MATHEMATICAL MODELING AND COMPUTER

SIMULATION OF THE WATER-FLOW

MECHANICS IN A COTTON

PLANT

By

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CHAPTER I

INTRODUCTION

Over 95 percent of the water supplied to a plant is lost by trans-
piration. A need to understand the mechanism of such losses and its
relation with various intensities of the evaporation demand is of sig-
nificance. However, before any effort can be made to increase the
water use efficiency of the plants it is necessary that a clear fund-
amental understanding of the processes involved be obtained.

Transpiration studies are common dating from the time of Vasque
(1878), who studied the water loss mainly from the physiological view
point. Later thinking regarding this process suggested that trans-
pirationrate may be governed by both physiological and the physical
forces. As early as 1948 van den Honert (1948) postulated that flow
rate in plants is a caternary process and is analogous to flow of
current in a conducting medium. The Ohms law analogy is accepted by
many modelers as a valid assumption and is employed as a starting
point. Several variations and modifications in the catena have
been introduced based upon the knowledge of the physiological reg-
ulation of the transpiration flow. The properties of the plant media
expressed by various parameters are constantly changing. An under-
standing and evaluation of the nature of those changes and the range
of the parameters are necessary ingredients to build a model of the
water flow through plants.

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The purpose of this study was to develop an understanding of the mechanism of water-flow and water-loss regulation in a cotton plant. The objectives included studying each basic component of the plant such as root, stem, and leaf and evaluation of those physiological parameters which affect the physical forces responsible for the flow of water in that component. Since the plant-water-atmosphere is a continuously changing system in the domain of time, the nature of these parameters as a function of time was also studied.

The study was divided into two phases. In phase one quantitative and qualitative experimental information was gathered for the various plant components. In the second phase these results were incorporated in a simulation model. Any additional information needed to establish conceptual validity was acquired from published sources or personal communication.

In the root component it was desired to determine the pattern of changes of root resistance to water entry under simulated applied suction. Skidmore and Stone (1964) reported that root resistance increased during the photoperiod in a cotton plant. Hence, the study included a quantitative evaluation of such an increase as a function of time, applied suction, and temperature of the root medium. Kuiper (1963) has reported the existence of a hysteresis effect in root resistance. In the present study this effect was investigated in cotton, tomato, and bean plants.

In the stem component knowledge was needed of the phase relations of transpiration stream at several locations on the stem.

In the leaf component a mid-day slump was attributed mainly due to water absorption lag behind the transpiration loss. Studies were

designed to establish the nature and magnitude of such lag in water up-
take and transpiration rates as well as in several other plant pro-
cesses. This was acheived by measuring simultaneously as many var-
iables as possible during short intervals of time.

The main objective of phase two was to formulate a model of the
transpiration stream which is simple, realistic, and identifiable with
plant components. Such a model should incorporate contemporary think-
ing in the area of plant-water-relations. A conceptual model consis-
ting of electrical analogies to the plant system was visualized. Mathem-
atical equations describing flux and changes in the path of water flow
were derived. The versatility of the simulation language, Continuous
System Modeling Program (CSPMI) was investigated by implementing the
model on operating system, IBM 360/65. Objectives included simulating
the experimental results.

Chapter II reports the results on root resistance. It was neces-
sary to modify the heat pulse technique for measuring sap velocity.
This is reported in Chapter III. Chapter IV contains the description
of the dynamic plant system. Those dynamics were simulated by the
electric analog model and these results are presented in Chapter V.
Chapter VI contains a description of the operation of the model. This
chapter should be of use to those attempting to further apply the model.

CHAPTER II

ROOT RESISTANCE AND TEMPERATURE EFFECTS

ON WATER UPTAKE BY PLANTS[1]

G. A. Shirazi, J. F. Stone,

L. Croy, and G. W. Todd[2]

Abstract

Root resistance of decapitated root systems of cotton, tomato,

and bean plants shows an exponential increase with applied suction up

to about #-1 bar. The water uptake rate was found to be path depen-

dent and showed presence of a hysteresis effect. Also, the root re-

sistance in a cotton plant increased about six-fold during the photo-

period of 12 hrs. The water uptake rate increased with increasing

temperature of the root medium up to 30 C in cotton and 25 C in

tomato and bean plants.

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Introduction

Several studies of simultaneous water uptake and transpiration rates have revealed that there is no simple relationship between the two. Kramer (1939) reported that in all of his experiments the water absorption through roots lagged behind transpiration. He suggested this lag was due to the inability of roots to absorb water in accordance with transpiration demand. Kramer (1939) also showed by decapitating various plant species that water uptake increased when the roots were removed, implying that root tissues offered much resistance to water uptake. Kuiper (1963) reported hysteresis effects in water rate as a function of applied suction in the roots of decapitated bean plants. He found that with increasing suction, water uptake rate increased exponentially, while with decreasing suction, the water uptake rate decreased linearly.

Maximum resistance to water movement in roots is encountered across the cytoplasmic membrane located in the epidermal cells of the root tips and the endodermis, Kuiper (1963). These membranes are susceptible to temperature and pressure changes, leading to changes in the water uptake properties of the roots. Thus, the resistance offered by the roots varies with time and other physical and chemical changes. Skidmore and Stone (1964) reported that root resistance in a cotton plant increased about five fold during the photoperiod. The effect of such variations in the root resistance on water flow mechanics in the plant is important.

The objectives of the present investigation of three species were:

(1) to determine the pattern of changes of root resistance to water entry under suction pressure.

(2) to determine the changes in root resistance as a function of time.

(3) to determine the magnitude of the pressure dependent hysteresis phenomenon.

Material and Methods

Cotton plants (Gossypium hirsutum L), tomato (Lycopersicum esculentum L cv. Rutgers) and kidney bean (Phaseolus vulgaris) were grown in nutrient solution in a controlled environment chamber. The plants were grown in 10-liter plastic containers made opaque with aluminum paint covering the outside. Each container was partitioned into four compartments by cross partitions of sheets of perforated plexiglass. One seedling was grown in each compartment. This kept roots separate and minimized breakage in handling. A Modified Hoagland's solution(Shirazi and Stone, 1973c) was used. The water lost from the nutrient solution was replaced daily with tap water, and the entire solution was changed every three weeks. The plants were clamped in position in a hole in the center of a wooden cover fitted to the containers. The root medium was continuously aerated.

A technique to facilitate aeration and protect roots from injuries due to turbulence was employed. The aeration assembly consisted of two concentric glass tubes. Air was introduced into the inside tube from the top. The escaping air bubbles were confined within the outer tube and uniform aeration was achieved due to convective mixing of the low density column of the air-water mixture. This aeration assembly was glued to one corner of the container so

as not to interfere with the root development.

A photoperiod of 13 hrs was maintained (11 hrs dark period). The light intensity was about 48k lux. Illumination was provided by 28 VHO 200-watt fluorescence tubes and 12, 75-watt incandescent light bulbs. The photoperiod temperature was 32.2 C and the dark period temperature was 26 C.

The cotton plants used in this study were 8-weeks old. Bean and tomato plants were over 7-weeks old.

The root system of the experimental plants was severed under nutrient solution about 3 cm above the roots. To avoid air entry into the xylem the decapitated root system was always kept immersed in the solution. Tygon tubing was connected around the xylem after removal of the bark. As an additional precaution against leakage the tubing was tied with a rubber band. This assembly was connected to a calibrated glass tube of 1 mm inside diameter (Fig. 1). This in turn was connected to a mercury manometer connected to a vacuum pump. This arrangement provided a maximum suction of 60 cm Hg.

The root system was subjected to incrementally varied suctions between 5 cm Hg and 60 cm Hg at intervals of 10 cm Hg in both ascending and descending paths of applied suction. The roots were kept in the same nutrient solution in which growth took place. The root volume at each run was determined by measuring the displaced volume of water.

The effect of different temperatures upon the rate of water uptake of decapitated plants was studied at a constant suction of 50 cm Hg. For this determination the plastic container was placed in a constant temperature bath. The temperature variation of the bath was

Hg MANOMETER

CALIBRATED   TUBE

VAC.
PUMP

CONST. TEMP.
BATH
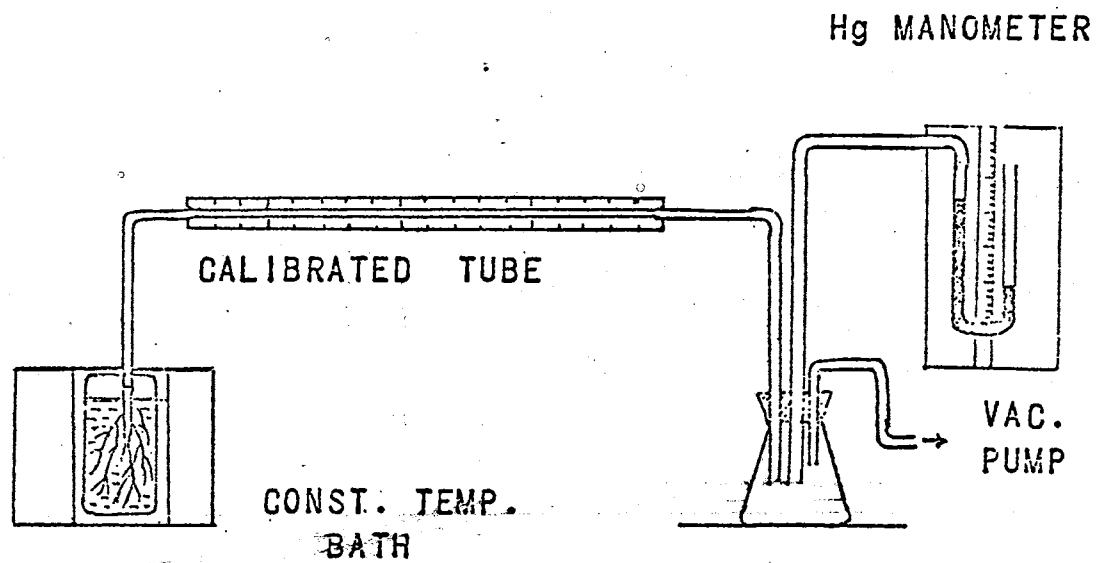
Figure 1.   Experimental Set-up for Root- resistance Measurement
on the Decapitated Stem

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less than $\pm$ 1 C. The temperature of the root medium was brought to equilibrium with the temperature of the bath for a period of 15 minutes before the root resistance was determined. One plant was studied in the bath at a time. Temperature ranged between 15 and 45 C in increments of 5 C.

Results and Discussion

Rates of water uptake as a function of applied suction to the decapitated root system of cotton, tomato, and bean are illustrated in Figs. 2, 3, and 4 and Table 1. These results are typical of several such runs on each type of plant and are meant to establish patterns of changes in the root resistance. Use of suctions on a decapitated plant to extract water through roots is, of course, conceptually different from the natural uptake phenomenon. In nature the suction pressure necessary to absorb water comes from metabolic and physical processes. However, the use of the term "water uptake" in this study is consistent with its use in the literature.

The results indicate that water uptake increases exponentially with increasing pressure. The decrease was also exponential. The study was repeated several times on several different plants with results in the same trend. Also, the magnitude of the water uptake on the descending path was higher than on the path of ascending suction. Thus, there were always two values of water uptake for each value of pressure indicating a path dependent nature of the water uptake rate. Several investigators have reported similar results (Mees and Weatherly: 1957a, Lopushinsky and Dramer, 1961: Kuiper, 1963). For the ascending pathway using positive pressure Mees and Weatherly

TABLE I

STATISTICAL SUMMARY OF THE RATE OF WATER-UPTAKE
AGAINST THE APPLIED SUCTION IN COTTON, TOMATO
AND BEAN PLANTS: LEAST SQUARE BEST FIT
LOG Y = A + B (TAU) WHERE Y = UPTAKE
AND TAU IS THE APPLIED SUCTION.
A = INTERCEPT, B = SLOPE
ON SEMILOG PLOT

	Root Volume (cm^3)	Age of the plant (weeks)		Y-intercept A	Slope B	Correlation Coefficient
COTTON						
Plant #1	149	8	Ascending	0.83	0.19×10^{-1}	0.999**
			Descending	0.97	0.17×10^{-1}	0.998**
Plant #2	150	8	Ascending	0.83	0.19×10^{-1}	0.999**
			Descending	0.90	0.18×10^{-1}	0.997**
Plant #3	138	6	Ascending	0.59	0.17×10^{-1}	0.999**
			Descending	0.68	0.10×10^{-1}	0.999**
TOMATO						
Plant #1	180	9	Ascending	1.20	0.14×10^{-1}	0.991**
			Descending	1.28	0.12×10^{-1}	0.998**
Plant #2	153	8	Ascending	1.27	0.13×10^{-1}	0.996**
			Descending	1.37	0.12×10^{-1}	0.998**
Plant #3	145	8	Ascending	1.19	0.14×10^{-1}	0.997**
			Descending	1.26	0.13×10^{-1}	0.996**
BEAN						
Plant #1	75	8	Ascending	0.41	0.19×10^{-1}	0.995**
			Descending	0.56	0.16×10^{-1}	0.999**
Plant #2	38	6	Ascending	$-.93 \times 10^{-1}$	0.17×10^{-1}	0.999**
			Descending	$-.92 \times 10^{-1}$	0.15×10^{-1}	0.990**
Plant #3	58	8	Ascending	0.42	0.17×10^{-1}	0.999**
			Descending	0.48	0.16×10^{-1}	0.998**
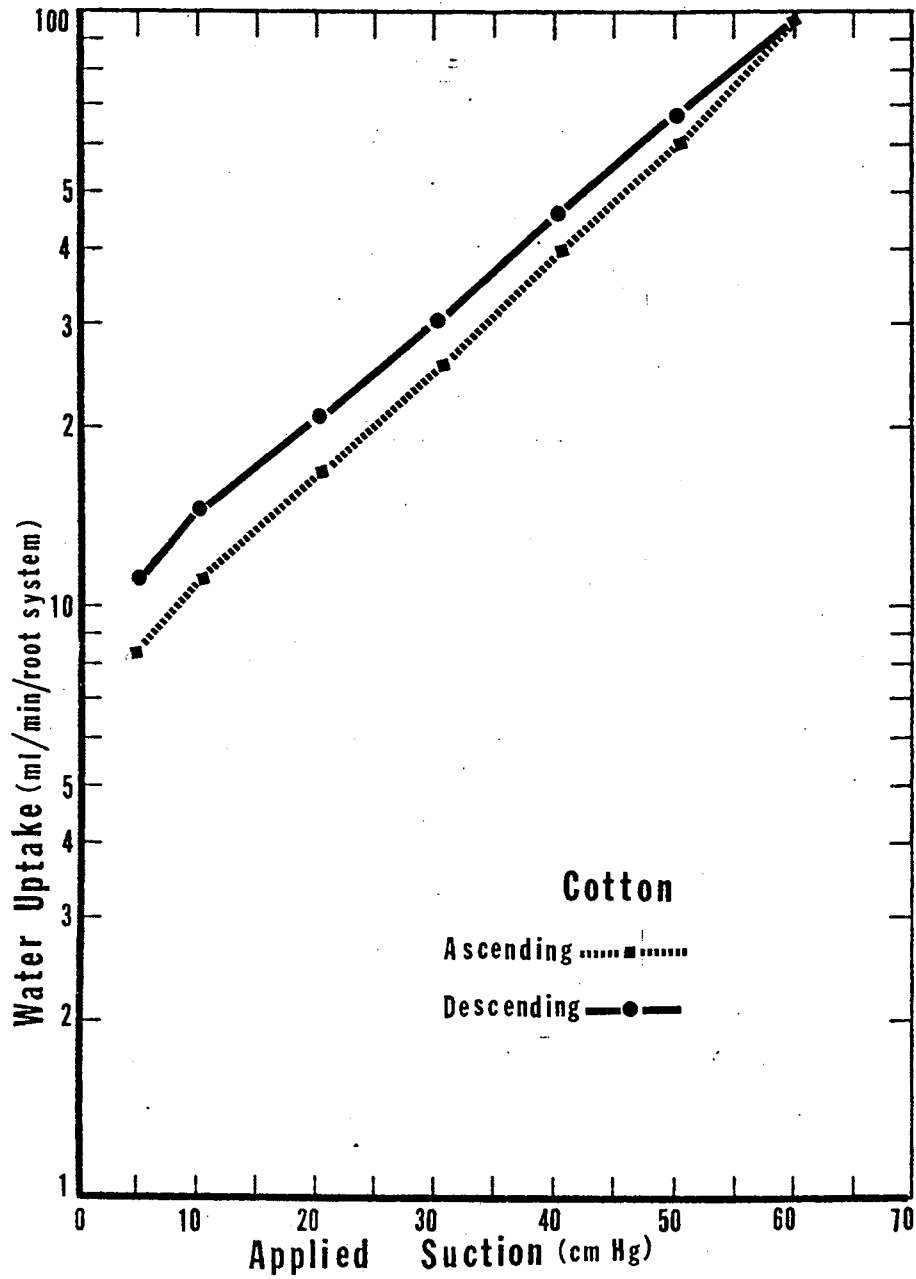
Figure 2. Rate of Water Extraction Through the De-
capitated Root System of Cotton Plant
Grown in Solution Culture and Constant
Environment
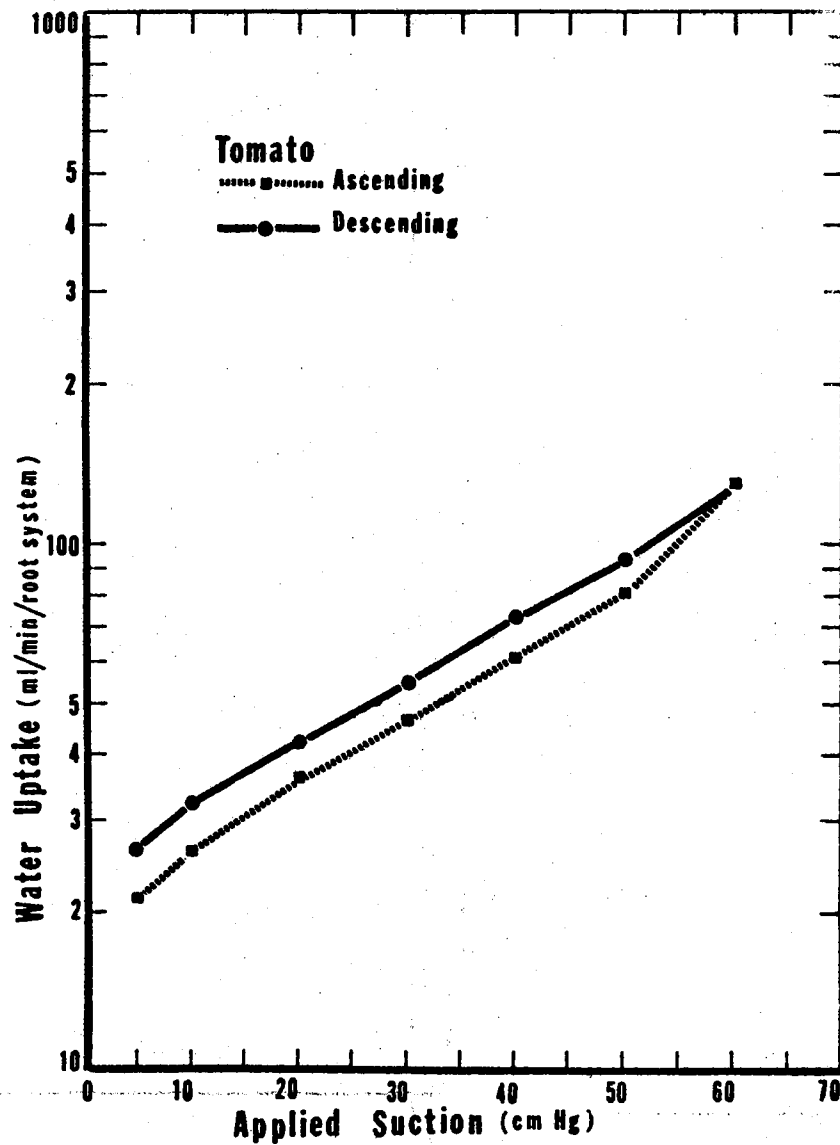
Figure 3. Rate of Water Extraction Through the
Decapitated Root System of Tomato
Grown in Solution Culture and
Constant Environment
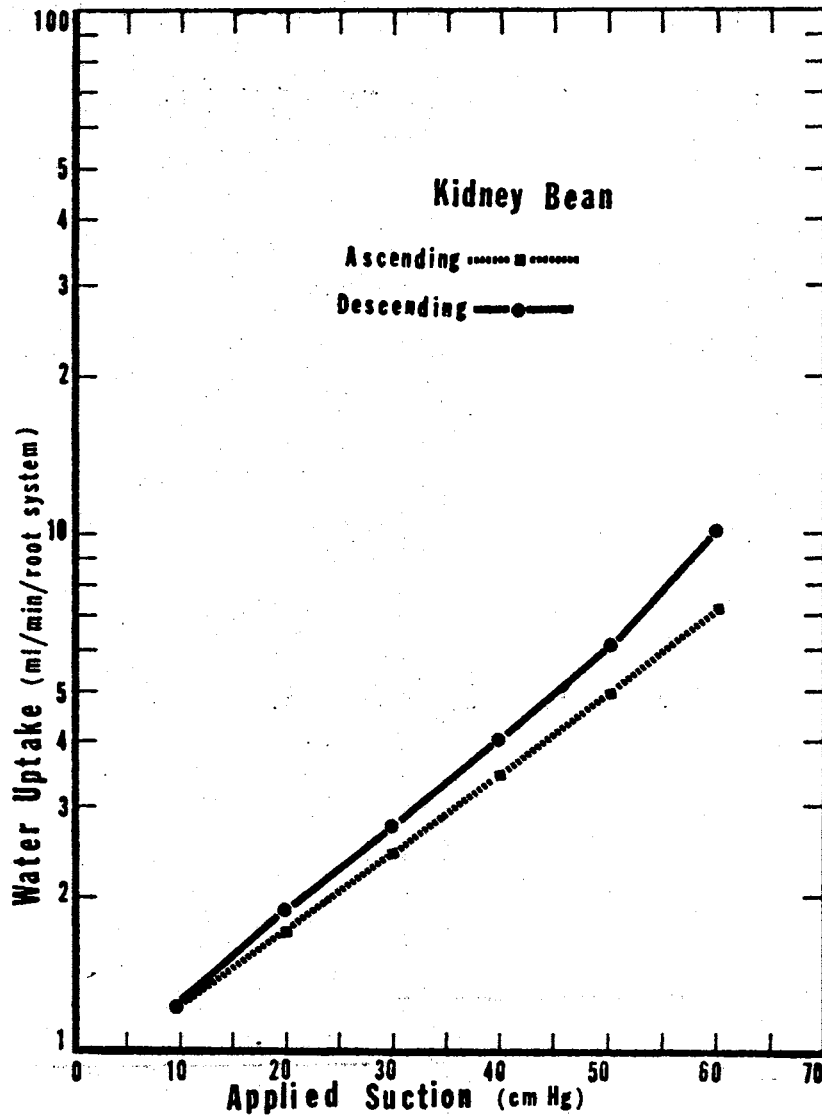
Figure 4. Rate of Water Extraction Through the
Decapitated Root System of Bean
Plants Grown in Solution Culture
and Constant Environment

(1957a) obtained a non-linear relationship up to 3 atm and linear for higher pressure. Lopushinsky and Kramer (1961) found a non-linear increase of water uptake up to 1 atm. Kuiper (1963) found a non-linear increase up to 60 cm Hg.

