xylem water potentials of -22 bars did not cause stomatal closure during this study. The forest tree did not experience the cumulative water stress demonstrated by seedlings in previous studies. Thus, the accumulation of stress related cell metabolites, possibly abscissic acid, responsible for sensitizing stomatal closure to water stress did not occur in the forest tree to the same extent as with the seedlings referenced above.

Energy balance calculations developed in this study compare favorably with those reported for cocklebur and black oak. Radiation accounted for at least 50 percent of the total heat loss. Evaporative heat loss accounted for up to 34 percent. The latter was about four times as great as convective losses. Larger values of total radiation input, VPD, wind speed, and temperature difference between the leaf and air resulted in more heat energy loss by evaporation and convection in the upper crown level than lower in the crown. The environmental variables that drive evaporative and convective heat losses became smaller as crown height decreased, thus radiative heat loss accounted for most of the heat loss in the lower crown.

Transpiration peaked at 1:15 P.M. closely following the responses of its controlling variables, with the

exception of xylem water potential that peaked approximately one hour earlier. All variables closely followed the diurnal cycle of total radiation input. Dew deposition on leaves in the morning delayed increases in transpiration, VPD, xylem water potential, and the difference between air and leaf temperature until 11:00 A.M. when the dew was evaporated. After 11:00 A.M. these variables increased rapidly to peak values. Diurnal stomatal diffusion resistance values varied directly with changing light intensity and were not increased by water stress.

To compete in the forest ecosystem, tulip poplar has evolved a mechanism by which it maximizes photosynthetic efficiency (i.e., greater CO_2 fixation per unit leaf surface or biomass) at the expense of large transpiration losses and resulting tissue water deficits. Water deficits incurred during rapid transpiration decrease the reservoir of water stored in the tree. The moist soil in which the study tree grew enabled recovery from water deficits to occur overnight. This recharge of water is critical, since cumulative water stresses can bring about increased respiration, hydroactive stomatal closure, and detrimental tissue and cell enzyme effects. Tulip poplar growing on drier soils would experience higher water stresses that would result in

stomatal closure, reduced photosynthetic efficiency, and lower growth rates.

Data presented in this study should prove valuable to modeling of the tulip poplar ecosystem. Measurements of plant water status are coupled with environmental variables that allow development of predictive formulas. Formulas could use atmospheric variables such as solar radiation, VPD, wind speed, and air temperature to predict transpiration rates. Subsequent models may find a broader data base for applications by relating plant variables to selected environmental variables. These data also shed some light on the reason why tulip poplar is found mainly on moist sites. Tulip poplar requires abundant moisture to balance high transpirational losses from open stomata necessary for maintaining a maximum photosynthetic rate for growth.

Areas needing further study are suggested by these data. Since only one tree was sampled, it would be interesting to repeat the study over a range of tulip poplar sites, from wet to moderately xeric, to see if the same relationships occur. The influence of stored water in the tree on developing water stresses and the effect of water stress on the growth of in situ forest trees would be valuable to modeling studies. Concurrent studies of photosynthesis, respiration, and plant water relations

would provide data coupling these important functions. Field data on the kinetics of water movement from soils into the roots, stems, and leaves would increase our understanding of how plant water stresses develop and are relieved. Such data would also be helpful in studies of nutrient movement from soils to leaves. While this study elucidates some of the control mechanisms operating at the plant-atmosphere interface, it also points to the need for continued research on the entire soil-plant-atmosphere continuum.

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APPENDIX

Table 11. Analysis of variance table and Duncan's new multiple-range test[a] for tulip poplar stomatal density distribution for four leaf quadrants and three crown levels.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Significance[b]
Total	359	5928	17		
Interaction	6	58	10	1.28	NS
Leaf quadrant	3	27	9	1.20	NS
Crown level	2	3216	1608	213.12	$P \leq .01$
Error	348	2626	8		

[a]Duncan's new multiple-range test for a 1 percent least significant range (Steel and Torrie, 1960): (1) leaf quadrant numbers: 1 3 4 2; (2) crown level: Bottom Middle Top.

[b]NS = not significant ($P \leq .1$).

Table 12. Analysis of variance table for numbers of stomata per leaf for tulip poplar by crown level.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Significance[a]
Total	15	69×10^{11}			
Crown level	2	4×10^{11}	2×10^{11}	0.43	NS
Error	13	65×10^{11}	5×10^{11}		

[a]NS = not significant ($P \leq .1$).

Table 13. Analysis of variance table and Duncan's new multiple-range test[a] for tulip poplar stoma slit length by leaf quadrant and crown level.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Significance[b]
Total	119	1568	13		
Interaction	6	30	5	0.53	NS
Leaf quadrant	3	61	20	2.12	NS
Crown level	2	439	220	22.87	$P \leq .01$
Error	108	1037	10		

[a]Duncan's new multiple-range test for a 1 percent least significant range (Steel and Torrie, 1960): (1) leaf quadrant numbers: 2 1 3 4; (2) crown level: Top Bottom Middle.

[b]NS = not significant ($P \leq .1$).

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