For the descending path, the effect of pressure potential on water uptake was inconsistent in the literature. Kuiper (1963) showed that water uptake rate for descending suction was higher than for ascending over the range of 60 cm Hg to about 0 cm Hg. The present results agree with his findings. Mees and Weatherly (1957a) showed similar results by applying positive pressure to decapitated tomato roots. Their data indicate presence of hysteresis type of phenomenon. Recently, Huck, et al., (1970) have shown that lateral roots undergo diurnal variation in diameter in rsponse to water potential changes in other plant components. Klepper, et al., (1971) observed hysteresis loop in the stem diameter due to changes in leaf water potential. In view of these observations it appears that root transport properties show a hysteretic response to changes in pressure potential in the plant.

The results of the study of water uptake over time are illustrated in Fig. 5. These experiments were also repeated several times. Fig. 5 shows a single set of data. Uptake characteristics were similar in all the runs.

The resistance of the roots to water flow was calculated as the amount of water extracted per unit of time for a given amount of applied suction (Kramer, 1940; Brouwer, 1953a, b; Mees and Weatherly, 1957a, b; Kuiper, 1963; Skidmore and Stone, 1964). The effect of applied suction upon the water uptake rate follows a relation of the
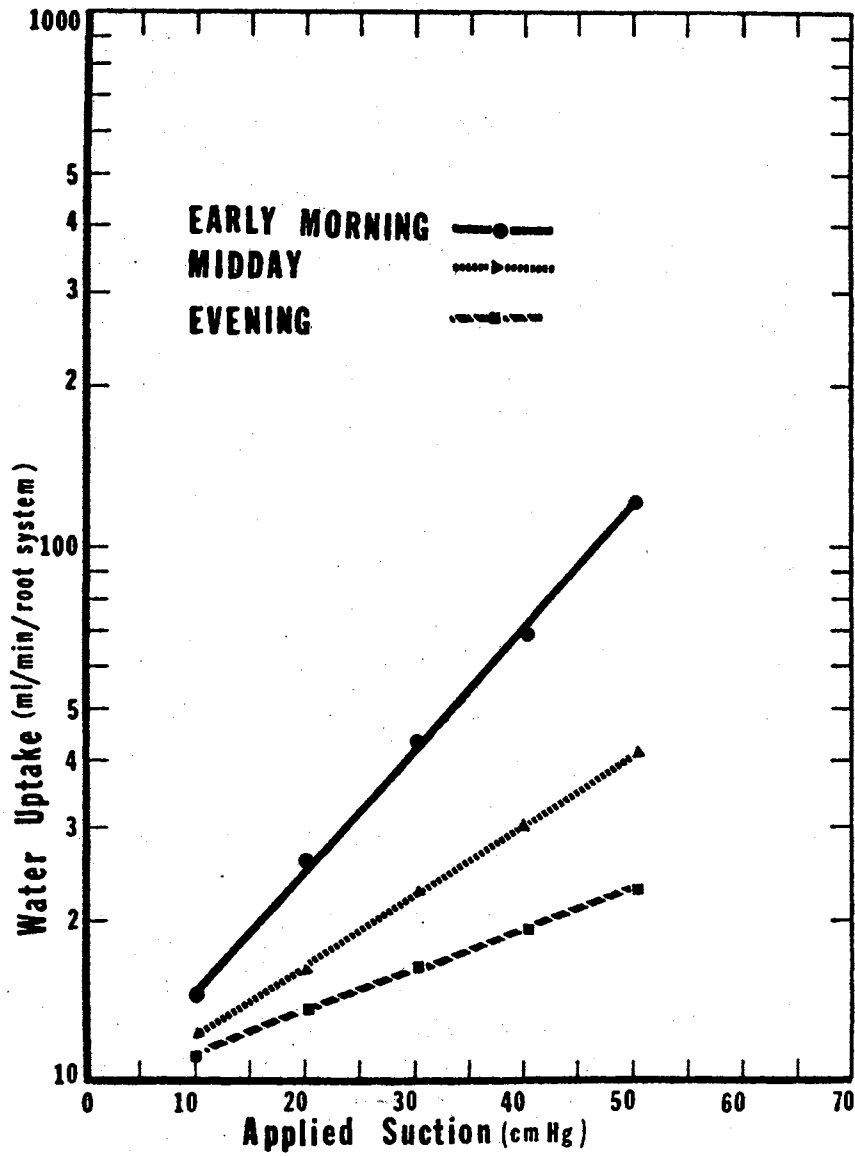
Figure 5. Rate of Water Extraction Through the
Decapitated Root System of an 8-
week-old Cotton Plant at Different
Times of the Day

type (Fig. 5).

$$\ln U = A + B \tau \tag{1}$$

where U is the rate of water uptake, τ is the applied suction. A and B are the intercept and the slope of the line. However, the rate of change of uptake with applied suction is a function of the lumped resistance to water flow in the roots. Therefore the derivative of the uptake rate with respect to applied suction would be a measure of water conductance:

$$\frac{dU}{d\tau} = B \exp (A + B \tau) \tag{2}$$

The inverse of conductance is hence the resistance R of the roots to the flow of water (Eq. 3)

$$R = \frac{\exp-(A + B \tau)}{B} \tag{3}$$

The values of A and B are different at different times of the day in the same plant species. Variation in uniformity of growth and age may change the magnitude of the water uptake and A, but seems to have insignificant effect on the slope B. B is, evidently, a function of plant species and time of day.

Since the relation of water uptake to suction change with time of day the resistance also changes. Skidmore and Stone (1964) reported 5-fold increase in the root resistance of a cotton plant through the day.

In order to estimate the time dependent root resistance the data

of Fig. 5 are utilized. Since the A value appears to remain constant

through the day a best-fit linear regression of the slope of the water

uptake and applied pressure curves in Fig. 5 was obtained. These

slopes are plotted against the time of determination to obtain a time

dependent linear equation:

$$B(t) = 1.57 - 1.58 \times 10^{-3} t \qquad (4)$$

Equation 4 along with the average value of A, 0.97, inserted in

3 yields:

$$R(\tau, t) = \frac{\exp-[0.97 + ((1.57 - 1.58 \times 10^{-3} t) \tau)]}{(1.57 - 1.58 \times 10^{-3} t)} \qquad (5)$$

Equation 5 can be considered a family of curves with τ as parameter.

A plot of two such relations is presented in Fig. 6.

Fig. 7 shows the effect of the temperature in the root medium up-

on the rate of water uptake on cotton, tomato and kidney bean plants

in a temperature range from 15 C to 45 C. In each case the rate of

water uptake increased with an increase in temperature from 15 C.

In cotton the increase was noted to 30 C and in bean and tomatoes to

25 C. Also, all plants studied showed a decline in the uptake rate

after a certain temperature was reached. In cotton the decline was

noted at 35 C, but in bean and tomato plants the decline was noted

at about 25 C. No explanation is offered for the observed decline.

However, further increase of temperature caused a significant rise

in the water uptake. This may have been due to breakdown of the

protoplasmic membrane eliminating the site of resistance in the roots.

Such a sudden increase of the water uptake was noted by Kramer (1933)
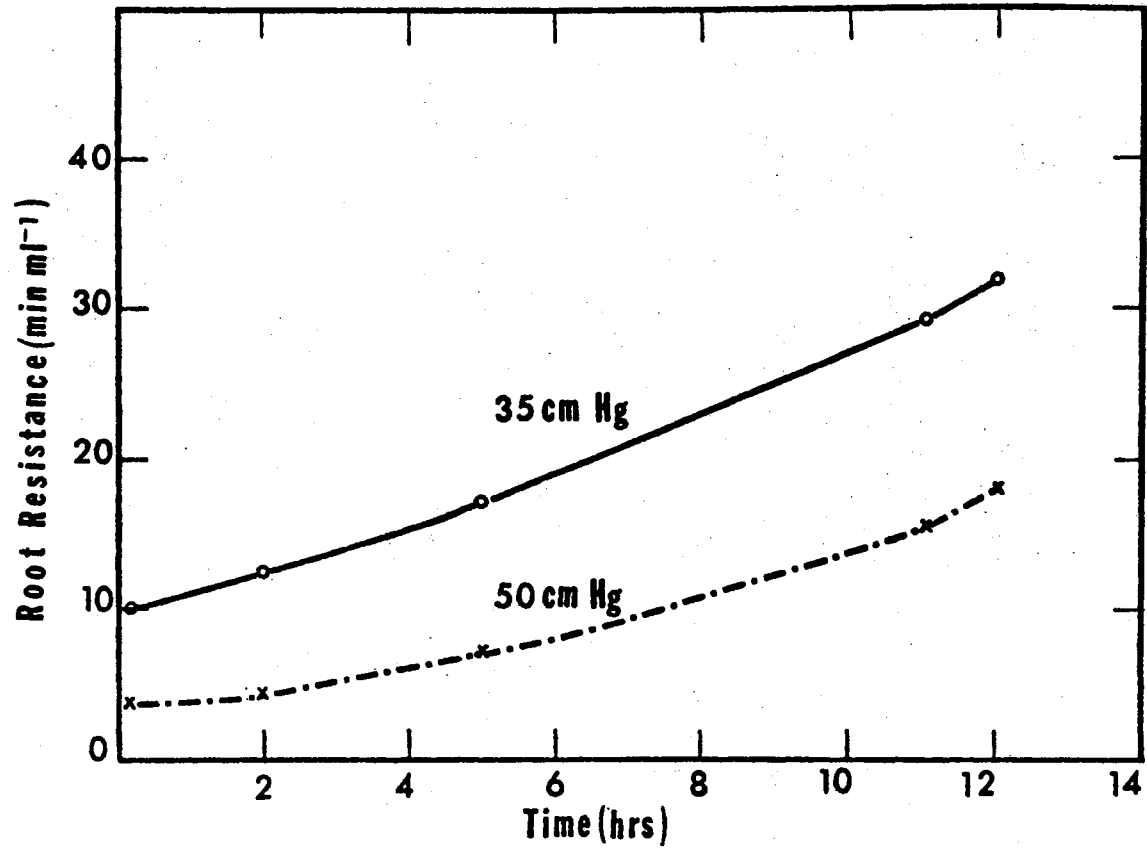
Figure 6. Time-dependent Root Resistance at Constant Suctions of 35 and 50 cm Hg in an 8-week-old Cotton Plant Grown in Solution Culture
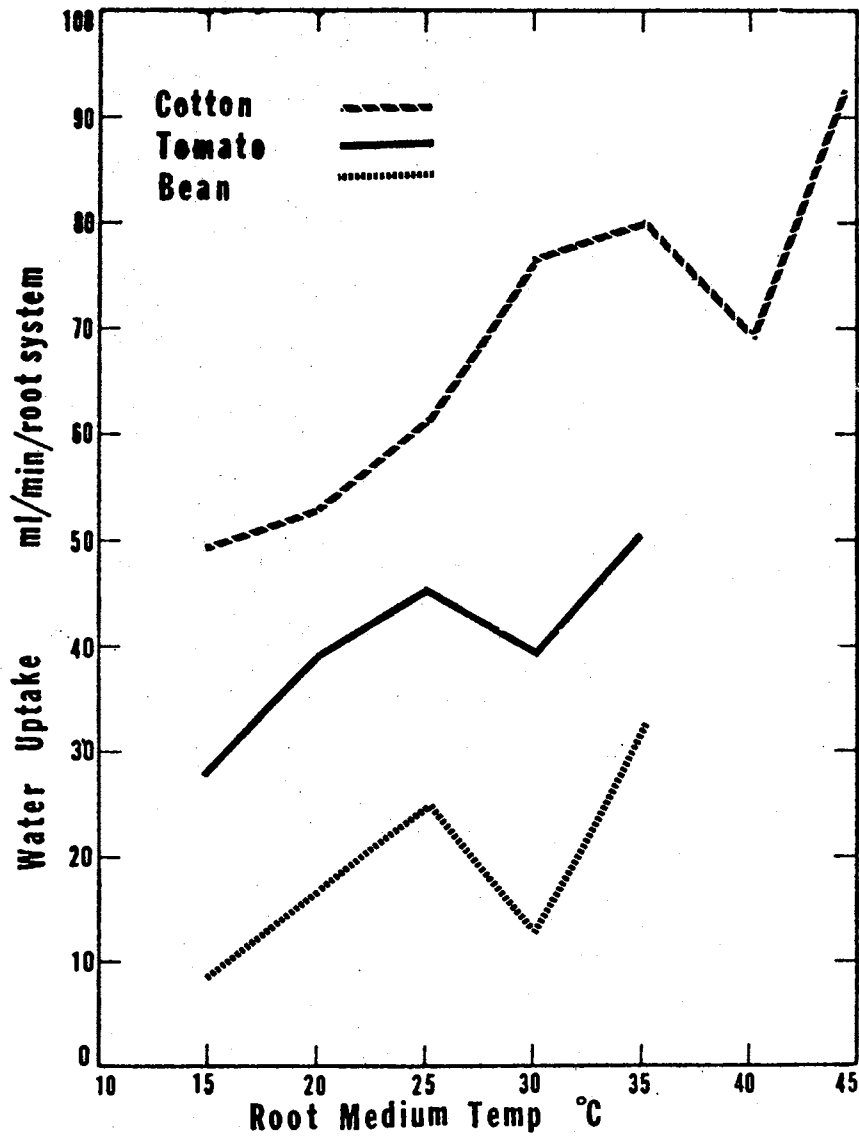
Figure 7. Effect of Temperature on rate of
Water Extraction for Cotton,
Tomato and Bean Plants

in dead roots. Mees and Weatherly (1957a) also noted higher water uptake rates in prolonged experiments of this nature where roots had died due to lack of aeration.

The results of Fig. 7 indicate that the resistance expressed in equation 5 is probably dependent upon temperature and should not be applied at temperatures significantly different from the 20 to 25 C range employed.

CHAPTER III

ON THE HEAT PULSE METHOD FOR THE MEASUREMENT

OF APPARENT SAP VELOCITY IN STEMS[1]

J. F. Stone and G. A. Shirazi[2]

Abstract

A temperature compensated system for the measurement of apparent

sap velocity in the stem of a cotton plant is presented. Output

variations caused by changes in the ambient air temperature in the

growth chamber were eliminated through use of opposing thermistors

in a bridge circuit which drove an operational amplifier circuit.

One thermistor was used as sensor while the other served as compensa-

tor for ambient temperature changes. A theoretical analysis of

temperature distribution from a plane source of heat in a stem and

its relationship with sap velocity shows that the time to achieve

the temperature peak is in phase with the apparent heat pulse velo-

city (AHPV).

Additional Index Words: sap velocity, transpiration rate.

In the heat pulse velocity method for the estimation of water uptake or transpiration rate a heat pulse is introduced on or in the stem of a plant and the resulting heat transient is sensed a fixed distance down the transpiration stream. The method has been employed by several workers. For example, since it was first introduced by Huber and Schmidt (1937), it has been used on cotton plants by Bloodworth et al. (1955, 1956), and Skidmore and Stone (1964). Marshall (1958) and Decker and Sakau (1964) have shown its validity in tall trees. Its use in monocotyledons was reported by Wendt et al. (1965).

A primary improvement has been to use two thermistors in the assembly: one at a point downstream and the other upstream of the heating element. This modification is reported to help measure the net sap velocity by distinguishing the convection and the conduction components of the heat flow. Marshall's (1958) analysis for a line source of heat perpendicular to flow is applicable in large trees where the heat source and the heat sensing devices are inserted in the trunk. For small plants this approach is too destructive.

The authors have used the heat pulse method in a controlled environment chamber and have experienced considerable difficulty due to ambient temperature variation caused by frequent cycling of the refrigeration unit. Variations of $\pm$ 2 C in the growth chamber have been accepted as common. Since the temperature increase caused by the thermoelectric heating element is of the same order of magnitude, it is necessary that the fluctuation of the ambient temperature be eliminated while sensing the heat pulse.

An electric circuit and a heat sensing device is presented which

has given satisfactory results in monitoring the applied heat pulse in a system of high evaporative demand. The following theoretical analysis of heat movement in the stem is adapted from the theory presented by Closs et al. (1958). The use of two thermistors to eliminate the effect of ambient temperature variation is described. Instrumentation and interpretations employed by authors using the heat pulse technique are not always elucidated. It is possible that others have used the bridge technique to eliminate ambient temperature fluctuation. However, the authors know of no other works giving complete instrumentation for the bridge technique and giving the theory justifying measurement of the time to the peak of the temperature wave for characterizing changes in sap velocity.

Theoretical

A heat pulse applied to the stem of a transpiring plant travels by two mechanisms: convection with the sap flow and conduction through the sap and stem tissue.

Carslaw and Jaeger (1954) presented the heat flow equation incorporating components of convection and conduction processes in a porous medium:

$$\frac{K}{\rho C} \frac{\partial^2 T}{\partial x^2} = \frac{\partial T}{\partial t} + \left[a v_s \frac{\rho_s C_s}{\rho C} \right] \frac{\partial T}{\partial x} \tag{1}$$

where C and ρ are specific heat and density of the wet interxylem material. The subscript s stands for the sap for the same parameters, K is the thermal conductivity of plant tissues, v_s is the sap velocity and a is the fractional area of the stem cross section occupied by

the xylem tissues. The thermal conductivity is strongly dependent

upon the water content of the medium.

In equation 1 the second term on the right-hand side represents

the convection flow. Carslaw and Jaeger (1954) describing wood point-

ed out that wood has different conductivities in the direction of

fibers, the rings, and the rays, and so the flow equation should be

modified for anisotropic media. The same is no doubt true for annual

plants. However, where the lateral dimension is small compared with

the dimension in the direction of flow, the system may be considered

one-dimensional for purposes of theory. Hence, equation 1 is valid

for small-stemmed plants and K refers to conductivity in the longi-

tudinal direction.

Closs (1956) and Marshall (1958) point out that the velocity of

the heat pulse in the transpiring plant then will be $v_h = v_s a \frac{\rho_s C_s}{\rho C}$,

the coefficient appearing on the right-hand side of equation 1.

Closs, et al. (1956) following Carslaw and Jaeger (1954), indicated

that the temperature at a point x distance downstram from the point

of application of a plane source of heat pulse on the stem of a

transpiring plant varies with time as the solution of equation 1:

$$T(x,t) = Q/(\Pi K t)^{\frac{1}{2}} \left[\exp -(X-v_h t)^2/4Kt \right] \qquad (2)$$

The boundary conditions include semi-infinite medium insulated sides

of the stem, and thermal uniformity across the stem, a good assumption

for young, small-stemmed plants. The pulse Q is realized at x = 0

at time t = 0. Results of equation 2 are illustrated in Fig. 1.

Marshall (1958) and Closs (1956) were interested in computation
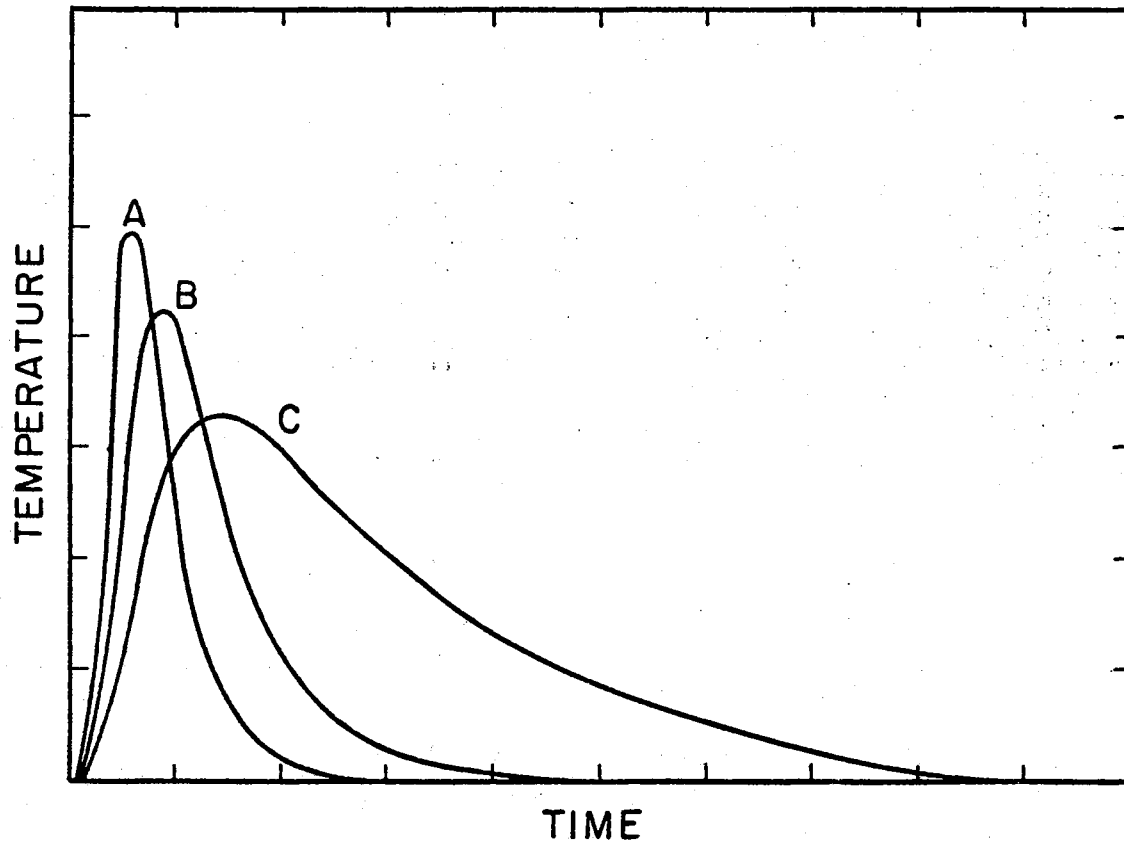
Figure 1. Theoretical Distribution of Temperature at
Increasing Sap-Velocities A, B, C in the
Stem at a Distance X from the Source

of the sap velocity and needed to eliminate Q from consideration. Also, they wished to evaluate both the diffusivity and conductivity. To achieve the necessary degrees of freedom for these computations Marshall measured temperatures at several times and Closs measured at two points on the stem. However, if only the phase relationships are of interest, a simplification is in order. Phase can be with respect to simultaneous velocities at different portions of the stem or can be the relationship of velocity to other variable, e.g., uptake or transpiration. A single measurement to characterize sap velocity would be desirable. In this regard consider the curves of Fig. 1. If one continuously records the output of the thermosensor, the observation of the peak of the curve is a simple matter. Mathematically this point can be represented by setting the time differential of equation 2 equal to zero and solving for the time t_p to achieve the peak temperature at a given distance x from the point of application of the heat pulse. Thus, the time differential is

$$\frac{\partial T}{\partial t} = Q/(\Pi K t)^{\frac{1}{2}} \left[(x^2 - v_h^2 t^2/4Kt^2) - (\Pi K/2\Pi K t) \right] \exp\left[-(x - v_h t)^2/4Kt \right] \qquad (3)$$

The time in this equation is the time t_p for the peak of the wave to pass point x. Thus, x/t_p can be regarded as the <u>apparent</u> heat pulse velocity v_a. Removing the trivial components of equation 3 and dividing by t_p^2 gives

$$v_a^2 - v_h^2 = 2K/t_p = 2Kv_a/x \qquad (4)$$

Thus, the difference between the square of the velocities v_a and v_h is related to the ratio of the thermal diffusivity of the stem and

sap and the time to achieve the peak of the pulse at point x.

Equation 4 can be rewritten

$$(v_h/v_a)^2 = 1 - \frac{2K}{v_a x} \tag{5}$$

By requiring $x > 2K/v_a$, the term on the right will always be positive.

For extremely large x, it can be seen that the ratio of the heat

pulse velocity and apparent heat pulse velocity would be unity. This

is because transfer of heat by diffusion would be negligible compared

to convection.

For v_a and v_h to be in phase, $\partial v_a/\partial t$ and $\partial v_h/\partial t$ would be zero

simultaneously, that is, they would reach peaks simultaneously.

Since v_a depends on v_h and v_h varies with t we can write

$$\frac{\partial v_a}{\partial t} = \frac{\partial v_a}{\partial v_h} \frac{\partial v_h}{\partial t} \tag{6}$$

If it can be shown that $\partial v_a/\partial v_h$ will be zero independently of $\partial v_a/\partial t$

then when $\partial v_a/\partial t = 0$, $\partial v_h/\partial t = 0$, showing in-phase behavior. Impli-

cit differentiation of equation 4 yields

$$\frac{\partial v_a}{\partial v_h} = \frac{v_h}{v_a} \left[1/(1 - K/v_a x) \right] \tag{7}$$

which can be zero only when $x = 0$, but $x > 2K/v_a$. Hence, from

equation 5, v_a and v_h are in phase. Velocity v_h is related to v_s

by a constant if one assumes densities and heat capacities over the

period and location of measurement. Hence, v_h would be in phase with

v_s.

Materials and Methods

Electronic Circuit

The thermistors R1 and Rs were connected with R3 and R4 to form

the temperature sensitive brdige circuit (Fig. 2). R3 and R4 are

temperature stable resistors (wire-wound is best) having resistnace

approximately the same as R1 and R2. It is unnecessary to use matched

thermistors for R1 and R2, but they should be of the same type number.

Changes of ambient temperature than effect R1 and R2 in the same man-

ner and cause no significant unbalance in the bridge output. Changes

in R1, mounted in contact with the stem, cause an unbalance in the

bridge. This unbalance appears in the feedback network of an opera-

tional amplifier, being connected to the inverting input and the

junction of R6 and R7. In this configuration the unbalanced voltage is

amplified in the ratio of R7:R6 or 600. The output of the amplifier

is lead through R8 to a meter or recorder. R8 is used to attenuate

the output to match the range of the meter. The thermistors produced

insignificant self-heating when the supply voltage E was held to less

than 0.4V. E must be a floating supply, so each bridge in use re-

quires a separate supply. A battery with potentiometric voltage

dropping or an adjustable dc supply can be used. The devices reported

here employed a commercial ac transistor-radio 9V power supply for E.

R10 was needed to load the supply for good regulation and R9 limited

the output to 0.4V. C_1 is an amplifier stabilizing capacitor. The

value is not critical. The starting and stopping of the refrigeration

compressor in the growth chamber induced great transients in the DC

power line. C_2 and C_3 were found necessary to suppress the effects
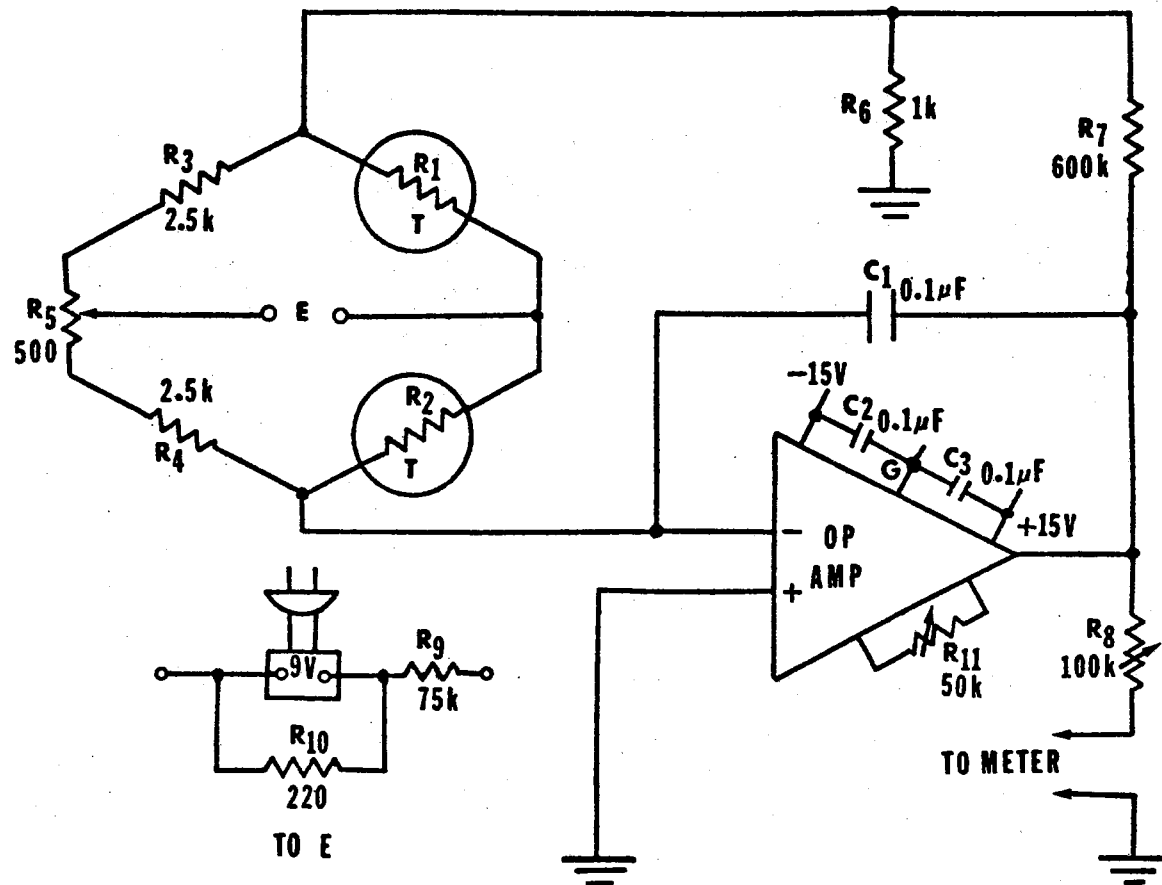
Figure 2.   Electronic Circuit

of voltage transients induced in the + and - 15V power supply leads.
(A Commercial operational amplifier power supply was employed.)

In the initial set up, R11 is adjusted to provide 0 output with
the inverting input grounded. This adjustment required no further
attention through the many months of the study. In subsequently con-
structed devices, a 47K ohm fixed resistor was substituted for R11.

R5 is used to bring the output meter to center scale at the
start of each run. Generally it is the only control requiring ad-
justment after the initial set-up.

The amplifier was an Analog Devices type 118A. This is an in-
expensive general purpose operational amplifier. Other inexpensive
types could be employed provided the noise figure is no worse than
the 118A.

Thermoelectric Probe

The probe block consists of two components: a heat pulse gen-
erator and a temperature sensor. The probe block (Fig. 3) contains
a heating element of no. 24 chromel wire. Heat is generated by
switching the element to a 3-volt battery. The element is bent to
conform to the plant stem with each placement on a plant. Voltage was
applied for 2 to 3 sec. The temperature sensor contains two therm-
istors mounted in a 1.25-cm diameter Plexiglass probe. One thermi-
stor protrudes farther than the other and is used to sense the term-
perature of the plant stem. The other thermistor senses ambient
temperature and compensates for extraneous temperature changes as
described earlier. The probe is contained in a Plexiglass block.

To make a measurement, the block containing the probe is mounted

Set Screw

Heater
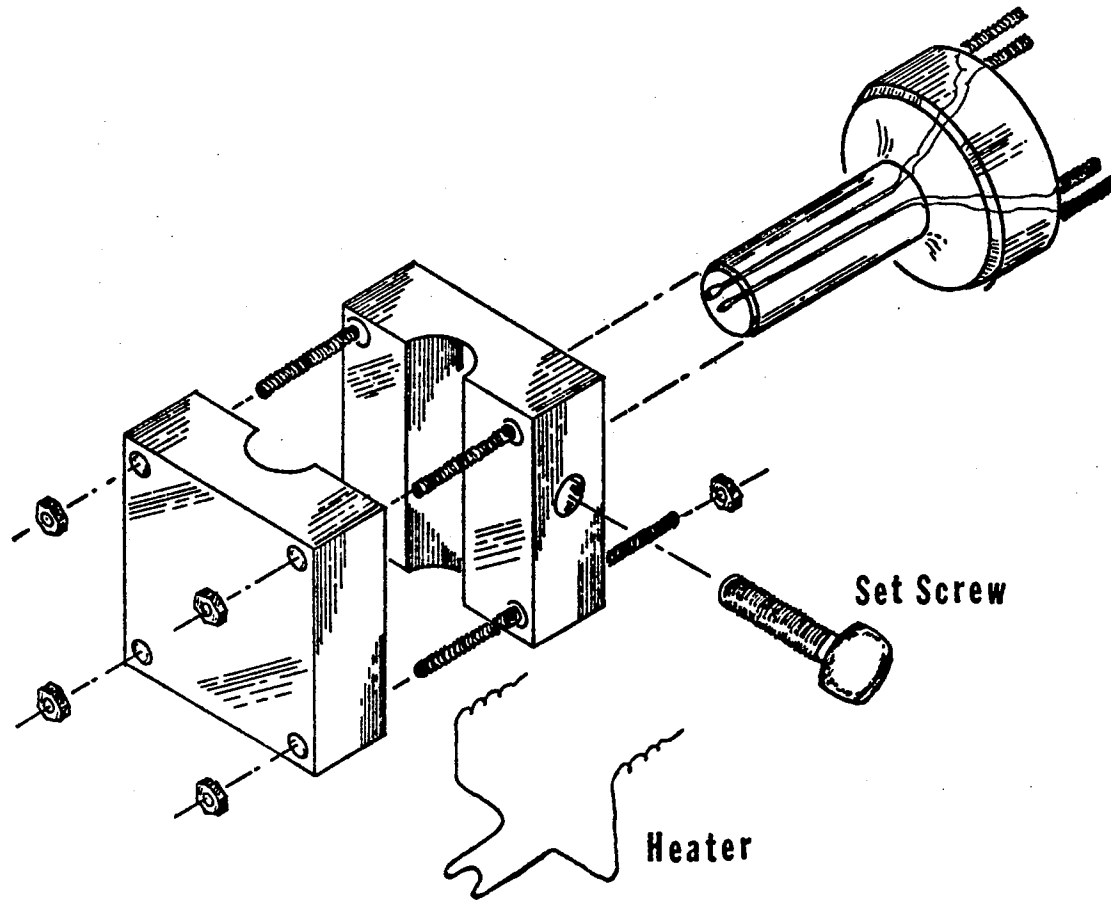
Figure 3. Thermoelectric Probe Assembly for the Measurement
of Apparent-Heat-Pulse Velocity in Stem

in the vicinity of the stem. The block derives support externally and

does not depend upon the stem for support. The thermistor probe is

adjusted to touch the stem. Then the probe is immobilized with the

set screw adjustment. Once the heat pulse has been generated, the

temperature recorder is turned on and the heat pulse passing the

thermistor probe is sensed. The time interval t_p for the peak to

reach the sensor is noted. The distance x between the heater and

sensor divided by t_p is the apparent heat pulse velocity v_a. Several

probes can be affixed to a single plant.

Plants

Use of the probe on cotton plants (Gossypium hirsutum, L.) is

reported here. Plants were 8-weeks old and grown in a growth con-

trolled environment plant growth chamber. Day temperature was 32.2 C

and night was 26 C. The daylight and nightime periods were 13 hrs and

11 hrs, respectively. Air flow was vertical upward. Light was pro-

vided by fluorescent lamps supplemented by incandescent lamps for

red enrichment. The illuminance indicated by Weston light meter was

48k lux. Plants were grown in nutrient solution which was continuous-

ly aerated.

Results

Water uptake and the apparent heat pulse velocity were measured

simultaneously at intervals of one-hour throughout the photoperiod.

Fig. 4 shows that these two quantities behave similarly. The theory

presumes the heat pulse is applied as a plane across the stem. The

effect of bark on this assumption is of interest. If the bark behaves

as an insulator the heat pulse reaching the xylem could be greatly distorted. To study this effect, the bark at the point of contact of a thermistor probe was removed during the observations in Fig. 4. The v_a for bark removed showed a 25 percent increase but the phase relationship was not distorted for the 1-hr intervals. The bark was about 2 mm thick and the stem was about 1.25 cm in diameter. The distance between the heater and sensor was the same along the direction of the flow, but with the bark, the heat-pulse had to travel the additional 2 mm distance through the bark. Therefore, the t_p for the bark is greater than the t_p for without bark.

In another set of measurements, v_a was measured at two points on the stem using two probes. One was about 6 cm above the root node and the other about 6 cm below the highest internode. The results are shown in Fig. 5. Note that at the start of the photoperiod the upper thermistor sensed a higher velocity than the lower. This suggests water was lost from the top of the plant first upon onset of transpiration. Shortly thereafter, the velocity in the lower probe on the stem was larger, suggesting the additional demand for recovery in the top of the plant.

Note the tendency for the v_a to oscillate. This oscillation is in accordance with other dynamic variables noted on the plants (Shirazi and Stone, 1973). Visual observations of the cyclic variation of the wilted and turgid conditions of all leaves of the plant confirm that v_a in the stem oscillated and was in phase throughout the length of the stem. The effects reported herein were noted on several plants studied over a period of several months.
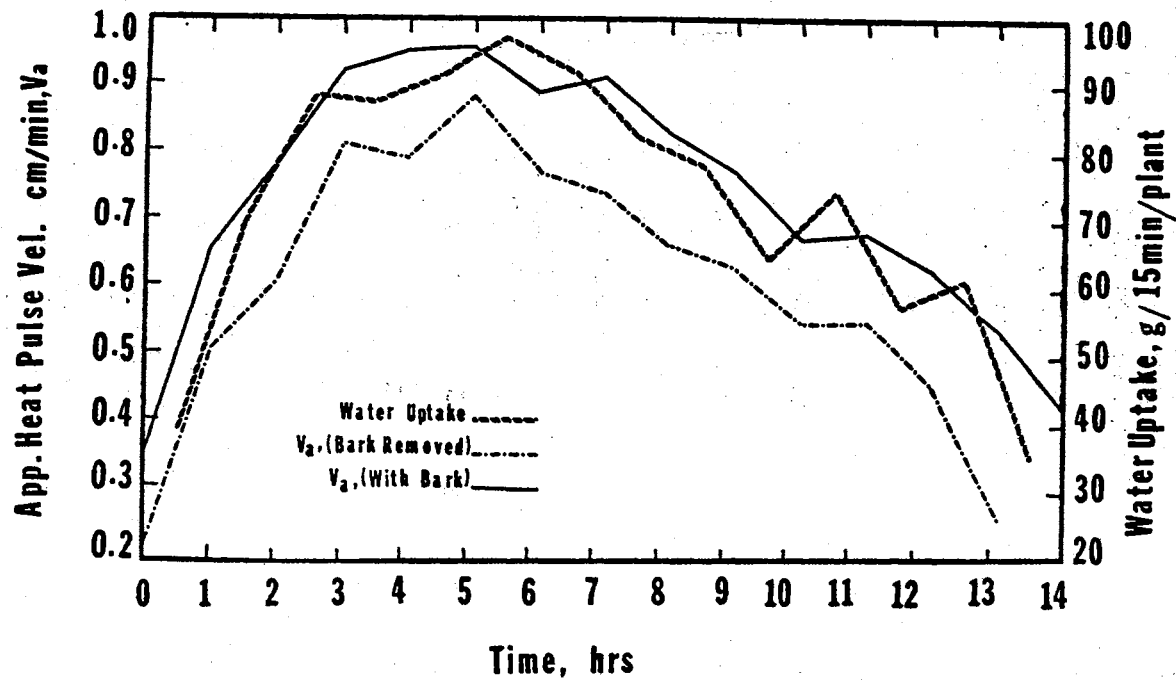
Figure 4. Simultaneous Measurement of the Rate of Water Uptake,
and Sap-Velocity in the Stem, With and Without
Bark, of an 8-week-old Cotton Plant
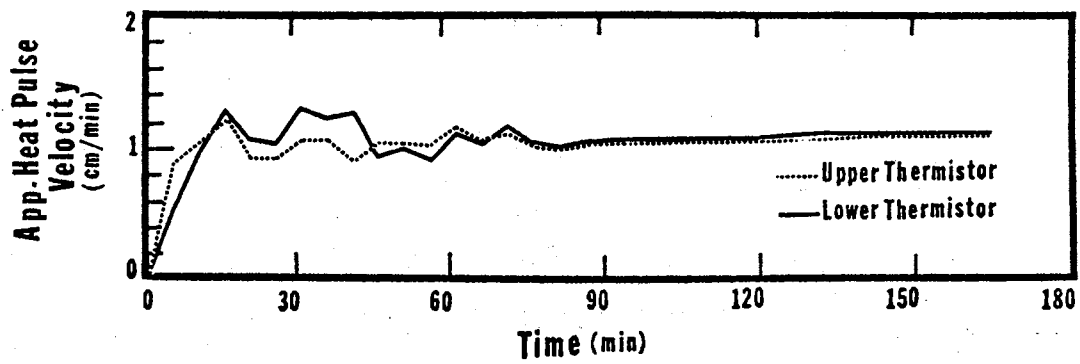
Figure 5. The Apparent-Heat-Pulse Velocity in a Cotton Plant
at Two Different Positions on the Stem

Acknowledgments

CHAPTER IV

CYCLIC VARIATIONS IN THE WATER-BASED RATE

PROCESSES IN A COTTON PLANT[1]

G. A. Shirazi, J. F. Stone,

and G. W. Todd[2]

Abstract

Simultaneous measurements of transpiration rate, rate of water
uptake, leaf temperature, changes in leaf density, leaf water poten-
tial, apparent sap-velocity in the stem at two locations, and visual
examination of the leaf response in a cotton plant growing in solution
culture and under constant environmental condition were made at short
time interval. The results indicate that plant processes undergo
through two sets of oscillations during the photoperiod. An early
day cycling is characterized by damping oscillations while sustained
oscillations were observed late in the day. The period of oscillation
was about 30 min. Phase differences in dynamic processes are reported.
The magnitude of the phase differences diminished in subsequent

---

cycling during early day period.

Introduction

Cyclic variations in the movement of stomates has been discussed by Hopmans (1971) and Cowan (1972). They categorize the process as having two distinct causal factors: internal carbon dioxide concentration and water stress. They postulate the CO_2-based oscillations are periods of 4 to 5 min. and the water stress-based of 20 to 40 min. Such variations in turn cause cyclic variation in related processes and quantities as transpiration, water uptake, sap velocity, leaf density, leaf temperature and state of turgor. The latter can be observed visually as alternate turgor and wilting.

Skidmore and Stone (1964) reported water-based oscillations in transpiration stream, leaf density and visual observations of the stomatal aperture. They suggested that an increase in the root resistance is the cause of initiation of the observed evening cycling. Ehrler, et al., (1965) observed cycling in leaf diffusion resistance, leaf temperature, transpiration rate and the leaf density in an environment which was constant with respect to light intensity, vapor pressure deficit, carbon dioxide concentration and the ambient temperature. Oscillations of the leaf water content were shown to exist in beans by Hopmans (1969). Barrs and Klepper (1968) and Lang, et al., (1969) showed such variations in leaf water potential, water flux and leaf density in cotton, pepper, and sunflower plants. Karmanov, et al., (1965, 1966) showed oscillations in the water absorbtion rate by roots which lagged behind the transpiration rate. Viktorov, et al., (1968) concluded that water based dynamic processes are

regulated by the transpiration stream at the site of stomata. Recently Hopmans (1971) and Cowan (1972) have shown the presence of oscillations in different plant processes and under a variety of environmental combinations.

Studies of such cyclic processes must be studied over sufficiently short time intervals to characterize changes over the course of individual cycles. Measurements must be repeated at intervals of no longer than one minute. Thus, many studies reported in the literature contributed little to the understanding of this cyclic process by virtue of long sampling intervals. The present study was undertaken to establish the phase relations and the interaction of the various dynamic processes by measuring them simultaneously at short time-intervals.

Plants

Cotton plants (Gossypium hirsutum L., cv Stoneville 7A) were germinated in sterilized vermiculite. One-week-old seedlings were transferred to nutrient culture in a controlled environment chamber. A 10-liter polyethylene container was partitioned into four compartments by cross partitions of perforated sheets of plexiglass. One seedling was cultured per compartment. This was done to avoid root entanglement and minimize root breakage in further handling of the plants. The nutrient culture solution was a modified Arnon and Hoagland (1947) solution. Iron was supplied by dissolving ferric chloride and acid free EDTA to obtain a 2 ppm concentration of iron in the nutrient solution. (Table 1). The pH ranged between 5.5 and 6.5 during the growth period. The loss of the solution was

TABLE I

COMPOSITION OF NUTRIENT SOLUTION

Compound	Mol. Wt. (g)	g/Liter	Molarity	ml of Stock per 10 Liters of Root Medium*	Molarity in the Root Medium
$Ca(NO_3)_2 \cdot 4H_2O$	236.15	472.0	2.0 $\underline{M}$	25	5 $\underline{mM}$
KNO_3	101.1	505.0	5.0 $\underline{M}$	10	5 $\underline{mM}$
$MgSO_4 \cdot 7H_2O$	246.48	246.0	1.0 $\underline{M}$	20	2 $\underline{mM}$
KH_2PO_4	136.0	136.0	1.0 $\underline{M}$	10	1 $\underline{mM}$
HCl (12N)	36.0	100 ml	1.2 $\underline{M}$	10	1.2 $\underline{mM}$
H_3BO_3	61.83	2.47	39.9 $\underline{mM}$	10	39.9 $\underline{\mu M}$
$MnSO_4 \cdot H_2O$	169.01	1.69	10 $\underline{mM}$	10	10 $\underline{\mu M}$
$ZnSO_4 \cdot 7H_2O$	287.54	0.288	1 $\underline{mM}$	10	1 $\underline{\mu M}$
$CuSO_4 \cdot 5H_2O$	249.68	0.05	0.2 $\underline{mM}$	10	0.2 $\underline{\mu M}$
$NaM_oO_4 \cdot 2H_2O$	241.95	0.097	0.4 $\underline{mM}$	10	0.4 $\underline{\mu M}$
$FeCl_3$ + EDTA		$FeCl_3$ = 10 g + EDTA (acid free) 10.5 g	61.6 $\underline{mM}$	10	61 $\underline{\mu M}$

*Tap water was used for preparing final volume.

replaced daily by adding tap water. The entire solution was changed

every three weeks.

The root medium was continuously aerated. A technique to

facilitate aeration and protect roots from injury was employed

(Shirazi and Stone, 1973a). The aeration assembly consisted of two

concentric glass tubes. The inside tube had an ID of 0.31 cm and

the outer tube was 1.25 cm. Air was introduced into the inside tube

from the top. The escaping air bubbles were confined within the outer

tube and uniform air mixing and solution circulation was achieved by

the resulting convective motion of the air-water mixture. This aera-

tion assembly was glued to one corner of the container to minimize

interference with root development. Four-week-old plants were trans-

ferred to a 10-liter container with a wooden cover. The container

was made opaque with an aluminum paint covering on the outside. The

plants were held in position by placing the base of the stem in a 1

cm hole in the center of the wooden cover. A 5-cm diameter hole in

the wooden cover accomodated a No. 11 rubber stopper and provided

visual and physical access to the root medium.

Plants of 7- to 8-week age were transferred to a 3 liter glass

jar whenever measurements were conducted. Plants of this age were

usually about 60 cm tall. The total leaf area on a given day of the

measurement was calculated by interpolating a regression equation

($\log Y = 0.1381 + 1.8115 \log X$, $r = 0.99$)[**] yielding a highly signifi-

cant relationship between the length of the mid-rib X, cm, and the

total leaf area Y, cm^2, according to the technique described by

Wendt, (1967). The total leaf area during the experimental period

on a 7- to 8-week-old plant ranged from 1.1 to 1.2 m^2. The root

volume was about 160 cm^3. Personal judgement for the uniformity of growth and vigor was made before a plant was selected for experimental determinations. Small plants referred to were 5 weeks old.

Aerial Environment

All experiments were conducted in a controlled-environment growth chamber, Model PGW-132 walk-in unit manufactured by Percival Refrigeration Mfg. Co., Des Moines, Iowa. The unit has a 6.45 m^3 internal volume with a working surface area of about 3 m^2. Illumination was provided by 28 VHO 200-watt fluorescent tubes and 12, 75-watt incandescent lights for red spectrum enrichment. Most experiments were conducted in the center of the working bench to avoid the large drop-off of light intensity at the edge of the bench. The chamber was provided with a readily removeable, sectional, Mylar thermal barrier separating the light chamber from the plant growth space. Air circulation was achieved by 6 fans, 3 at each end of the chamber. The re-circulated air was expelled at floor level and was distributed uniformly through the chamber, vertically upward. The chamber was equipped with controls for regulation of photoperiod and temperature. The chamber had no humidity control but the temperature and the relative humidity was recorded on a bi-metal and hair type hygrothermograph. A photoperiod of 13 hrs. was maintained (11 hrs. dark period) and started at 9 a.m. local time. Light intensity at plant top was about 48k lux and this was maintained by adjusting the distance from the lamp bank with the moveable bench. The lamps were changed when aging lowered their intensity by 20 per cent. The mean photoperiod temperature was 32.2 C and the dark period temperature was 26.6 C.

Measurement of the Water Uptake

The water uptake rate was measured by a technique involving periodic refilling of the root solution container to a reference level. Achievement of the reference level was determined by the use of an electric circuit. The circuit consisted of two platinum wire electrodes and a milliammeter connected in series with a 6-volt cell. The electrodes were confined to a stilling basin of wire mesh to avoid contact with foreign material and air bubbles.

At the start of the run the solution culture was brought to a desired reference level in the container. At that level the electrodes were adjusted to make electrical contact through the solution culture. Water was then extracted by the plant for a convenient increment of time (usually 5 min. in smaller plants and 15 min. in larger plants). The amount of water uptake was measured by back filling the container from a burette until the level reached the datum. The amount of water needed to re-establish the electrical contact was taken as the amount of water uptake during the time interval.

Transpiration Rate

The rate of transpiration was measured by periodically weighing the pot and plant system on a sensitive balance. A Pennsylvania Scale Co. Balance, Model No. 1-10, cap. 5 kg, was used. Weights were taken at 15 min. intervals. The balance was capable of reading changes as small as one gram. The 5 min. interval measurements reported were made on a top-load Metler balance (Type, Model P-1200, cap. 1200 g) and capable of reading 0.1 g changes.

Leaf and Air Temperature

Leaf and air temperatures were measured with thermocouples. A fine bead copper-constantan thermocouple was mounted in contact with the lower epidermis and was cemented with Dynaloy Sealant (Dynaloy Inc. Neward, N. J.). This sealant did not injure the leaf surface. Direct and continuous reading of the thermocouple output were read on a microvoltmeter (Wescor Inc., Model M.J. 55). The temperature sensitivity of the system was about 40 uV/C.

Leaf Density Measurement

Leaf density was measured by the method described by Mederski (1961), Skidmore and Stone (1964), and Ehrler and Nakayama (1964). The beta-ray emmiting radioisotope, ^{14}C, was used for the density measurement. The fourth leaf from the top of the plant was interposed between the source and the thin window G. M. detector tube. A cushion of felt was inserted between the leaf and the bottom of the G.M. tube to avoid damaging the leaf. The fourth leaf was chosen for its vigor of growth and the gauging was done on the leaf surface at a location where no large vein encountered the counting geometry. A Nuclear-Chicago rate meter, Model 1620A, was used to read the count-rate. The output count signal was passed through a preamplifier, and a continuous record of the leaf density was plotted on a strip chart recorder (Bausch and Lomb, Model VOM-5).

Measurement of the Apparent Sap-Velocity in the Stem

The heat-pulse method of measuring the apparent sap-flow velocity

was adopted after Bloodworth (1956) and Skidmore and Stone (1964).

In this measurement, a unit containing a stem heater and a heat pulse

sensor is mounted in contact with the stem. The time required for the

heat pulse to travel the distance between the heater and sensor is

measured. The apparent heat pulse velocity was calculated from the

distance to time ratio (Stone and Shirazi, 1973).

The apparent sap-velocity was determined at two positions on the

stem of 8-week-old plants. Two units of heater and heat sensing

assembly were placed on the stem, one was at 10 cm above the root top

and the other was four internodes above.

Measurement of the Leaf Water Potential

Leaf water potential was measured on leaf disks at different

times of the day during the oscillation phase of the transpiration

process. Leaf disks of 0.625 cm diameter were placed in the sample

holder in a sample-chamber psychrometer (Wescor In., Model C-51) and

were allowed to reach equilibrium for 2 min. The micro-volt output

readings were recorded on a psychrometeric microvoltmeter (Wescor

Inc., Model MJ55). The water potential of the leaf was interpolated

from a calibration curve with a sensitivity of about 0.427 uV/bar,

valid in the range of -2 to -30 bars.

Visual Examination of the Leaf Response

The visual observations were made on a continuous basis by noting

the leaf response to the evaporative demand throughout the photo-

period. To record the continuity of the leaf response, a time-lapse

movie with a scaled time ratio of 1:320 was made for the entire

photoperiod. Data from Skidmore and Stone (1964) was used to deduce the stomatal opening and closing sequence.

Results and Discussion

Principal results on four different plants are shown in figures 1, 2, and 3, and Table 2. In the early phases of the study, only a few combinations of the several variables were studied simultaneously. When techniques were perfected such that results became consistent, other variables were added. For example, water uptake always lagged behind transpiration by about 5 to 10 minutes; leaf temperature was 180° out of phase with leaf density; water uptake closely followed apparent sap velocity in the stem; apparent sap velocities at two locations, one above the other, were in phase. Also the plant went through two sets of oscillations each day. One set of oscillations was observed at the beginning of the photoperiod and the other at the end. Figure 1 was a day-long observation of transpiration and uptake on an 8-week-old plant. Figures 2 and 3 represent an attempt to measure simultaneously as many combinations of the variables as possible. Figure 2 is data from a 5-week-old plant and Figure 3 is from an 8-week-old plant. Data on five additional plants is summarized in Table 3.

Uptake and Transpiration

From Figures 1, 2, and 3 it is obvious that phase relations in these two cyclic processes are consistent under the controlled environment conditions. These oscillations have a period of about 30 min. which is characteristic of water-based oscillations (Hopmans,
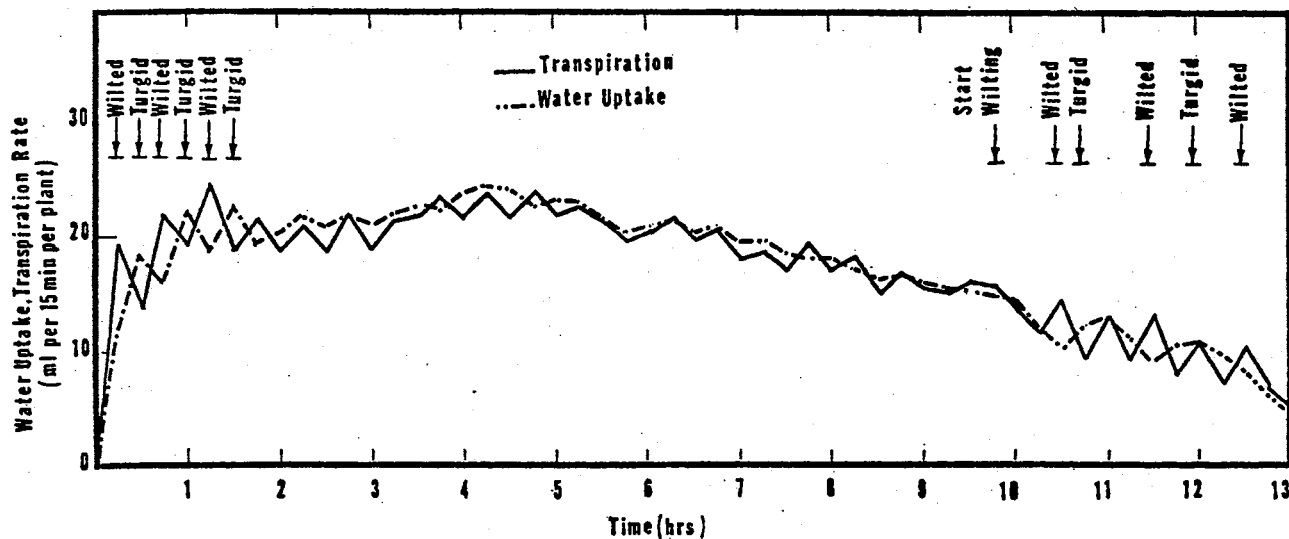
Figure 1. Simultaneous Measurement of Transpiration Rate and Rate of Water
Uptake in an 8-week-old Cotton Plant in Solution Culture and
Control Environment Chambers for the Entire Photoperiod
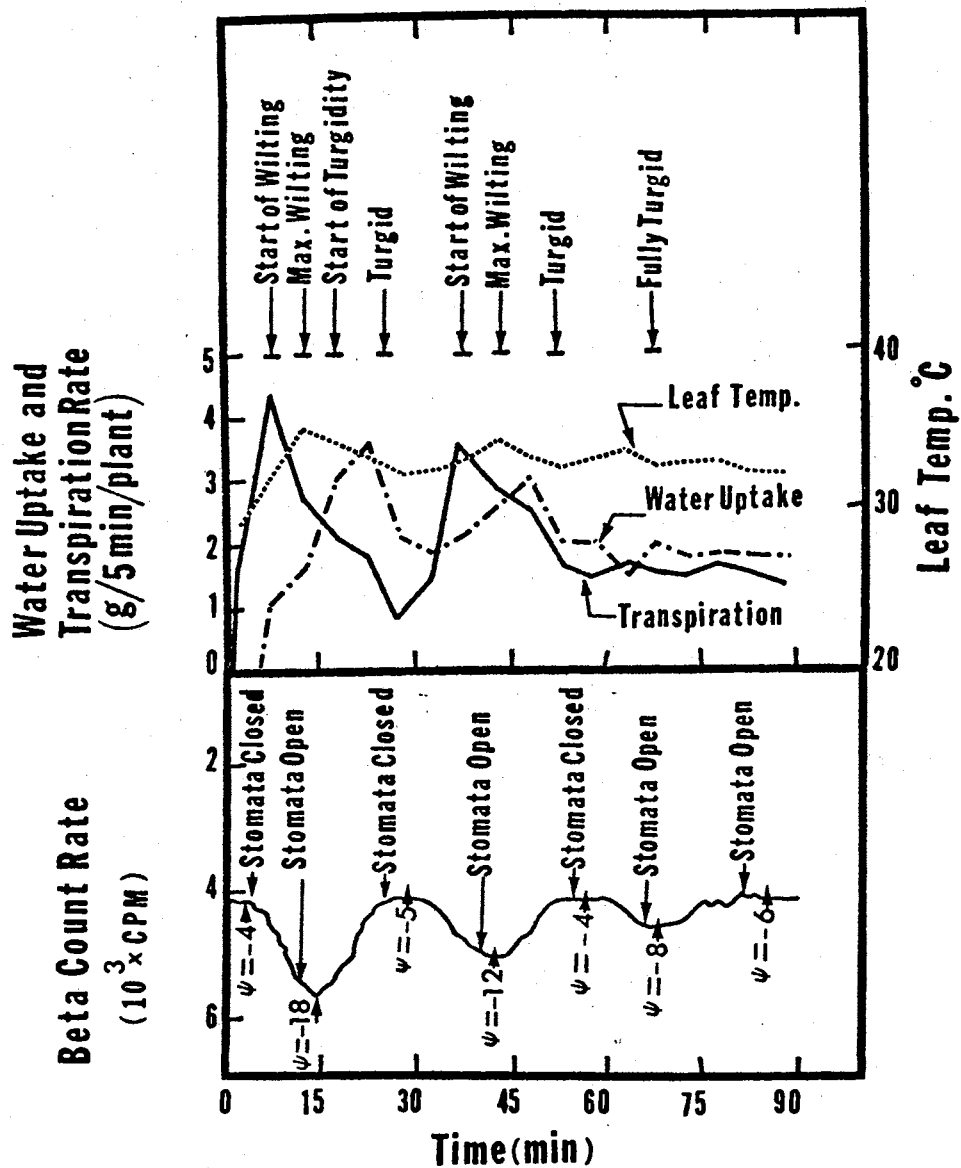
Figure 2. Simultaneous Measurement of Transpiration
Rate, Water Uptake Rate, Leaf Tempera-
ture, Leaf Density, Water Potential in
the Leaf of 5-week-old Cotton Plants.
Stomatal Action Was Deduced from
Skidmore & Stone (1964)
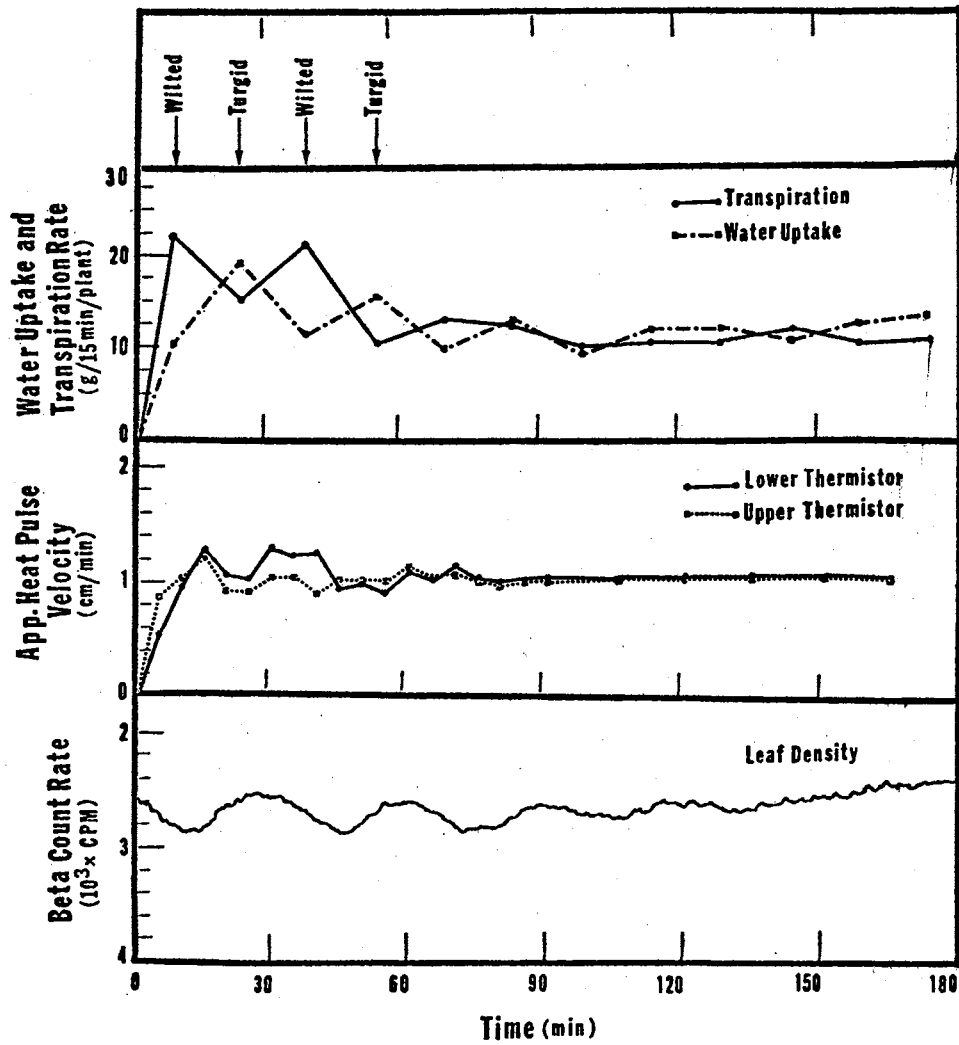
Figure 3. Simultaneous Measurement of Transpiration,
Water Uptake, Apparent-Heat-Pulse
Velocity and Leaf Density on a 9-
week-old Cotton Plant

1971). During the period when transpiration exceeded uptake, the plants were observed to wilt. Plants recovered when uptake overtook transpiration. Figure 1 shows detail of alternate turgid and wilted condition. The oscillation in these processes show a higher amplitude during the early-day cycling than the late-day cycling. The two cycling periods are separated by a period of non-oscillatory conditions where no visible wilt is observed. The late-day oscillations were persistent and never damped out before the end of the photoperiod. The period of oscillation on a 5-week-old plant averaged 32.7 min. as determined by the examination of time-lapse movies, (Table 2). In figure 2 it is seen that at the start of the photoperiod, when the leaf is turgid, transpiration loss commences almost immediately and continues to increase for 10 min. The roots did not start absorbing water until after 5 minutes from the start of the photoperiod. Harris (1968) measured an absorption lag of 3.77 minutes in cotton. At this time the net difference between the amount of transpiration loss and the water uptake was maximum and the leaf showed "incipient wilt" even though the uptake rate is continuously increasing. The maximum wilting occurred after about 15 minutes of the photoperiod. The water uptake lagged behind the transpiration but the net difference was reduced. The leaf started re-gaining turgor soon after the water uptake rate exceeded the transpirational loss. The second cycle started with similar leaf conditions and phase-relations, but the amplitude of the oscillation was smaller. The net difference between the transpiration and uptake, although smaller, was sufficient to cause visible wilting. At the third cycle of oscillation the net difference between these two variables was such that visual wilting was not seen.

TABLE II

PERIODICITY OF LEAF OSCILLATIONS IN A
COTTON PLANT UNDER CONSTANT
ENVIRONMENTAL CONDITIONS

| | Morning Cycling in Cotton | | |
	Leaf Position	T (min)	Time Per Cycle (min)
9:07a.m.*	UP	xxx	xxx
9:22	DOWN	15	
9:37	UP	15	30
9:50	DOWN	13	
10:05	UP	15	28
10:20	DOWN	15	
10:40	UP	20	35
10:56	DOWN	16	

	Evening Cycling in Cotton		
6:20p.m.	DOWN	xxx	xxx
6:35	UP	15	
6:55	DOWN	20	35
7:12	UP	17	
7:25	DOWN	13	30
7:45	UP	20	
7:57	DOWN	12	32
8:14	UP	17	
8:36	DOWN	22	39
8:49**	UP	13	
			AVG = 32.7

*Lights on at 9:00 a.m.
**lights off at 9:00 p.m.

TABLE III

CYCLING VARIATION IN TURGIDITY DURING MORNING
AND EVENING PHASE OF THE PHOTOPERIOD*

| | Morning Cycling | | Evening Cycling |
Date	Period of Cycles	No. of Cycles Before Steady-State	Period of Cycles
4-16-71**	30 min.$^+$	2	30 to 35$^+$
4-23-71**	30 min.$^+$	5	35$^+$
10-5-71***	30 to 32 min.	3	33
10-7-71	30 to 32 min.	3	32
10-13-71***	30 min.	3	32

*In all observations, transpiration rate, water uptake rate, and leaf
 density cycled with same period as wilted-turgid condition.
**Leaf density was not measured.
***Measurements on transpiration rate and water uptake rate were not
 made in evening.
$^+$Visual only

Minor variations of the two processes was noted during the subsequent

6-hour period, but the magnitude of the variation was small, indicat-

ing that the roots were able to absorb enough water to maintain

turgor. Figure 1 indicates that average values of both the water up-

take and the transpiration rate decrease with time. During the steady

state condition the average rate of both the processes was about 22 ml

per 15 min. per plant system, but later in the photoperiod the average

rate decreased to about 15 ml per 15 min. per plant system. Figure 1

shows that at 10 hrs. an abrupt reduction in water uptake was accom-

panied by a reduction in transpirational loss preceded the late-day

oscillation. Unlike the early-day oscillation, the late-day oscilla-

tions did not damp out. They were similar to the oscillations noted

by Skidmore and Stone (1964). They attributed the oscillatory

behavior to an increase in root resistance to water uptake which

developed through the day and postulated the resultant reduction in

uptake might trigger wilting. Shirazi and Stone (1973a) made a

quantitative study of root resistance on plants similar to those in

the present study and found a consistent, 3 to 6 fold increase in

root resistance by late day.

(B) Leaf Temperature and Transpiration

Figure 2 shows cyclic changes in the leaf temperature with time.

The leaf temperature and the transpiration rate show some phase dif-

ference.

In the first cycle, the increased leaf temperature lags behind

transpiration. The maximum transpiration occurs before the maximum

of leaf temperature. After 60 minutes of light period temperature

and transpiration are in phase. In the subsequent cycle the lag was smaller and by the third cycle was almost negligible. The interaction of the temperature and the transpiration has been studied in greater detail by Hopmans (1971) and Gates (1966, 1968). The transpiration process is a measure of the heat energy dissipation from the leaf and is an important part of the cooling system in the plant-water relations. In conditions where plants are growing in unlimited water supply, the transpiration will continue at a rate determined by the heat-load on the system.

Skidmore and Stone (1964) measured the transpiration rate, the leaf density and the stomatal condition simultaneously. Their data indicate a 5 to 7 min. lag between the stomatal opening and closing and the maximum and minimum transpiration rates. In this study the maximum transpiration occurred about 5 min. before the maximum wilting and the maximum uptake was seen 10 min. after the maximum wilting. Thus the maximum wilting, minimum leaf density and the maximum leaf temperature had about the same phase relationships as reported by Skidmore and Stone (1964). Thus we assume a similar pattern in the stomatal conditions and the phase relations between transpiration and visual wilting observations.

In Figure 2 it is seen that when the lights were turned on, the stomata opened and the transpiration was initiated immediately. The loss of water from the leaf reduced its density and the magnitude of the heat sink, thereby causing the temperature to rise. The maximum temperature coincides with minimum leaf density.

For the plants growing in such conditions, the transient response and cyclic variations could make the relationship between leaf

temperature, leaf density and transpiration more complex. Many workers have reported a decrease in the leaf temperature with the increase in transpiration on the basis that transpiration is a part of cooling system, Mellor, et al., (1964) and Gates (1966).

Lowering of the temperature is observed during the time when the stomata are closed. This is possible in a dynamic situation such as this, where the high transpiration demand causes the water uptake rate to increase. Figure 2 shows that lowering of the leaf temperature is observed whenever the water uptake and transpiration curves cross each other. The incoming water is cooler than the water in the leaf, and hence can act as a heat-sink.

(C) Phase Relations Between the Leaf Density and Transpiration

The measurement of leaf density gives a good indication of the relative water content of the leaf. It is a macro property and as such is affected by the overall changes in the leaf cells and the input-output relations in both liquid and vapor phase. The leaf density measurements were accompanied by water potential measurements at critical points of maximim wilting or full turgor. The leaf water content and the water potential oscillated between the initial turgid value and the extreme value at maximum wilting encountered in each cycle. After passing through the state of incipient wilting the leaf always returned to its near initial density (Figure 2). The amplitude in the leaf density cycling decreases indicating that the water uptake is increasing correspondingly. Fig. 2 reveals that transpiration loss and the leaf density are nearly 180° out of phase. Minimum transpiration occurs when the leaf reaches full turgor, but the leaf density

minimum is observed after about 8 min. after maximum transpiration in the first cycle, and after about 5 min. in the second cycle. The third cycle is not clearly defined. Similarly, the leaf did not achieve maximum density until after about 8 min. after maximum water uptake rate in the first cycle, and after about 5 min. in the second cycle.

The water potential in the leaf at the start of the photoperiod was found to be -4 bars. After the evaporative demand was impressed upon the plant system, the leaf water content diminished. The minimum water potential during the first cycle was measured at maximum wilt and was found to be -18 bars. At the end of the first cycle when the leaf regained its turgidity the water potential increased to about -5 bars. The maximum wilt at the second cycle corresponds to -12 bars and the turgid state corresponds to about -4 bars. The third cycle, which did not produce appreciable wilt had its minimum water potential of about -8 bars, and the steady state water potential was recorded at -6 bars.

(D) Apparent Sap-Velocity Changes in the Stem

Fig. 3 shows that the sap-velocity was higher at the upper thermistor in the initial 10 min. of the photoperiod, but the velocity at the lower thermistor increased in the later time-interval and remained higher thereafter. The visual observations as indicated by the leaf response in the time-lapse movie suggest that all leaves exposed to the same evaporative demand oscillated in phase. These observations are in agreement with the findings of Lang, et al., (1969). Stem shrinking and radial expansion have been recently reported by Namken,

et al., (1971) who showed that some amount of hysteresis effect is observed in the stem water content. In the present study the sap-velocity was in phase at both the thermistors. The sap-velocity was more closely in phase with transpiration rate than the water uptake rate.

CHAPTER V

CONCEPTUAL MODEL OF AUTO-OSCILLATION IN THE

TRANSPIRATION STREAM IN A COTTON PLANT

UNDER CONSTANT ENVIRONMENTAL

CONDITIONS[1]

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Abstract

A conceptual model of the transpiration stream in a cotton plant

growing in nutrient solution under constant environmental conditions

is presented. The model is based upon phase relations between water

uptake, transpiration rate, sap-velocity in the stem, leaf density

changes, leaf temperature variation, and visual observations of wilted-

turgid cycles. These water-based dynamic processes are simulated by

an RC electric network model. A nonlinear coupling consisting of a

hysteresis loop with time-variant constraints is used as the mechan-

ism operating on the stomatal resistance to cause auto-oscillation

in the plant. Mathematical equations based on the network variables

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were solved via the simulation language Continuous System Modeling Program (CSMP1-IBM-360/65). The model showed gradually damped oscillations early in the photo-period and sustained oscillations late in the photo-period in all dynamic variables. The resulting simulation output agrees with the pattern of auto-oscillations observed in the in vivo system in terms of relative magnitude of potential changes and periodicity of oscillations.

Introduction

Modeling has become an important tool in the study of water flow mechanics in biological systems. Since van den Honert (1948) cited Gradman, who first applied an analog of Ohm's law to water transport in a plant, several workers (Gardner and Ehlig, 1965; Rawlins, 1963; Skidmore and Stone, 1964; Slatyer, 1960) have used modified forms of van den Honert's basic equation. Skidmore and Stone (1964), accepting the conceptual validity of the Ohm's law analogy, proposed that future models should include elements of capacitance, delayed feedback, switching mechanisms, and variable root resistance. Rawlins (1963) suggested that resistance in the gaseous phase should be modified to accomodate the nonlinear behavior of the vapor transport. He further proposed that since the entire process is dynamic, all resistances in the plant should be regarded as variable.

Several models describing the plant-water relations have been proposed in recent years. Woo et al. (1966) presented conceptual models of transpiration and stomatal control mechanisms using a mass-spring-friction mechanical system as an analog of the turgor pressure mechanism. They assumed that such a system is linear. It was capable

of self-oscillation by virtue of a second-order lag property which created up to a $180°$ phase shift in the system. Second-order systems with positive feedback loops have been presented (Karmanov et al., 1966; Meleshchenko and Karmanov, 1966; Viktrov, 1968). They use a hydraulic model in which the functions are not clearly analogous to the plant system. Positive feedback was postulated by Rashcke (1970) on the basis that the decrease in the turgidity of the epidermal cells increases the stomatal aperture. He recognized another loop in which lowering the turgidity in the epidermis causes removal of water from the guard cell. This represents a negative feedback path. Cox (1968) working on sunflower suggested that during high evaporation demand, water may flow from the leaf tissues which are not directly in the transpiration stream. Hopmans (1971) presented a model in the support of negative feedback, with a minor positive feedback loop involving water flow through epidermal cells only. Cowan (1972) presented a closed loop model of the mechanism of sustained oscillation in trans-piration, leaf water content, and water flux measurements in a cotton plant. Cowan's model accounted for the free running oscillations but did not account for non-oscillatory steady state conditions. Penning de Vries (1972) presented a first order simulation model using a first-order lag function for the transpiration stream in a non-growing leaf under varying environmental conditions. He advanced a hypothesis that the control mechanism of the guard cell is affected by several factors including water potential, and that the function of the subsidiary cell is affected by the water potential only. The model of Lang et al. (1969) seems to be the most logical and simple model. However, they indicated that their model was incapable of oscillation unless a 180

degree phase-shift, requiring an additional 3 RC units, was introduced between the guard cell and the mesophyll potential.

This paper introduces a model with the following objectives.

1) The model should be simple, realistic and able to simulate the experimental results reported by Shirazi and Stone (1973 a, b) in a manner consistent with the contemporary literature.

2) The model should conceptualize a coupling between guard cell and stomatal resistance which can produce oscillations in the model of Lang et al. (1969) without creating a 180 degree phase shift.

3) The model should allow determination of the sensitivity of parameters in the model dynamics.

Formulation of the Model

The model of Lang et al. (1969) is the simplest and the most realistic among all those reviewed above. It shows plant components which are easily identified. The functional relationship of the various electric analogies are close to the present-day understanding of the plant-water relations. Figure 1 is a model adapted from Lang which incorporates the features of the phase relations in water-based rate processes reported in the literature (Barrs and Klepper, 1968; Rawlins, 1963; Shirazi and Stone, 1973a,b; Stone and Shirazi, 1973; Skidmore and Stone, 1964). Several modifications were found necessary in the Lang model.

First, Skidmore and Stone (1964) and Shirazi and Stone (1973a) showed root resistance to be dependent upon time, water potential, and temperature. Hence a variable resistance in the root component is introduced. (See R1 and R2 in Figure 1.) Also, the gaseous phase
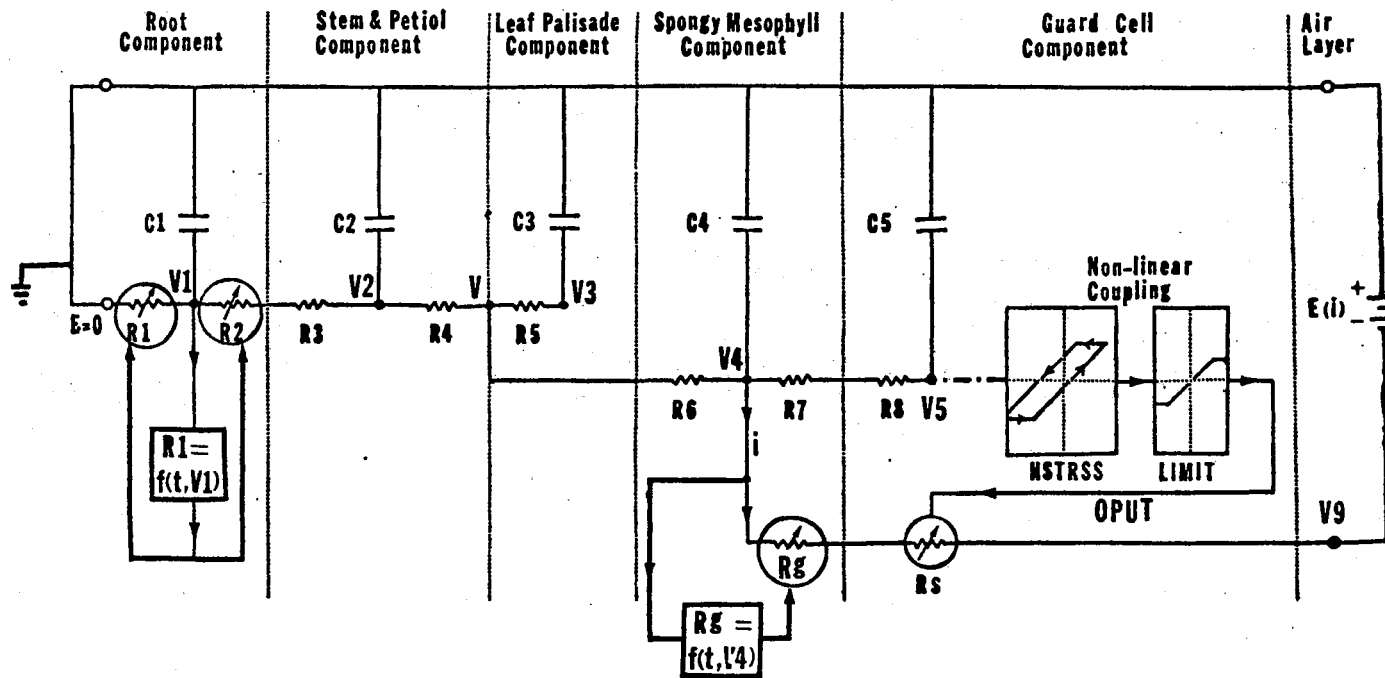
Figure 1.   Electric Analog Model of the Transpiration Stream.
Roots Are at Zero Potential

resistance should be recognized as a unique function of vapor pressure and concentration as suggested by Slatyer (1960) and Rawlins (1963). The resistance Rg is incorporated as additive to the stomatal resistance Rs. The magnitude of these resistances is potential dependent. Since potential is time-variant, these resistances are shown in Figure 1 as functions of time and potential.

Several authors including Skidmore and Stone (1964) have shown that stomatal action lags behind leaf turgor changes. Such lag may be due to changes in the water permeability properties of the guard cell walls and could account for the delay-action of changes in shape similar to a hysteresis effect (Figure 1). Hopmans (1971) cited Stalfelt who proposed the phenomenon of "spannungsphase", in which guard cells accumulate the effect of previous impulses over a period of time, building up the turgor pressure gradually to a level when stomatal opening is initiated. Therefore, the pattern of stomatal opening and closing is postulated to occur through a non-linear coupling between the guard cell potential V5 and the stomatal resistance Rs. This will be elucidated later.

Evaluation of the Parameters and Constants

The evaluation of the magnitude of the resistances and the capacitances and other related constants and parameters in the network model was based upon observations reported by Shirazi and Stone (1973a,b) and Stone and Shirazi (1973).

The capacitances simulate the water storage capacity in various plant components. These capacities are expressed as lumped parameters. Since the behavior of all leaves in a single plant appear to be in

phase, as reported by Lang et al. (1969) and Shirazi and Stone (1973b), all leaf components are assumed to behave as parallel capacitors and are lumped into a single value C_2. Each leaf could have been regarded as a discrete unit with a characteristic value at any given time, i.e., the magnitude of C_3, C_4, and C_5 could be modeled in each leaf. Thus, the largest value of the capacitance was assigned to the mesophyll C_4 components and C_3 was taken to be equal to C_4. The root storage C_1 was assumed to be about 1/4 of the combined capacitance of palisade and mesophyll. The capacitance C_5 of the guard cells was set at about 1/100 of the mesophyll. After the results for this study were obtained Cowan (1972) published data on computed values. He assigned the capacitance of the subsidiary cell and guard cell to be 1/15 and 1/30 of the mesophyll capacity respectively.

The water-based auto-oscillations reported by Shirazi and Stone (1973b) in the various dynamic variables show a period of about 28 to 30 min. during the entire photoperiod of nine hours. For a first approximation, a 30 min. period was assumed for calibrating the model. All physical systems require a certain amount of time to transmit signals from input to output. This time is characterized in the model by system time constants dimensionally given by the product RC. "Complete" charging of the R-C network requires about 6 time constants.

The network model contains five capacitors and is thus described by a fifth-order system of differential equations. The model is nonlinear due to the nonlinear relations between R_1 and R_2 and the voltage V_1 and between R_g and V_4 and between R_s and V_5.

Although the concept of a fixed time constant is valid only for a linear time-invariant network, the network parameters were established

from the desired time constant values as observed from data. Reasonably good results were obtained by considering the charging and discharging cycles separately and focusing on the dominant (largest) time constant in each case. Assuming the dominant time constant during the discharge cycle (uptake of water) is about 2 minutes in length and the dominant time constant during the charging cycle is 3 minutes and further recognizing that about six time constants are needed for nearly complete transient excursions, the total period of the oscillations was established as 6 X (2 + 3) = 30 minutes as desired.

The root resistance (R1 + R2) was arbitrarily set to be two units at the start of the photoperiod (t = 0). R1 is equal to R2. R3 to R6 were given constant values of 2.5 units. The values of R1, Rg, and Rs were variables calculated by mathematical expressions described later. The time constants for charge and discharge cycles then fixed the values for the largest capacitors C3 and C4. (Note: both resistance and capacitance were of arbitrary units with product equal to time in minutes). This produces a time interval of one minute of real time for a unit of time on the computer simulation.

The water potential at the root was assumed to be zero (osmotic potential component neglected). The potential at the leaf boundary layer was assumed to be -200 bars. The electric network model assumes a one-to-one relation between pressure potential and voltage. The potential above the boundary layer is usually much lower _in vivo_ but this feature was not modeled. Shirazi and Stone (1973b) found leaf water potential to be -4 bars in the morning. This represents an initial condition of potential in the leaf just prior to initiation of light period. With these values of potential at the two extremities

and the measured value of -4 bar in the leaf, the magnitude of Rg =
Rg + Rs sufficient to drop the voltage from -4 to -200 was calculated
as 487 units. This represents the maximum value of stomatal resistance.
the minimum value was assumed to be zero. For the time constant cal-
culation of (Rg + Rs)C4, Rs was taken as zero and Rg was scaled to
give the 5 min. time constant.

Evaluation of the Variable Root Resistance

Shirazi and Stone (1973a) used a decapitated root system technique
and showed that the effect of applied suction upon the water uptake
rate follows an exponential path as

$$U = \exp(A + B^\tau) \tag{1}$$

where U = rate of water uptake, τ is the applied suction and A and B
are the intercept and the slope of the straight line on a semi-log
plot. However, the rate of change of uptake with applied suction is
a function of the lumped resistance of the pathway of water flow in
the roots. The time-dependence of the root resistance was evaluated
by incorporating an observed linear relationship between the slope of
the line and the time of the day, resulting in a mathematical expres-
sion for uptake rate.

The present model utilizes the Ohms' law analogy relating the
flow of water to the flow of electric charge. Thus the following
equation was used in the simulation of the time-dependent root
resistance.

$$R(\tau, t) = \frac{-(V_o - V_1)}{U} = \frac{V_1}{U} = \frac{\tau}{U} \tag{2}$$

where Vl, shown in Fig. 1, Vo = 0 and U and τ are both time-dependent.

Shirazi and Stone (1973a) showed

$$R(\tau,t) = \frac{\exp - \left[0.96 + (1.57 - 1.58 \times 10^{-3}t)\tau\right]}{(1.57 - 1.58 \times 10^{-3}t)} \tag{3}$$

This equation was scaled to give unit value at time zero.

Evaluation of Resistance in the Gaseous Phase

The expression for the gaseous resistance variable models the dimensionally uniform resistance for the gaseous transfer as suggested by Rawlins (1963)

$$Rg = \frac{RT}{DMb} \ln \frac{\theta s + bl}{\theta s} \tag{4}$$

where D = diffusivity of the water vapor for the total effective cross-sectional area, M = molecular weight of water, R = universal gas constant, T = absolute temperature, θs = vapor concentration at saturation, and θ = vapor concentration and is linearly related to the "effective path length" l by, $\theta = \theta s + bl$ where b is constant. Herein, let RT/DMb = K1, a constant.

In the vapor phase, θ and θs, and water potential, ψ are related by the well known expression

$$\psi = \frac{-RT}{M} \ln \frac{\theta}{\theta s} \tag{5}$$

such that at $\psi = 0$, the $\theta = \theta s$. Solving for θs gives

$$\theta s = \theta/\left[\exp(-M\psi/RT)\right] \tag{6}$$

However, in this model, $\theta s + bl = -200$ bars. Substituting these

expressions in eq (4) gives

$$Rg = K1\left[\ln\left[\frac{-200}{\theta} \exp(-M\psi/RT)\right]\right] \tag{7}$$

collecting terms which are constant for the present boundary conditions and calling them K2, gives

$$Rg = K1 \ln K2 + K1 \frac{M}{RT} \psi \tag{8}$$

In here potential ψ is equivalent to V4(t) (Fig. 1). Thus, V4 (t) in equation (8) simplifies to

$$Rg = \overline{A} + B\left[-4V(t)\right] \tag{9}$$

There is a threshold value of -4 bars (the night time equilibrium potential) at the turgid state of the leaf. Therefore, the value of $\overline{A}$ is small and was neglected. Initially, the value of the slope B was adjusted to produce Rg $\approx$ 50 units when V4 = -18.

Nonlinear Coupling and Stomatal Variation

An analysis of the pattern of water potential change in the leaf component and the degree of stomatal aperture as reported by Shirazi and Stone (1973b) is presented in the phase plot diagram of Fig. 2. It shows that at the beginning of the photoperiod the leaf water potential is about -4 bars. The stomata begin to open immediately after the lights are turned on, followed immediately by transpirational loss. The leaf water potential starts to drop after a slight delay. At the time of maximum transpiration, which corresponds to maximum opening of the stomatal aperture, the leaf water potential drops to about -9 bars. At this stage incipient wilt is observed due to
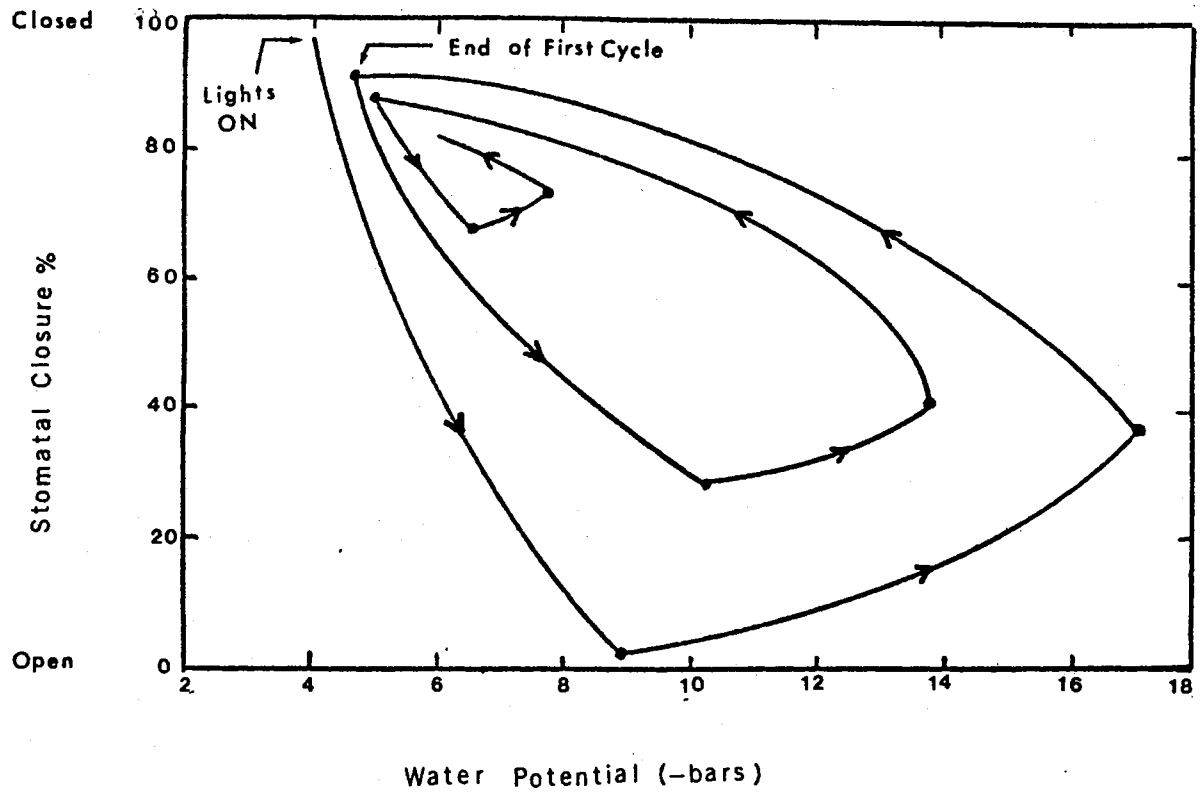
Figure 2. Phase-Plot Diagram of the Stomatal Resistance and
the Leaf Water Potential

desiccation. Finally, the initiation of the stomatal closure follows even though the leaf water potential continues to decrease until the maximum wilt is reached at about -18 bars. At this stage the water uptake rate increases in accordance with the deficit demand and subsequently exceeds the transpiration rate until leaf gains full turgidity. The leaf water potential then increases to a near-initial value.

The second cycle starts with similar initial conditions of leaf water potential and the state of turgor and passes through a similar sequence of events until the water potential reaches to its near-initial value again. In subsequent cycles however, the magnitude of the potential drop is smaller and on the third cycle, no visible wilting is observed even though water potential shows oscillations.

This pattern of the stomatal action lagging behind the water potential suggests a hysteresis loop in which the process returns to the initial reference position at the end of each cycle. In Figure 1, the hysteresis loop is visualized as part of the nonlinear coupling between the guard cell potential and the stomatal resistance. The lag is about 6 minutes. Hopmans (1971) and Lang et al. (1969) proposed a time delay in the information pathway to be due to high resistance for water transport to the guard cell. This delay tends to cause a time-lag in the stomatal response with the changes in the water status. In the present model the magnitude of this component of delay is simulated by R8C5 (Fig. 1). A 5-to 7-minute delay in the stomatal action and the transpiration rate was reported by Skidmore and Stone (1964).

The lag effect on guard cell potential (V5) action is generated by letting V5 traverse a hysteresis loop with width equal to (W1, W2)

(Fig. 4). The dependent lagging function is called V5H and becomes the controlling function for the stomatal action. V5H will follow V5 to any value but a window of control equal to (K1, K2) on stomatal opening (resistance) is set (Fig. 4). When V5H $\leq$ K2, stomata are closed and when V5H $\geq$ K1 stomata are open. For intermediate values of V5H (K2 < V5H < K1) stomata are partially open. As indicated earlier, stomatal resistance is set to vary between 0 and 500 units. A function dependent upon V5H is needed to generate a zero when V5H $\geq$ K1 and a unity when V5H $\leq$ K2 and a CSMP limiter function is used for this purpose. Additionally, the limiter generates an output which changes linearly with V5H for intermediate values of the window.

Thus, if one wants the stomatal resistance to vary linearly between 0 and 500, it is necessary to multiply the function by 500. However, such a variation does not seem realistic as pointed out by DeMichele and Sharpe (in preparation). A exponential rate of change seems more reasonable (Fig. 3). Consequently, stomatal resistance was modeled

$$Rs = 500[\exp\{-N(OPUT + 4.0)\}-1.0]/[\exp(DN)-1.0] \qquad (10)$$

where N and D are constant. The variable OPUT is the output of the function generator block called LIMIT. The use of this function is discussed in detail by Shirazi and Stone (1973d). This function is utilized to generate values of zero or unity. When the stomata are open and the OPUT is equal to K1, the term multiplying the constant 500 is zero, so that Rs = 0. When the stomata are closed and OPUT is equal to K2, the ratio multiplying the constant 500 is equal to unity, so that Rs = 500. The exponential function is defined for
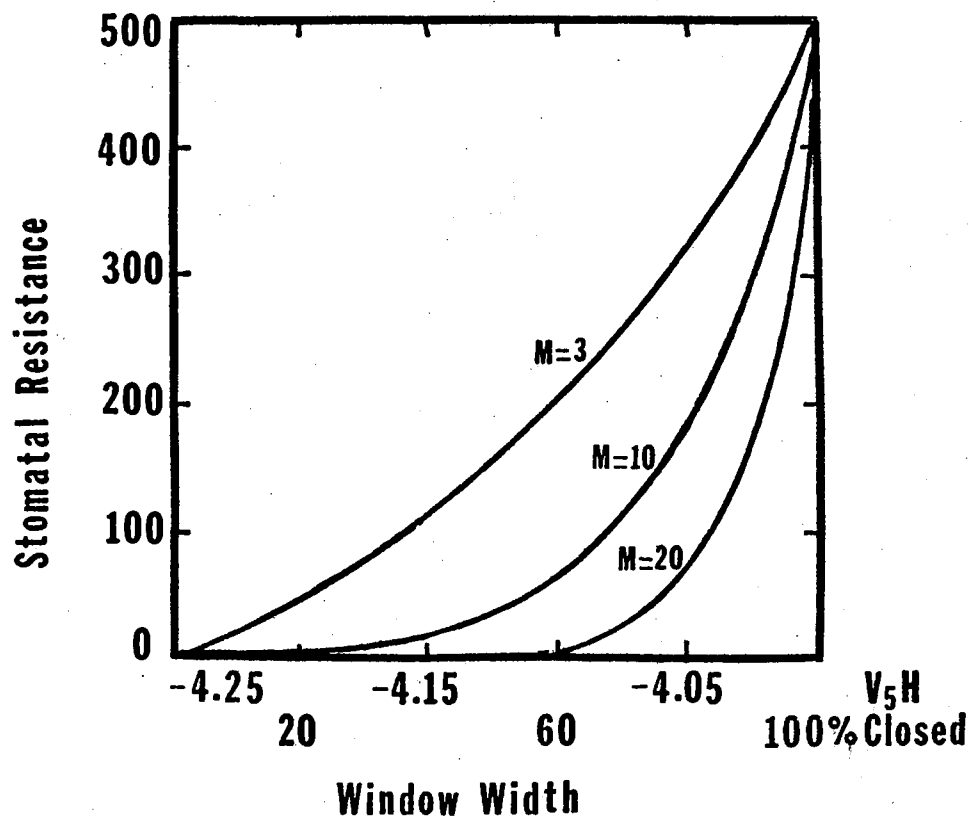
Figure 3.   Effect of Window Opening Upon the
Stomatal Resistance
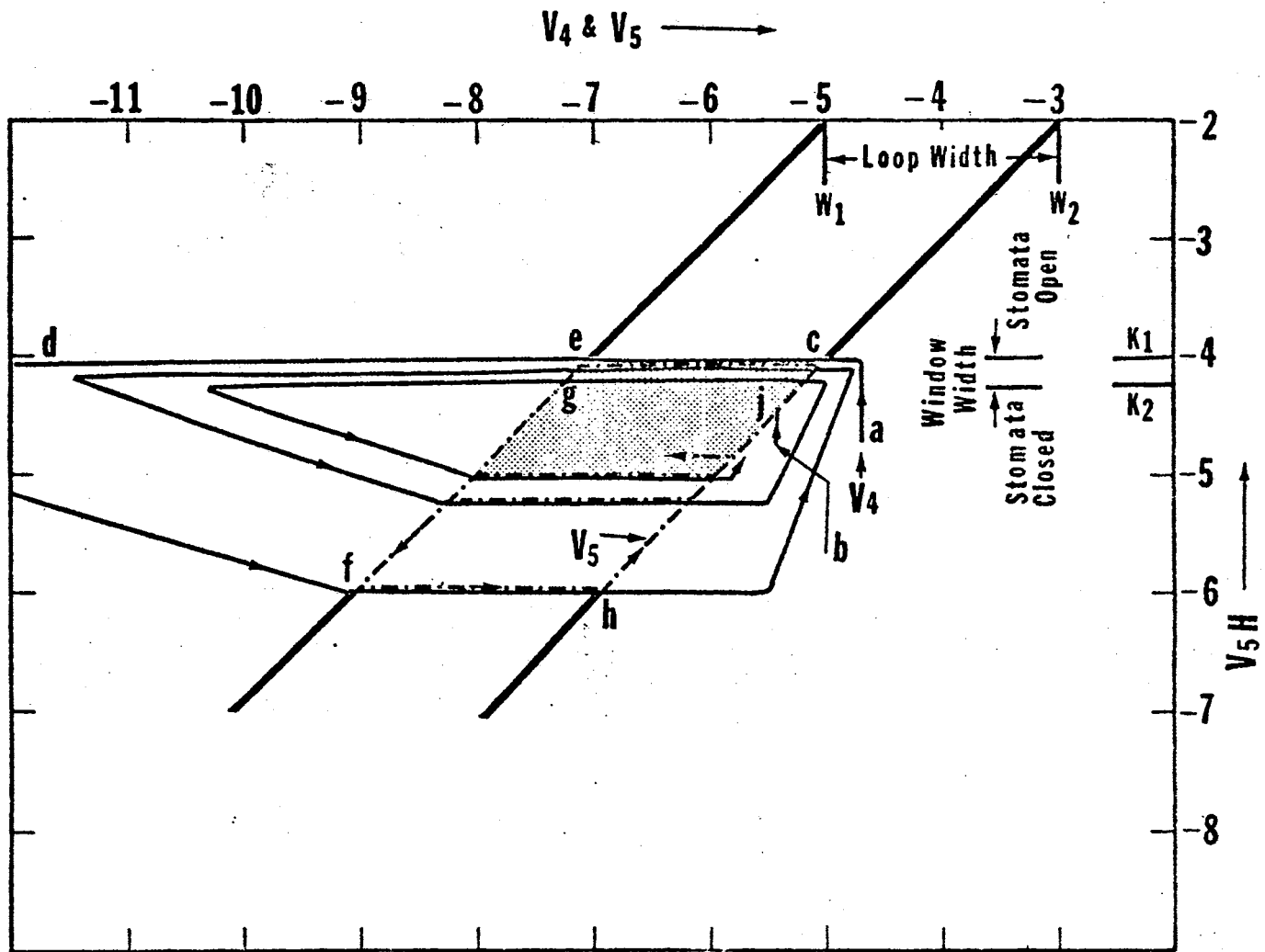
Figure 4. Hypothetical Interaction of V4, V5, and V5H Variables, as Affected by the Magnitude of the Parameters W1, W2, K1, and K2

$K2 < V5H < K1.$

Figure 4 illustrates a typical scan showing how V5 follows V4 and how V5H is generated. The points a and b represent initial conditions on V4 and V5 respectively. Dark diagonal bars delineate the width of the hysteresis loop. Initially, the stomata are closed ($V5H \leq K2$), and V5 approaches V4 and they tend to equalize at about -5 bars. However, at this point, $V5H \geq K1$ and the stomata are open, causing V4 to drop rapidly, going from c to d and beyond. V5 follows V4 to the lower limit of the hystersis bound e, and then follows this bound towards f, changing V5H as it goes. When V5 passes point g, $V5H \leq K2$ and the stomata are closed. V4 then recovers and moves towards f, overtaking V5 and moving rapidly past h. V5 follows to h, and is then constrained to follow the upper bound of the hysteresis loop towards e. As V5 passes j, $V5H > K2$ and stomata start to open, initiating a new cycle.

While offscale in Figure 4, the water potential in the mesophyll (V4) dropped to about -18 bars while V5 dropped to about -9 bars. This variation in V4 is consistent with initial cycles reported by Shirazi and Stone (1973b).

Adjustment of the Parameters

Once the approximate values of the constants and parameters were established, the model was tested with the System/360 Continuous Modeling Program (CSMP1) language. The width of the hysteresis loop corresponding to the range of potential variation in the leaf was maintained for the morning phase of oscillations. The magnitude of the window-width was established based upon the damping characteristics

of the leaf oscillations reported by Shirazi and Stone (1973b).

In the absence of any constraints on the hysteresis parameters, the model produced sustained and symmetrical oscillations. Hence, the constraints (K1, K2) were established on the hysteresis function. Larger window width caused overdamping of the system and smaller window caused sustained oscillations. The oscillations were satisfactory in terms of their period but the drop in potential was smaller than reported by Shirazi and Stone (1973b). To achieve larger drops in potential the window width (K1, K2) was narrowed and the hysteresis loop was readjusted in the more negative region. However, it was seen that assigning discrete values to these parameters would be unrealistic and, therefore, an arbitrary time-variant mathematical function was generated as

$$Y1 = A[exp(Z \times time)] \tag{11}$$

where A and Z are constants. There were several advantages to this function. First, it provided a continuity in the process of opening of the window, and a condition where K2 is $\leq$ K1, thereby allowing V4 to traverse through a larger negative potential region. Second, it gave control on the time desired for the window to reach its final value. Furthermore, it is more logical to open the window slowly since very few biological processes change states abruptly.

The relationship between window width and stomatal resistance is presented in Fig. 3. Window width is postulated to change between -4 units to -4.25 units of V5H. The variation of the constraint upon the V5H is simulated according to the following equation

$$K1 = -0.25[\exp\{-M(Y1 + 4.0)\}-1.0]/[\exp(MD)-1.0] \qquad (12)$$

where D and M are constant and Y1 is defined above. Fig. 3 indicates

that the behavior of the stomatal resistance is dependent upon the

degree of change in the OPUT and a factor M. It appears that at larger

M, the stomatal resistance is smaller for a given width of window. The

factor M holds the stomatal resistance to a lower value at a given

degree of closing. Recently, DeMichele and Sharpe (in preparation)

identified the length of the stomata to have similar effects.

In the later part of the day it was observed that both the water

uptake rate and transpiration rate declined. The plants showed indi-

cation of gradual wilting as reported by Shira.i and Stone (1973b).

At about 600 minutes after the lights were turned on, the water uptake

rate lagged behind the transpiration rate. This could be due to

increase in root resistance. Evening cycling has been reported by

several workers (Barrs and Klepper, 1968; Hopmans, 1971; Shirazi and

Stone, 1973a,b; Skidmore and Stone, 1974). In the present model, the

root resistance increased six-fold over the length of the photoperiod.

This caused instability in the system and slight tendency for oscilla-

tion was noted. To achieve the evening oscillations, it was necessary

to readjust the width of the loop and the window width. The width

of the hysteresis loop was increased to twice the initial value and

its location was moved towards the more negative region. Also the

window was reduced by 80% of its steady-state value. These adjust-

ments were made as a function of time and were simulated by the

following equation

$$K1 = 0.15[\exp\{-M(Y2 +4.0)\}-1.0]/[\exp(D\ M)-1.0] \qquad (13)$$

where D and M are constants and Y2 is the expression to simulate the closing of window and is developed as follows

$$Y2 = -4.0 - 0.25 \left[\{exp(C \times time) - exp(CZ2)\}/[1 - exp(CZ2)] \right] \qquad (14)$$

where C and Z2 are constants. A detailed treatment of the significance of these parameters and a CSMP program listing is presented by Shirazi and Stone (1973d).

As indicated in Fig. 4, when V4 and V5 are traversing the paths towards more negative potential, V5H stays unaltered which might be conceptually similar to a sort of resilience in the characteristics of the guard cell wall. Increasing the hysteresis loop width is, there- fore, visualized to be analogous to an increase in the resilience during the evening. Decreasing the window width on V5H causes stomata to close rapidly, thereby allowing the leaf to regain its turgor. This variation along the path of the window is, therefore, visualized to be analogous to permeability characteristics of the guard cell walls.

Results and Discussion

The results of the computer simulation are shown in Fig. 5. The water potential changes in the root, an average of leaf palisade and mesophyll cavity, and guard cell are plotted as function of time as the variables V1, V(aver.), and V5, respectively; variation in Rg = Rs + Rg is also plotted. The changes in water uptake and transpiration rate are illustrated in Fig. 6 and 7. The plots of other variables are not shown here but are available through the computer plotting instruc- tions. See details of input-output by Shirazi and Stone (1973d).
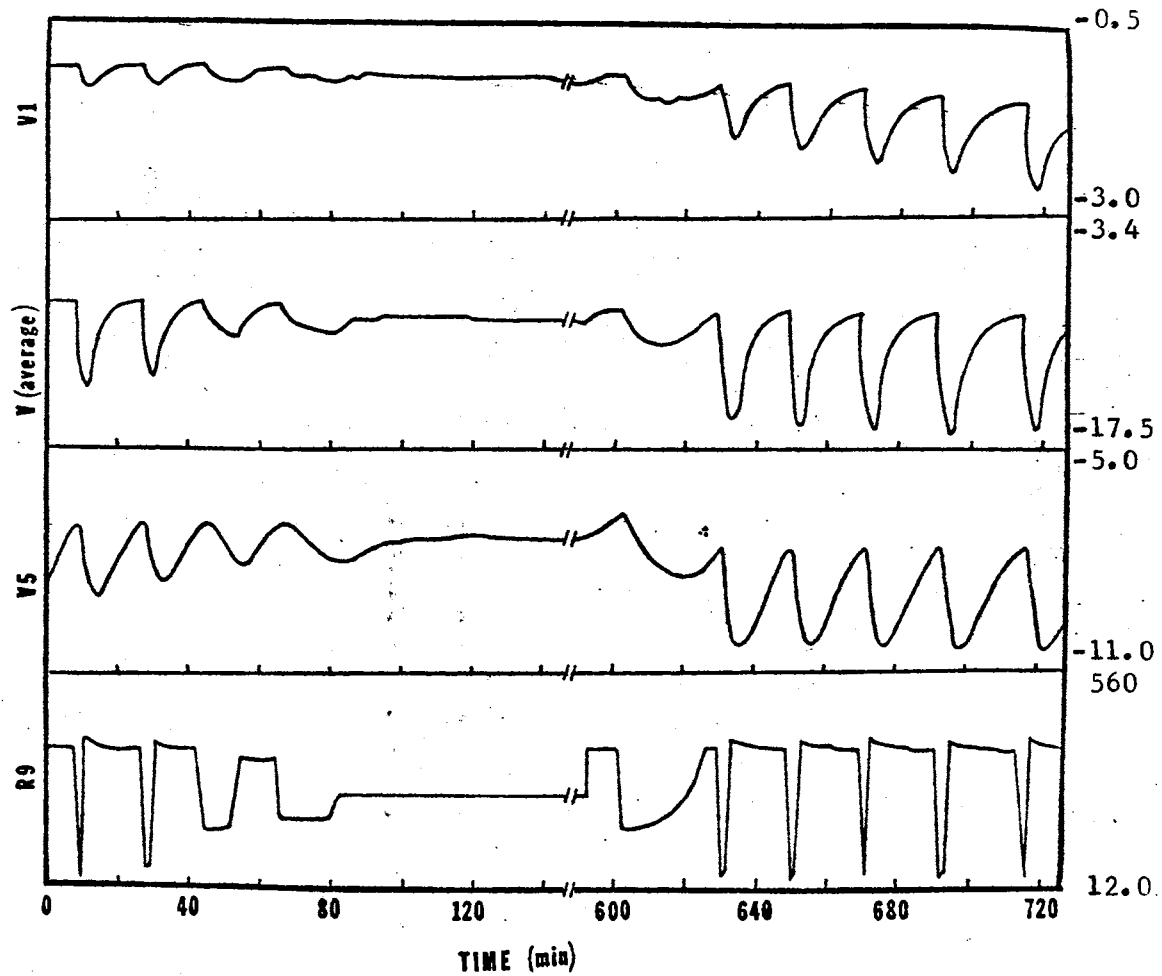
Figure 5. Computer Simulation Output of the Potential in Different
Plant Components and Total Leaf Resistance
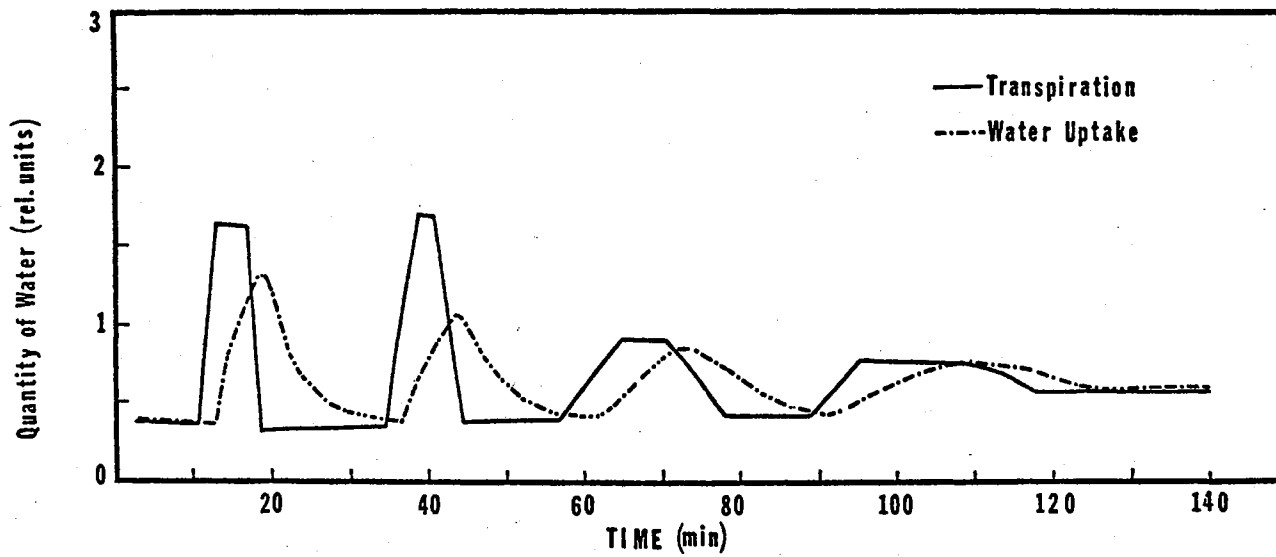
Figure 6.   Computer Simulation Output of the Transpiration and Water
            Uptake Rate for the Morning Phase
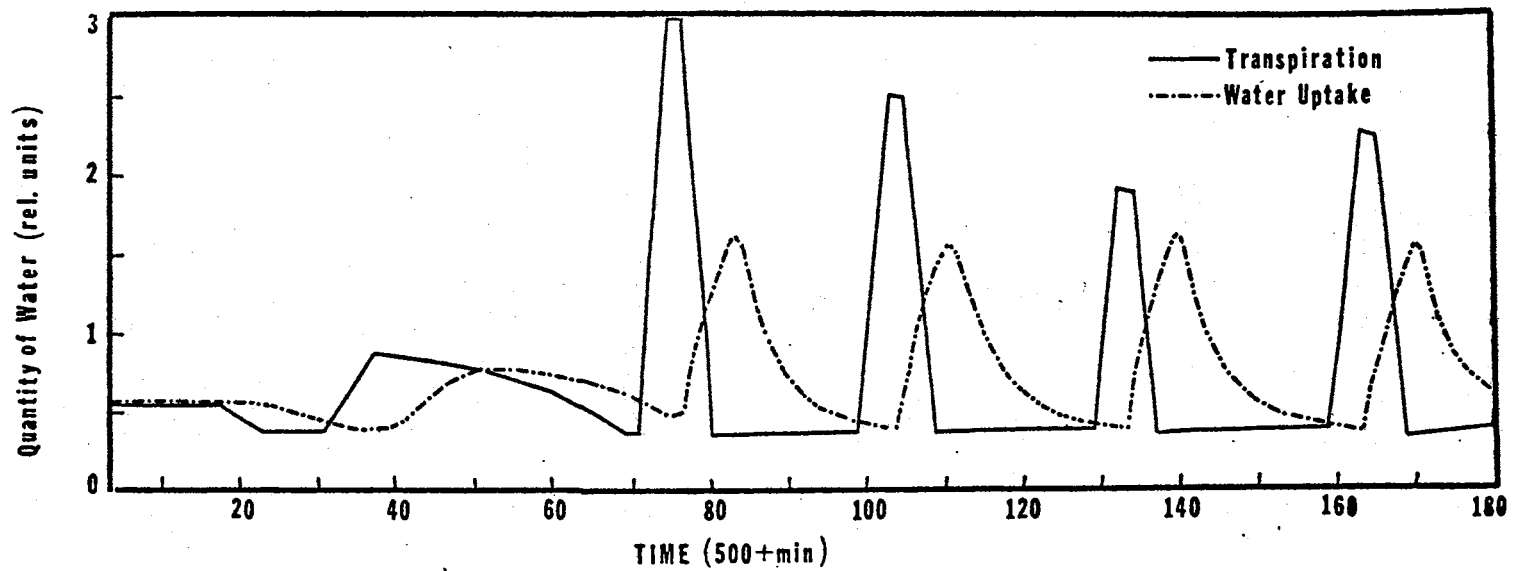
Figure 7. Computer Simulation Output of the Transpiration and Water-Uptake
Rate for the Evening Phase

In the model, the effect of an increase in root resistance was noted late in the photoperiod as the system became unstable, and a slight tendency to oscillation was noted. The magnitude of the root resistance at that time was such that it alone could not produce the extent of instability in the system found necessary to initiate auto-oscillation. However, in conjunction with the adjustment of parameters it had its effect upon creating reasonable lag of water uptake behind transpiration at about 600 min. of the photoperiod (Fig. 6 and 7).

The pattern of potential changes in the stem petiole component, indicates similar oscillations. These patterns are comparable with the sap-velocity measurements in the stem reported by Stone and Shirazi (1973) and Skidmore and Stone (1964).

The water potential in the palisade component also oscillated with slight phase differences with the mesophyll component. In the absence of any reported values for the potential variations in this component, it is conjectured that computer output is a fair approximation of the potential changes in the leaf palisade.

The largest variation in the water content is considered to take place in the mesophyll cavity. Loss of water from the leaf surface through the stomata takes place from palisade and spongy mesophyll cells exposed to the intercellular spaces. For the purpose of comparison with the leaf water potential changes reported by Shirazi and Stone (1973b), and average of $(\frac{V3 + V4}{2})$ was plotted in Fig. 8 as V(Aver.). The result indicates good agreement in terms of ranges of potential and period of oscillation.

In the guard cell component, the potential (V5) increased as soon as driving force was applied at zero time. Unlike V3 and V4, there
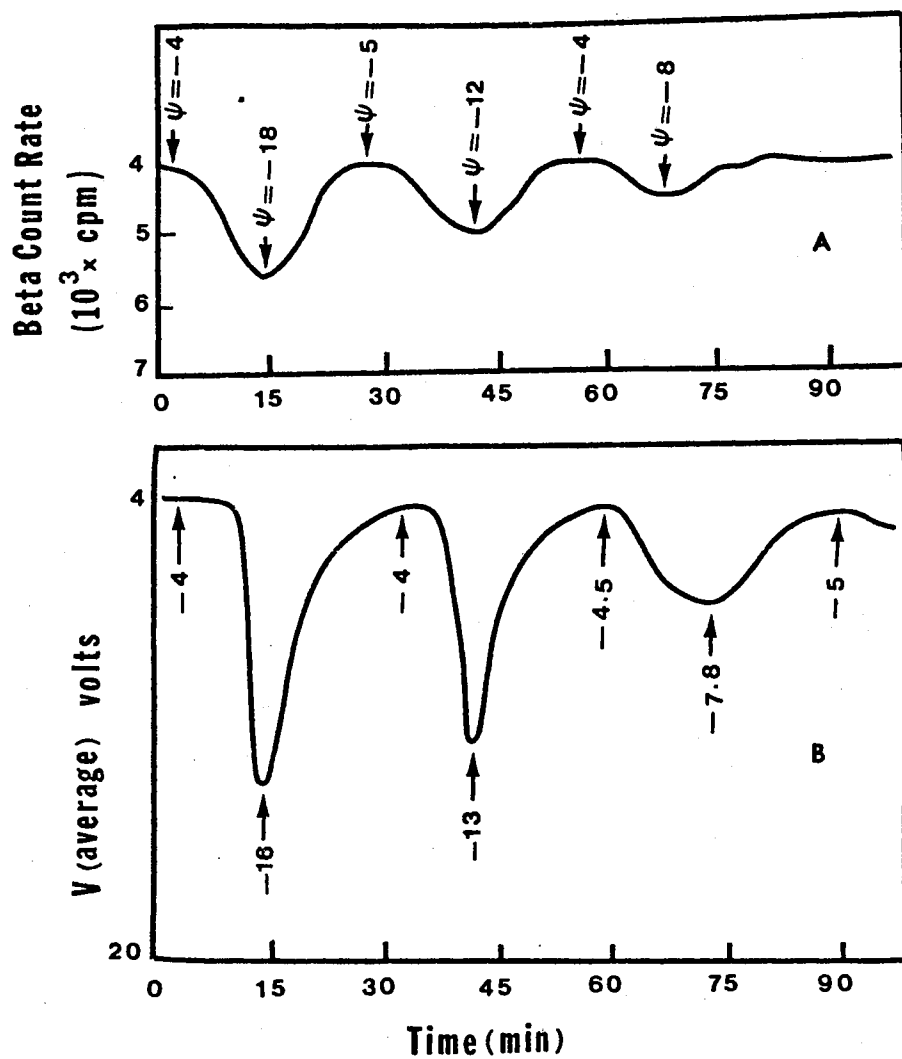
Figure 8. Comparison of Experimental and Analog
Results of Water Potential in the
Leaf. A. Leaf Density as Measured
by Beta Ray Gauging. Water Poten-
tial was Measured on the Same Leaf
at 15 Min. Intervals. B. A Computer
Output of Average Water Potential
Change in V3 and V4

was no delay in the variation of the guard cell potential. No experimental data was found in the literature to compare with the computer output.

Skidmore and Stone (1964) reported a 5- to 7-minute lag between the stomatal opening and closing, and the maximum and minimum values of the transpiration rate. In the computer simulation output, the phase relation between the average of the palisade and mesophyll components and the combined resistance of the stomatal and the gaseous phase is compared. The lag between the maximum and minimum of these two variables was found to be about 3 minutes in the first and second cycles and about 8 minutes in the third cycle.

Transpiration and the water uptake rate were plotted calculating the moving average of 6 minutes and is presented in Fig. 6 and 7. The moving averages were used to simulate the interval of measurement in vivo. These figures illustrate similar phase differences and pattern of changes in vivo reported by Shirazi and Stone, (1973a,b).

After the onset of oscillations at the beginning of the day, a steady-state condition in all dynamic variables was achieved, both in the experimental data and the simulation output. However, late in the photoperiod, auto-oscillations were observed in all dynamic processes. Several workers have reported such cyclic patterns for the evening (Barrs and Klepper, 1968; Hopmans, 1971; Shirazi and Stone, 1973a,b; and Skidmore and Stone, 1964). Skidmore and Stone (1964) have attributed the evening oscillations to the increase in the root resistance, which they documented to be 5-fold higher. Barrs and Klepper (1968) related this phase of oscillation with the diurnal changes in root resistance. Several possible mechanisms to induce

or eliminate oscillations by changing growth conditions in **root and**
shoot environment were discussed by Cowan (1972). In **the experimental**
procedure of Shirazi and Stone (1973b), no external element **in growth**
environment was altered to induce oscillation in the evening. **Also,**
the evening oscillation continued to the end of the photoperiod.

The presence of a nonlinear relation between transpiration and
leaf conductance was postulated by Cowan, (1972). He assumed the
presence of a finite external boundary layer and further assumed leaf
conductance to be smaller than the external conductance. Thus, a
given change in leaf conductance would have more effect upon transpir-
ation than for the case when the leaf conductance is greater than the
external conductance. He pointed out that additional nonlinearities
might be operating in vivo.

The inception of evening cycles was regarded by Cowan (1972)
due to intrinsic noise in the plant or the plant environment. In the
present model, the final adjustment of the parameters to cause simula-
tion was made in the portion of the model which was least satisfying
conceptually (stomatal control). The previously suspected primary
cause, root resistance, did not appear to be responsible for the
evening oscillations. However, the implications of adjusting the
parameters would suggest diurnal variation in the ability of stomata
to control transpiration. It seems that stomatal behavior takes time
to build the ability to adapt to daylight and that a "fatigue" seems
to operate late in the day.

Of course, the abrupt application of the evaporative demand
simulated herein is unrealistic. However, the authors made time-
lapse movies of cotton plants growing in the field and noted a tendency

for early-day and late-day cycling. Additionally, the model was tested on the computer where the evaporative demand E; varied sinusoidally through the day, peaking at -200 volts at mid-day. This run produced output similar to Fig. 5.

It should be emphasized that the model in its present form is only a first approximation of what is a complex phenomena. The role of stomatal control in the transpiration process seems crucial and needs further examination. Biochemical, photochemical, and water stress relationships must be elucidated. Much refinement in the palisade and mesophyll components is needed. There are several assumptions which must be validated on a rational basis through future research. However, the systems approach seems to have definite merit in the study of plant physiological behavior.

CHAPTER VI

SIMULATION OF THE DYNAMICS OF AUTO-OSCILLATION

IN A COTTON PLANT UNDER CONSTANT

ENVIRONMENTAL CONDITIONS[1]

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INTRODUCTION

In recent years there has been wide acceptance of the analogy

between the flow of electricity through a conductor and that of water-

flow through the plant-atmosphere pathway. The movement of water

through the plant and into the air is assumed to be proportional to

the water potential gradient, which is the driving force, and is in-

versely proportional to the resistance in the pathway. The concept

first developed by van den Honert (1948) has been utilized by several

workers (Slatyer 1960; Rawlins 1963; and Philip 1966). However,

Slatyer (1960) and Rawlins (1963) objected to the liberal use of con-

stant resistances in different plant components. Skidmore and Stone

(1964) and Shirazi and Stone (1973a) showed experimentally that the

root resistance is temperature and water potential dependent. Also, it

changes as much as six-fold through the day. Rawlins (1963) developed

an expression for the resistance to flow through the gaseous phase

from liquid-water to water-vapor change that takes place in the meso-

phyll cavity. Additionally, the resistance in the leaf component

operates in a more complex fashion than postulated by earlier modelers.

Earlier workers made no allowance for capacitive effects and these

could be of great importance during transient conditons.

Auto-oscillation in the transpiration stream has been modeled by

first-order systems as well as second-order systems. Most models have

incorporated elements which are either not present in the plant system

(Meleshchenko and Karmanov, 1966) or are difficult to recognize as

operative mechanisms (Woo et al. 1965). Among the models of water-

based auto-oscillations, Karmanov (1966) emphasized the site of the

controlling mechanism as being in the leaf and neglected the possible

role played by roots. Cowan (1972) presented a third-order system

simulating free-running oscillations in dynamic properties such as

leaf conductance, water flux, and water content in a cotton plant in

a controlled environment. He assumed constant resistances in the mo-

del. Since his model was meant to duplicate (rather than model) the

free-running oscillations he built large positive feedback on stomatal

conductance into the action of the subsidiary cells. The model pre-

sented by Lang et al. (1969) shows plant components which are easily

identified. It is simple and realistic and has conceptual validity.

The present work incorporates the experimental results and the

conceptual features of the transpiration phenomena as reported by

Shirazi and Stone (1973 a, b, c) and Stone and Shirazi (1973). The

electric analog model used herein is that of Shirazi and Stone (1973c)

and was adapted after Lang et al. (1969). The model is implemented
in the simulation language Continuous System Modeling Program (CSMP1-
IBM/360).

Simulation Model

Development of the State Equations

In the model (Fig. 1) various plant componenets are visualized as
parts of an electric network consisting of resistance and capacitance.
Ei is the driving force simulating the constant evaporative demand.
A convention followed in the present analysis is that since the
evaporative demand is a negative water potential, the driving force
Ei is negative. This approach is consistent with the concept that
during transpiration all potentials in the plant are negative.

The basic method of formulating the state equations for the net-
work of Figure 1 is based on Kirchhoff's Current Law which states that
the sum of the currents directed into (or out of) a node is zero.
The voltage-current relationships for the resistance and capacitance
elements are then used to directly write the node currents in terms of
the node voltages. For example, summing the currents at the node
labeled Vl in Figure 1 gives $i_{C1} = i_{R1} + i_{R2}$ where i_{C1} is assumed
to be directed out of the node while i_{R1} and i_{R2} are directed into the
node. The element equation gives

$$C1\frac{dV1}{dt} = \frac{E-V1}{R1} + \frac{V2-V1}{R2+R3} \tag{1}$$

Noting that E = 0 and introducing the notation dVl/dt = VlDOT, Equation
(1) becomes
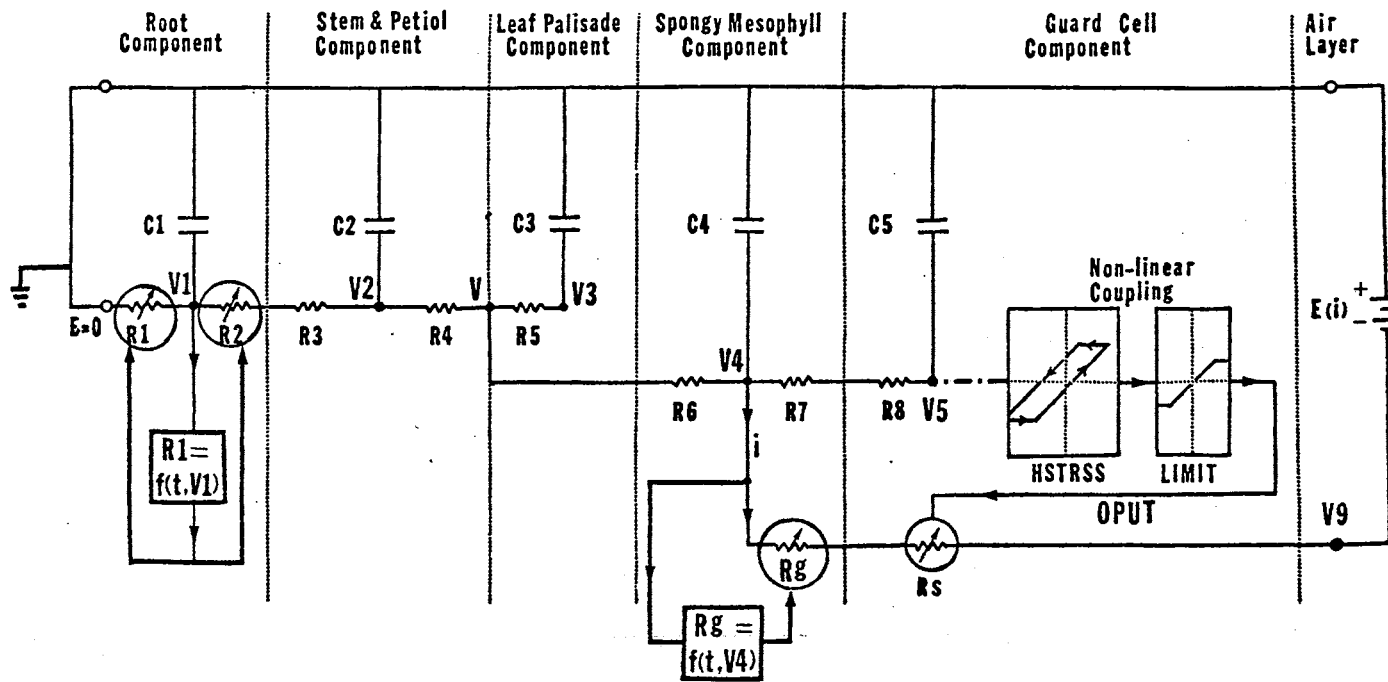
Figure 1. Electric Analog Model of the Transpiration Stream.
Roots Are at Zero Potential

$$V1DOT = -\left[\frac{V1-V2}{C1(R2+R3)} + \frac{V1}{C1R1}\right] \qquad (2)$$

The resistances R1 and R2 are time-varying quantities representing the total root resistance of the plant. This feature is consistent with the data reported and the concept advanced by several workers (Skidmore and Stone, 1964; Shirazi and Stone, 1973a; Rawlins, 1963; Barrs, 1971).

Shirazi and Stone (1973a) have given a quantitative estimate of the root resistance at different times of the photoperiod. They reported an increase of the root resistance up to six-fold from early morning to late evening. From that analysis a time-dependent equation for average slope of the line plotted on a semi-log scales of water uptake versus applied suction was obtained as follows

$$UPTAKE = \exp[2.303(\overline{A} + K(t) \, TAU]] \qquad (3)$$

where TAU in the applied suction in the roots, $\overline{A}$ is average uptake intercept and $K(t)$ is the time-variant slope of the water uptake and applied suction line respectively. The value of $K(t) = [1.57 - 1.58 \times 10^{-3} \, (time)]$ and TAU is modeled as $TAU = (-1.0 \, (V1))$. From the analogy to Ohm's law, then the time-varying root resistance can be expressed as

$$R(t) = \frac{V1 \times 137.3}{(UPTAKE)} \qquad (4)$$

Here the factor 137.3 is used to scale the root resistance to unity at the start of the photoperiod. The time varying resistance $R(t)$ given by Equation 4 is represented equally between the root resistances R1 and R2 in Equation 2. Since both R1 and R2 depend upon the water potential V1 in the root component, it is clear that a closed-loop

feedback mechanism exists in the model.

The state equation for the stem and petiole component (Fig. 1) at the node V2 is derived using a similar approach to that used to develop Equation 2. The result is

$$V2DOT = -\left[\frac{(V2-V)}{R4C2} - \frac{(V1-V2)}{R2(t)C2+R3C2}\right] \tag{5}$$

In the leaf, two components, leaf palisade and the spongy mesophyll , were identified by Lang et al. (1969). They are also the site of evaporation and liquid to vapor transformation. The uniqueness of the process and the nonlinear relation between the potential and vapor concentration for this component were developed by Rawlins (1963). These concepts were incorporated in the present model by Shirazi and Stone (1973c). The state equations for these components are

$$V3DOT = -\left[\frac{(V3-V)}{R5C3}\right] \tag{6}$$

for leaf palisade, and for the mesophyll component

$$V4DOT = -\left[\frac{(V4-V9)}{R9C4} - \frac{(V5-V4)}{(R7C4+R8C4)} - \frac{(V-V4)}{R6C4}\right] \tag{7}$$

where R9 = Rg + Rs shown in Fig. 1. The mathematical expressions describing these resistances are as

$$Rg = -B(V4) \tag{8}$$

and $$Rs = \frac{500\left[\exp\left[-N(OPUT+4.0)\right]-1.0\right]}{\left[\exp(D2N)-1.0\right]} \tag{9}$$

where N and D2 are constants.

In Fig. 1 the potential change in the guard cell component is calculated at the node V5. The potential rate of change is

$$V5DOT = - \left[\frac{(V5-V4)}{(R7C5+R8C5)}\right] \quad (10)$$

At the node between the palisade and stem/petiol components, the potential is

$$V = \frac{(V2/R4 + V3/R5 + V4/R6)}{(1/R4 + 1/R5 + 1/R6)} \quad (11)$$

The transpiration rate analog is expressed at the point where flow leaves the system. This flow occurs through Rs and Rg and can be expressed as

$$I = \frac{(V4-V9)}{R9} \quad (12)$$

The rate of water intake (uptake rate) is represented by the flow through the variable root resistance R1. Therefore

$$INTAKE = \frac{\left[-1.0(V1)\right]}{R1} \quad (13)$$

An analog computer mechanization of R1 equation (2) to (11) is presented in Fig. 2. Equations defining the time-constants and multipliers are summarized in Table I.

The network model contains five capacitors and is thus described by a fifth-order system of differential equations. The model is non-linear due to the nonlinear relations between R1 and R2 and the voltage V1 and between Rg and V4 and between Rs and V5.

Athough the concept of a fixed time constant is valid only for a linear time-invariant network, the network parameters were established from the desired time constant values as observed from data. Reasonably good results were obtained by considering the charging and discharging cycles separately and focusing on the dominant (largest) time
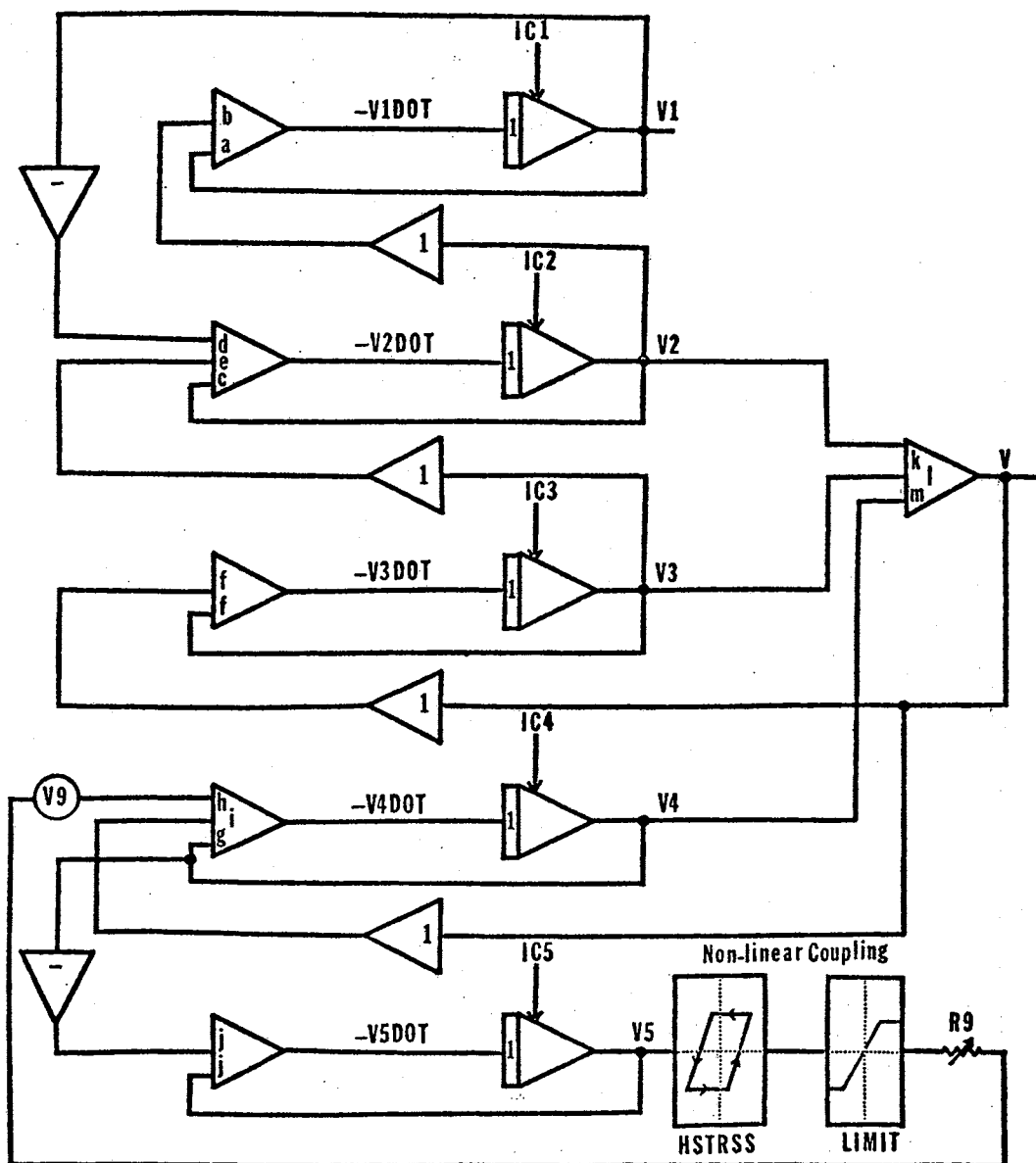
Figure 2. Analog Computer Mechanization of the
Transpiration Model

TABLE I

THE TIME-CONSTANTS AND THE CONSTANT MULTIPLIERS
FOR THE ANALOG COMPUTER DIAGRAM OF FIGURE 2.
(NOTE THAT SOME RESISTANCES ARE NOT
CONSTANT. SEE TEXT.)

$$a = \left[\frac{1}{R2C1 + R3C1} + \frac{1}{R1C1} \right]$$

$$b = \left[\frac{1}{R2C1 + R3C1} \right]$$

$$c = \left[\frac{1}{R4C2} + \frac{1}{R2C2 + R3C2} \right]$$

$$d = \left[\frac{1}{R2C2 + R3C2} \right]$$

$$e = \left[\frac{1}{R4C2} \right]$$

$$f = \left[\frac{1}{R5C3} \right]$$

$$g = \left[\frac{1}{R9C4} + \frac{1}{R7C4 + R8C4} + \frac{1}{R6C4} \right]$$

$$h = \left[\frac{1}{R9C4} \right]$$

$$i = \left[\frac{1}{R6C4} \right]$$

$$j = \left[\frac{1}{R7C5 + R8C5} \right]$$

$$k = \left[\frac{1/R4}{1/R4 + 1/R5 + 1/R6} \right]$$

$$l = \left[\frac{1/R5}{1/R4 + 1/R5 + 1/R6} \right]$$

$$m = \left[\frac{1/R6}{1/R4 + 1/R5 + 1/R6} \right]$$

constant in each case. Assuming the dominant time constant during the discharge cycle (uptake of water) is about 2 minutes in length and the dominant time constant during the charging cycle is 3 minutes and further recognizing that about six time constants are needed for nearly complete transient excursions, the total period of the oscillations was established as 6 X (2 + 3) = 30 minutes as desired.

Simulation of the Stomatal Resistance Regulation Mechanism

Skidmore and Stone (1964) reported a 5 to 7 min. delay in the stomatal action and water potential change in a cotton leaf. They emphasized that future models should include time delay and switching mechanisms in the feedback path. Phase differences in water uptake, transpiration, and leaf density changes were reported by Shirazi and Stone (1973b). Based upon these results a time delay mechanism hysteresis was incorporated in the guard cell component. In order to simulate the limits on the stomatal resistance a limit function operating on the output of the hysteresis block was introduced. These CSMP blocks constitute the nonlinear coupling. Since both functions are nonlinear and multi-valued in the time domain, a functional form of the relations cannot be easily stated. However, their switching mechanisms within the system are utilized to control various parameters and establish their interaction.

The expression of the stomatal resistance was obtained by operating the nonlinearity upon the output of the guard cell potential (V5). The voltage V5 was obtained by integrating the state equation (10) with the initial condition on V5 taken to be the assigned equilibrium potential of the guard cell at the start of the photoperiod. The

utility of a hysteresis loop was documented by Shirazi and Stone

(1973c). A function V5H is generated through a function generator

block HSTRSS of the CSMP as follows:

$$V5H = V5-W2 \ (V5-V5_{n-1}) \geq 0, \ V5H \leq V5-W2_{n-1} \tag{14}$$

$$V5H = V5-W1 \ (V5-V5_{n-1}) \leq 0, \ V5H \geq V5-W1_{n-1} \tag{15}$$

The parameters W1 and W2 establish the width of the hysteresis loop.

As can be seen from the relations above. The hysteresis function is

a history element and its output depends upon both the present input

and the past value of the output. At $t = 0$, V5H is set equal to

V5(0). For all other conditions not designated above, V5H is equal to

the last output.

The variable V5H is further controlled by a limiter as shown in

Figure 1. OPUT is the name of the function output, and K2 and -4.0

are the lower and the upper bound parameters respectively. This limiter

produces an output equal to V5H except when V5H is equal to or greater

than K2, the output is set equal to K2. Also, if V5H is equal to or

greater than -4.0, the V5H output is set equal to -4.0.

Other than the present nonlinear coupling, the authors did not

want to add any components in the model which would lack in vivo jus-

tification. The necessary degree of freedom to make the model simulate

the plant behavior was achieved by adjusting the parameters on the

coupling mechanisms. In generating the lower and upper bounds of the

LIMIT, the upper potential was maintained at -4.0 volts corresponding

to the state when stomata are open, Shirazi and Stone (1973b). The

lower limit K2, corresponding to the state when stomata are closed

was gradually changed from -4.0 to -4.25 according to the following

time-variant mathematical expressions:

$$Y1 = -4.0[exp(Z \times time)] \qquad (16)$$

$$K1 = \frac{-0.25[exp[-M(Y1 + 4.0)]-1.0]}{[exp\ (DM)\ -1.0]} \qquad (17)$$

$$K2 = -4.0 + K1 \qquad (18)$$

where D, Z and M are constants. The constant M relates stomatal

resistance to the degree of stomatal closing. It is discussed by

Shirazi and Stone (1973c).

Finally, based upon the value of the output of the limiter on

V5H, the potential dependent stomatal resistance Rs is calculated as

$$Rs = \frac{500[exp[-N(OPUT+4.0)]-1.0]}{[exp\ (D2N)\ -1.0]} \qquad (19)$$

where D2 and N are constant (see Appendix 2). It is seen that when

OPUT is equal to -4.0 volts the Rs is equal to zero and stomata are

open and when OPUT is equal to -4.25 Rs is equal to 500 units and the

stomata are closed.

Results and Discussion

The graphical results of the simulation can be obtained by the

CSMP instruction PRTPLT for several variables. Numerical values of

associated variables can be printed on the side of the graph. One

such output (V4) is presented in Fig. 3. The behavior of oscillations

was found to agree with the experimental results of Shirazi and Stone

(1973b,c). The pattern of simulation results, the periodic relations,

and the relative magnitude of the changes in the potential of different
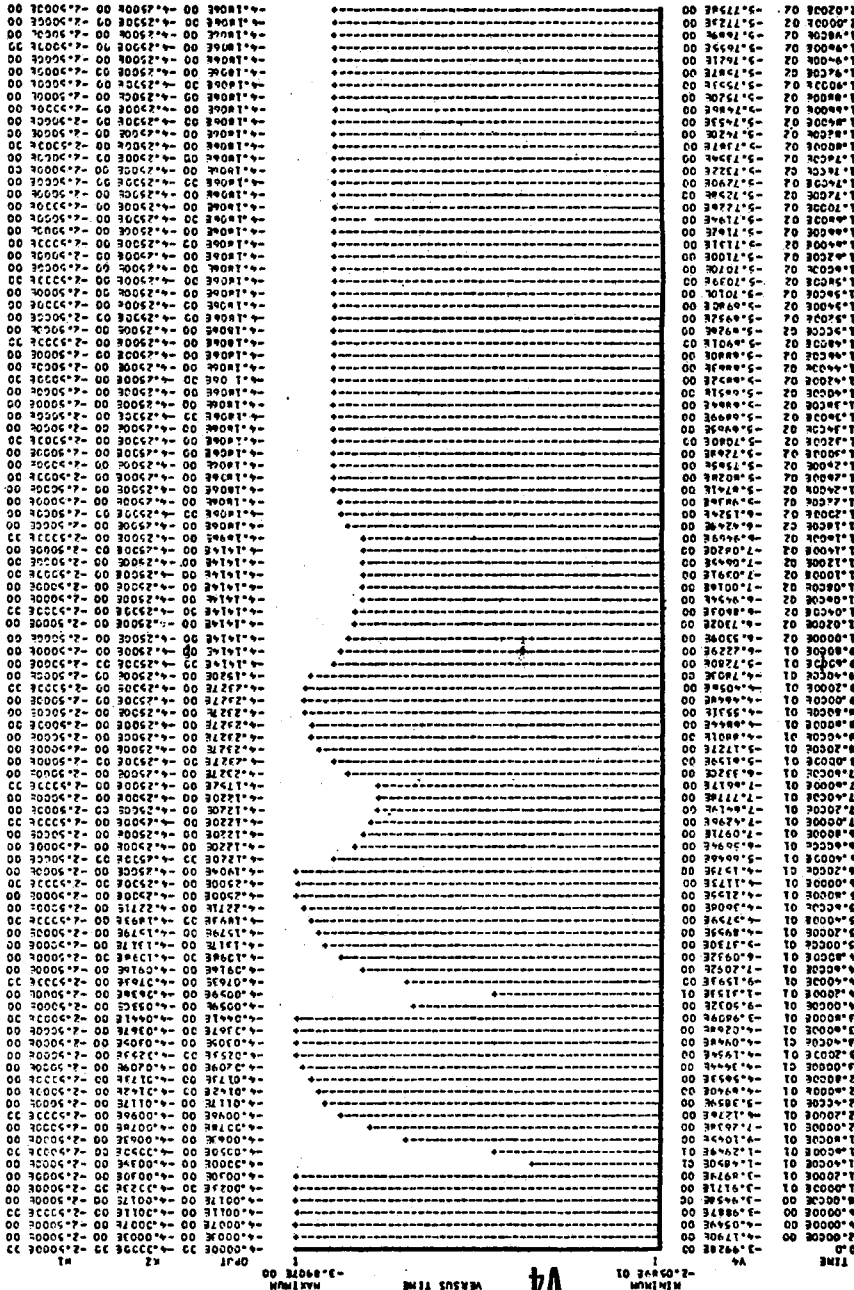
Time (min)

Figure 3. Typical CSMP Print-Plot of V4 State
Variable as a Function of Time

plant components are within acceptable limits of the data reported by Shirazi and Stone (1973a,c).

During the early stage of model development, sustained and symmetrical oscillations were obtained by the use of the hysteresis function alone. These oscillations were similar to that simulated by Cowan (1972). However, the data and the time-lapse movies of the leaf response obtained by Shirazi and Stone (1973b) showed damped oscillations in the morning phase and sustained oscillations during the evening phase. Therefore in the present model, the constraints discussed above on the V5H were adjusted as described to simulate the morning and the evening oscillations.

A hypothetical combination of parameters interacting on the nonlinearity was presented by Shirazi and Stone (1973c). It was observed during the parameter adjustment phase that for given values of W1 and W2, and while changing the limits K1 and K2 on V5H, the system response adjusted itself to over-damped or under-damped oscillations. The physical significance of these parameters and their effect on the output of potential in different plant components is documented by Shirazi and Stone (1973c).

In the model, readjustment of the parameters was made to simulate the conditions necessary for the evening oscillations (see the program listing in Appendix 2). A function TLAPS (for the elapsed time) was defined late in the photoperiod as

$$TLAPS = (TIME - 650) \tag{20}$$

Evening oscillations have been reported by several workers including Skidmore and Stone (1964), Hopmans (1971), and Shirazi and Stone

(1973a,b). Skidmore and Stone (1964) and Shiraz and Stone (1973a) reported 5 to 6 fold increase in the root resistance during the photo-period. Computer output showed that the system becomes unstable with higher root resistance. However, the magnitude of the instability was too small to initiate oscillations in the water-based dynamic processes. To simulate the evening cycling, two parameters, the limits K1 and K2 on V5H and the arguments of the hysteresis loop were readjusted. The value of K2 was reduced by about 80 per cent of the steady-state con-dition. Thus, equations 16, 17, and 18 for the morning phase were modified as follows:

$$Y2 = \frac{-4.0-0.25[\exp(C \times TLAPS)-\exp(C \times Z2)]}{[1 - \exp(C \times Z2)]} \tag{21}$$

$$K1 = \frac{-0.15[\exp[-M(Y2 + 4.0)]-1.0]}{[\exp(Dm) -1.0]} \tag{22}$$

$$K2 = -4.0 + K2 \tag{23}$$

Thus, in the morning K2, gradually rises to a value of -4.25 and remains constant until time = 650 min. At this time the control was transferred to Y2 which causes K2 to decrease by 80 per cent. The behavior of K2 was potulated to be analogous to "fatigue" effect in the plant. Similarly, it was necessary to relocate and redefine the hysteresis width by changing the parameters W1 and W2 as a function of time. This was achieved by the following mathematical functions

$$W1 = -2.5[\exp[1.59 \times 10^{-2}(TLAPS)]] \tag{24}$$

$$W2 = -1.0[\exp[2.73 \times 10^{-2}(TLAPS)]] \tag{25}$$

FORTRAN branching and conditional transfers were made in the NOSORT section of the CSMP program to obtain final values of the

parameters and run control (see Appendix 2). For rapidly rising and falling functions such as the state variables in the model, a variable-step size method of integration was found to consume considerable central processing time of the computer. Therefore, the trapezoidal method was used to integrate the state equations. It was found that the integration interval must be smaller than the smallest time-constant in the analog RC model. The rationale behind this limitation is outlined in Appendix 1.

The authors are aware of the criticism that model builders are prone to construct models which merely duplicate experimental results. Modeling and simulation techniques have some inherent credibility pro-blems. However, the merit of the systems approach, such as presented in this paper, lies in the appreciation of these limitations. Systems analysis represents a philosophy of computing which emphasizes an in-depth study and interpretation of the processes involved in the real system. Thus the modeling effort produces a clearer understanding of the real system.

Summary

An electric analog model of the transpiration process in a cotton plant growing in solution culture in a constant environment chamber is presented. It represents a first approximation of a complex process in water flow mechanics. The transpiration stream is modeled by an RC circuit containing resistances simulating vascular resistances in root, stem and leaf. The corresponding fluid capacitances are modeled and a nonlinear coupling consisting of a hysteresis loop and a limit function is introduced between the guard cell potential and the time-variant, potential dependent stomatal resistance.

The model accounts for the cyclic variations previously observed during the transient periods and the midday steady-rate, characterized by damped oscillations. The "lumped parameter" approach modeling the transpiration process is employed. The model is adapted from Lang et al. (1969) and was chosen for its conceptual validity. Lang et al. (1969) reported that the model could not oscillate without incorporating three additional RC circuits in the leaf component. Thus, in their model the nature of coupling was left open for future modelers. Shirazi and Stone (1973c) observed a hysteresis phenomenon in the phase plot diagram describing stomatal action and introduced the function as a nonlinear coupling to simulate the observed results.

The model was written in the simulation language Continuous System Modeling Program (CSMP 1-0 S/360) and the trapezoidal method of integration was employed. This method is adapted to rapidly changing variables and the integration interval was found to be limited by

the value of the smallest time-constant in the circuit.

In the absence of required data explaining the mechanism of the guard cell and stomatal action, a certain amount of artificiality in the model is inevitable. However components wholly without conceptual basis are not proposed in the model.

APPENDIX 1

The Limitation of DELT Upon the Method

of Integration

The Continuous System Modeling Program (CSMP) language offers several options of methods of integration to its users. The methods are braodly classified as either as fixed-step size or variable-step size routines. In view of the fact that a large number of integration steps were required for the entire photoperiod some sophistication was sacrificed to make the overall run economical.

The simulation runs were tried using variable-step and the fixed-step methods. The Trapezoidal method was finally adopted. The method does not use a corrector equation but uses the estimation equation only, along with the predictor equation.

The predictor; $Y^p_{t+\Delta t} = Y_t + X_t \Delta t$, where $X_t = \left.\frac{dy}{dt}\right|_t$

and the estimate; $Y_{t+\Delta t} = Y_t + (X_t + X_{t+\Delta t}) \frac{\Delta t}{2}$

The estimate uses the average of the derivatives calculated for time t and $(t + \Delta t)$, where $(t + \Delta t)$ is based upon predictor value $Y^p_{t+\Delta t}$. This computation therefore involves two calls to update at each DELT.

In the nodal analysis of the RC circuit model, it was found critical to choose a proper DELT for the integration routine. The

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importance of the DELT can be shown by a simple RC block as in Fig. 4.

Let the node be at V1 and let V2 = -E. As before, the flow of current

coming into the node is positive and the flow going out of the node

is negative. Thus since V2 = -E, and for small changes in voltage at

each iteration we have

$$\frac{\Delta V_1}{\Delta t} \cong - \frac{1}{RC}(V_1 + E) \text{ or}$$

$$\Delta V_1 = \frac{-\Delta t}{RC}(V_1 + E)$$

The boundary conditions are such that V1 = 0. Therefore, the

first iteration gives

$$^1Y_{t+\Delta t} = 0 + \frac{-\Delta t}{RC}(0 + E)$$

and the second iteration gives

$$^2Y_{t+\Delta t} = \frac{-\Delta t}{RC} E + \frac{-\Delta t}{RC}(\frac{-\Delta t}{RC} E + E) \text{ or}$$

$$\frac{^2Y_{t+\Delta t}}{E} = \frac{\Delta t}{RC}(\frac{\Delta t}{RC} - 2)$$

at any given time the value of $\frac{\Delta t}{RC}$ cannot be zero, therefore only

$$(\frac{\Delta t}{RC} - 2) = 0 \quad \text{or}$$

$$\Delta t = 2 RC$$

Hence the DELT for integration would be < 2RC so that output will carry

proper sign. Furthermore a much smaller DELT, say 0.1RC, would be

necessary to insure accurate integration. Unlike SIMP and MILNE

methods the TRAPZ method of integration does not use a corrector term.

Therefore it is advisable to use somewhat smaller DELT than what
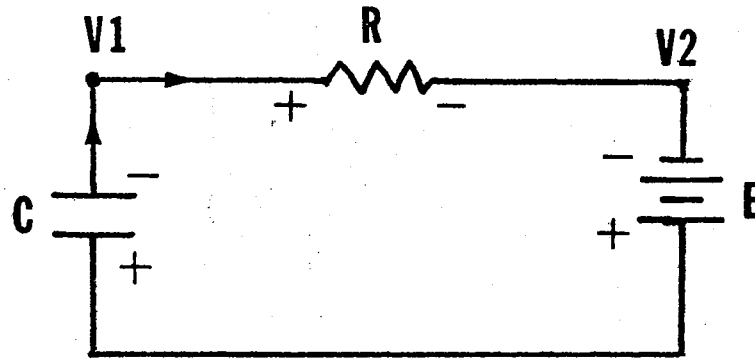
Figure 4.   RC Circuit

seems to be the limiting value. This analysis is true for the RECT

method of integration as well.

****CONTINUOUS SYSTEM MODELING PROGRAM****

*** VERSION 1.3 ***

```
     INITIAL
 TITLE   SIMULATION OF TRANSPIRATION STREAM IN A COTTON PLANT
     CONSTANT R3=2.5,R4=2.5,R5=2.5,R6=2.5,R7=2.5,...
 E=200., C1=1.66E-01, C2=8.66E-03, C3=0.350, C4=0.3500,...
R8=3000.0,B=-3.0,A=0.9605,N=3.0, C5=3.50E-03,Z2= 55.0,C=0.1
  INCON    IC1=-0.4964,IC2=-1.9928,IC3=-2.9928,IC4=-3.9928,...
     IC5=  -7.5
     PARAMETER    W1=-2.5,W2=-1.0,Z=1.0625E-03,SW=1., M=20.0
     V9=-E
     DYNAMIC
     R2=  R1T
     R1T=    -(V1/UPTAKE)*137.3
     INTAKE=   -(1.0/R1T)*V1
     KSUBT=     (1.57394-0.00158*(TIME))
     TAU=    -1.0*V1
     UPTAKE=    EXP(2.3026*(A+KSUBT*TAU))
     RSUBG=   B*V4
     R9=  RSUBG+RSUBS
     I=   (V4-V9)/R9
V=  (V2/R4+V3/R5+V4/R6)/(1.0/R4+1.0/R5+1.0/R6)
V1DOT= -((V1-V2)/(R2*C1+R3*C1)+V1/(R1T*C1))
V2DOT=  -((V2-V)/(C2*R4)-(V1-V2)/(C2*R2+C2*R3))
V3DOT= -((V3-V)/(C3*R5))
V4DOT=  -((V4-V9)/(C4*R9)-(V5-V4)/(C4*R7+C4*R8)-...
(V-V4)/(C4*R6))
     V5DOT=   -((V5-V4)/(C5*R7+C5*R8))
     V1=   INTGRL(IC1,V1DOT)
     V2=   INTGRL( IC2,V2DOT)
     V3=    INTGRL(  IC3, V3DOT)
     V4=   INTGRL( IC4,V4DOT)
     V5=   INTGRL(IC5,V5DOT)
     V5H=    HSTRSS(-7.5   ,W1,W2,V5)
     VD=   (V3+V4)/2.0
NOSORT
TLAPS= (TIME-650.0)
IF (TIME.GE.650.0) GO TO 20
IF  (SW.EQ.0.0)  GO TO 20
Y1=  -4.0*(EXP(Z*(TIME)))
IF( Y1.LE.-4.25) Y1= -4.25
   D=0.25
   K1=   -0.25*((EXP(-M*(Y1+4.0)))-1.0)/(EXP(D*M)-1.0)
   K2= -4.0+K1
OPUT=  LIMIT(K2,-4.0,V5H)
D2=  -(K2+4.0)
RSUBS= 500.00/((EXP(D2*N))-1.0)*((EXP(-N*(OPUT+4.0)))-1.0)
GO TO 3
```

```
20   Y2= -4.0-0.25*((EXP(C*TLAPS)-EXP(C*Z2))/(1.0-EXP(C*Z2)))
          IF (Y2.GE.-4.10) Y2=-4.10
      SW=0.0
      W1=   -2.5*(EXP(1.5917E-02*TLAPS))
          IF (W1.LE.-6.0) W1=-6.0
      W2=   -1.0*(EXP(2.7347E-02*TLAPS))
          IF (W2.LE.-4.0) W2= -4.0
          M=0.1
          D=0.15
          K1=    -0.15*((EXP(-M*(Y2+4.0)))-1.0)/(EXP(D*M)-1.0)
          K2= -4.0+K1
      OPUT=  LIMIT(K2,-4.0,V5H)
          D2=   -(K2+4.0)
      RSUBS=  500.0/((EXP(D2*N))-1.0)*((EXP(-N*(OPUT+4.0)))-1.0)

3    CONTINUE
     TERMINAL
         METHOD  TRAPZ
         TIMER   FINTIM=720.0,DELT=1.5E-02,OUTDEL=2.00
     PRTPLT  V1(R1T),V2,V3,V4(OPUT,K2,W1),V5(V5H,Y2,W2),VD,I,INTAKE,...
         R9(RSUBS,RSUBG)
     END
     STOP
```

```
OUTPUT VARIABLE SEQUENCE
V9      TAL     KSUBT   UPTAKE  R1T     R2      V1DOT   V1      V       V2DOT
V2      V3DOT   V3      RSUBG   R9      V4DOT   V4      V5DOT   V5      INTAKE
I       V5H     VD      TLAPS   ZZ0006  Y1      Y1      D       K1      K2
OPUT    D2      RSUBS   Y2      Y2      SW      W1      W1      W2      W2
M       D       K1      K2      OPUT    D2      RSUBS
```

```
PARAMETERS NOT INPUT OR OUTPUTS NOT AVAILABLE TO SORT SECTION***SET TO ZERO***
RSUBS
```

```
  OUTPUTS     INPUTS    PARAMS   INTEGS + MEM BLKS   FORTRAN  DATA CDS
  51(500)     118(1400)  31(400)    5+   0=  5(300)   51(600)     12
```

```
        ENDJOB
```

SUMMARY AND CONCLUSIONS

Cyclic variations in different dynamic processes have been re-
ported in plants growing under water-stess conditions. Such changes
when observed under constant environmental conditions offer a unique
opportunity to understand the cause-effect relations in plant
processes.

Measurements of transpiration rate, rate of water uptake, changes
in leaf density, leaf temperature, leaf water potential, and the sap-
velocity in the stem were made to elucidate the mechanics of water
flow in a plant. The plant was grown in nutrient solution and under
constant environmental conditions.

It was felt that systems approach as a tool to gain insight in
the dynamics of flow could be utilized through an electric analog
model of the transpiration stream. A model was formulated after Lang
et al. (1969). It was modified in terms of incorporating time-
variant and potential dependent resistances in root, gaseous phae, and
the stomatal regulation mechanism. The plant was composed of five
components, namely root, stem, leaf palisade, spongy mesophyll, and
the guard cell in the path of water flow. In each component at least
one element of resistance to flow and one element of storage was
visualized. A lumped parameters approached was adopted in the formu-
lation of the model.

In order to define various resistances, their nature and magni-
tude, the capacitance, the delay functions, and the switching mech-
anisms several studies were undertaken.

In the root component, root resistance measurements were made on

a decapitated root-system of cotton, tomato, and bean plants. The water extraction rate as a function of applied suction along the path of increasing and decreasing suction was measured at different times of the day and in different root media temperature. It was noticed that the root resistance increased and deceased exponentially as a function of applied suction in all the plant species. The water extraction rate was always higher when suction was changed from higher value to a lower value. A hysteresis effect was observed in this determination. The root resistance was found to be time-variant and increased about six-fold during the photoperiod. Also, the water extraction rate increased with increasing temperature.

In the stem component the apparent sap-velocity (ASV) was determined by measuring the apparent heat pulse velocity (AHPV) by a thermoelectric technique. Two thermistors in a bridge circuit, one as a heat pulse sensor and the other as compensator of the ambient temperature variation in the evaporative demand were used. It was found that the apparent sap velocity and the apparent heat pulse velocity oscillated in phase. The apparent heat pulse velocity was in phase at two different locations on the stem and was found to be correlated with the transpiration rate.

In the leaf component, simultaneous measurements of leaf density and leaf temperature and water potential were made. Visual observations of leaf conditions were recorded through a time-lapse movie. The results showed that all these plant processes oscillated at the same time. Two sets of cycling were observed; one at the beginning of the photoperiod and the other late in the photoperiod. The early-day cycling damped out while the late-day cycling persisted until the

end of the photoperiod. Water uptake rate lagged behind the transpiration rate by about 5 minutes during the first cycle. The lag decreased in subsequent cycles until the water uptake rate was higher than the transpiration rate. This stage was characteristic of the steady state condition.

A conceptual model of the transpiration stream was formulated. A nonlinear coupling between the guard cell potential and the stomatal resistance, composed of a hysteresis function and a limit function was established. The parameters defining the operation of these non-linrearities were evaluated by adjustment to make the model simulate the experimental results. Mathematical equations of the state variables in each plant component were solved in a simulation language CSMP1 on IBM- 360/65 computer. The model was successful in simulating the characteristics of the auto-oscillations observed in the dynamics processes of transpiration, water uptake, potential changes in the leaf. The overall response of this R-C model was governed by the parameters defining the width of the hysteresis loop and the limits assigned to the limit function. The delay mechanisms formulated in the development of stomatal resistance were arrived at by using conditional branching in the simulation program. It was found that the parameters operating on the nonlinearities were highly sensitive in creating over-damping or sustained oscillation in the system.

Several authors Skidmore and Stone (1964) and Barrs and Klepper (1968) have postulated that the late day oscillations might be due to increase in the root resistance. In the present model an increase in root resistance created unstability late in the photoperiod. But the effect was not severe enough to trigger oscillations. However,

when the parameters on the hysteresis function and the limit function were adjusted the model initiated sustained oscillations. The parameters causing auto-oscillations were conceptually related to the permeability and the resilience of the guard cell wall.

In the conclusion it can be said that the present model is only a first approximation of what seems to be a complex process. Future testing and refinement of the model demand more detailed and accurate information about the behavior of real plants. Such data is scanty at present. Realistic data for the resistances in each plant components and specially in the leaf is needed. The stomatal mechanism as affected by the water stress is the main area where much of the future research efforts should be directed. The direction indicated by the analysis of the nonlinear coupling seems to be a fruitful area for further research.

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