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THE ENERGY BUDGET AT THE EARTH'S SURFACE: WATER RELATIONS AND STOMATAL RESPONSE IN A CORN FIELD

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UNITED STATES ARMY ELECTRONICS COMMAND
Atmospheric Sciences Laboratory
Fort Huachuca, Arizona
Microclimate Investigations, U. S. Department of Agriculture
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NOTICES

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ABSTRACT

The study described is an attempt to separate the effects of light intensity and water stress on stomatal behavior under field conditions. A simple model has been developed as a means of systematically approaching the problem. The model is based on measurements of leaf resistance and relative water content through the day for a range of different stress conditions. The results of the model indicate that after-effects of stress must be considered and that a more complete model must include the effects of internal CO_2 concentration.

Testing of the changes in stomatal resistance in response to changes in leaf water relations shows how the effects of water stress can be included as a sub-model in the larger plant community model. The agreement between the energy balance measurements and the model calculations using the measured resistances strengthens the confidence in the approach. Comparison of the total flux values for the crop appears to be a good test of the model and illustrates how small differences in profiles can influence the overall exchange processes.

The modeling approach has been discussed as an example of how the plant parameters and meteorological parameters can be combined in a systematic way to evaluate the plant response to a change of a large number of factors. The model can be manipulated to arrive at "answers," but this is a dangerous procedure. The value of the exercise lies in the fact that it forces us to systematize our approach and helps to identify areas where more precise information is needed.

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INTRODUCTION

A look at recent literature indicates that much has been done toward bettering our understanding of plant-soil-water relationships [1-3]. The impression is often given that no further work is needed. On the contrary, these volumes and the bibliography contained therein show that even with this impressive surge in fundamental work there still remain a number of questions unanswered.

One motivation behind this interest centers around the concern for conservation and sensible utilization of water supplies. The study undertaken here has these goals in mind although it is necessary to concentrate on more specific aspects of the problem.

Kozlowski [2] summarized some aspects of plant-soil-water relationships where more fundamental knowledge is needed. He considers the characterization and measurement of the water status in plants, the transport of water in plants, the nature of the effect of water deficits on plant growth, and the possible control of the internal water balance in plants. All of these areas are fruitful fields of research, but for sufficient depth and detail leading to fundamental laws, a sharper focus is necessary. Hopefully the findings can be integrated into solutions of the overall problem. A comprehensive review of the subject is not attempted, and the volumes cited earlier are recommended.

The approach taken in this project is on the level of the plant in the natural community. Natural community implies a "field laboratory" and emphasizes the complexity of the environment and the difficulty in maintaining control over variable conditions. Some interactions are observed that might not occur with simulated natural environments. With the possibility of manipulating the agronomic crop community, the study of natural plant-environment interaction takes on added significance.

The advent of computers has made possible the development of mathematical models to predict relationships between soil, plant, and atmosphere [4,5]. A model can be used to vary factors and relationships and can lead to quantifying physical relationships much faster than long field or laboratory experiments. However, there is a danger of relying too completely on the model, because it is impossible to build a model including all the possible factors in the system. Models are extremely useful tools, along with the computer, in systematizing the approach and identifying the most or least important factors for consideration. There is still a need for experimental measurements to verify the relationships assumed in the model. Ideally the combination of modeling and experimental measurements might be the best approach.

The research problem to be discussed in this dissertation stems from earlier developments from both the modeling and the experimental approach, namely the interaction of water deficits, stomatal diffusion resistance and subsequent plant processes. The models cited earlier have been concerned with the movement of water through the plant, soil, atmosphere system, and are involved in predicting evapotranspiration and photosynthesis. The influence of stomatal closure has been included (Waggoner, [5]) but as yet very little has been done to include the effect of water deficits into these models.

Indeed this would seem a next logical step in the approach to the problem of the effect of water deficits. The premise, as a first approximation, will be to relate the effect of water deficits on plant processes via the influence of water deficits on stomata as suggested by Slatyer [6]. In summarizing the effects of water deficits he stated:

> "...it can be stated that there is increasing evidence that stomatal closure, directly by impeding CO_2 supply and indirectly by increasing leaf temperature may be the primary mechanism by which water stress leads to reduced net photosynthesis under natural conditions."

Indeed this may be a gross over simplification and there may be innumerable approaches. Taking the above approach does not mean that direct effects of water deficits are not recognized. The suggestion made by Idso [7] as to a different type of water deficit effect being operative in photosynthesis and in transpiration bears consideration.

In keeping with the above comments, the work reported here considers the modeling approach and experimental approach. This project was part of a larger project in which a team of researchers were involved, each concentrating on various aspects of the measurement of natural exchanges of CO_2, heat, and water vapor between a corn crop and the atmosphere, as well as measuring various physiological parameters of the plant community.

CHAPTER I

INTERACTION OF LIGHT INTENSITY AND WATER DEFICITS ON STOMATAL ACTIVITY UNDER FIELD CONDITIONS

Review of Literature

This research project stemmed from previous work at this location reported by Shinn and Lemon [8]. Studies of the variation of leaf water potential at different heights in a corn crop were made during a period of increasing drought stress. Soil moisture tension and evapotranspiration were also measured. A relatively small gradient in water potential between the lower and upper leaves in the canopy was measured; however, the gradient was significant and agrees with the concept of flow in the direction of the potential gradient. A bimodal trend in water potential of the upper leaves was found while the lower leaves exhibited a more constant water potential through the day. Evapotranspiration, as calculated by an energy balance technique, did not show the same bimodal characteristics. There was no evidence that evapotranspiration decreased even though plants had visible signs of wilting. As soil moisture tension increased (became more negative) over a drying cycle of several days, the gradient of water potential (expressed as maximum gradient measured in late afternoon) also increased. The same bimodal trend could be expected in stomatal closure. Since evapotranspiration for the crop was not bimodal, it was concluded that 1) stomatal closure was ineffective in reducing transpiration, or 2) the transpiration decrease from upper leaves due to stomatal closure was compensated by the evapotranspiration from the lower leaves where water potentials apparently did not reach values to induce stomatal closure. Stomatal aperture was not measured in this study.

In addition, plant growth parameters over a persistent drought period showed that growth decreased, but even with decreased (more negative) leaf water potentials and larger potential gradients, transpiration relative to the amount of energy available was not decreased. The corn plants were responding to the water deficit by increasing the potential driving force for transporting large amounts of water to maintain transpiration.

Begg et al. [9] suggest how transpiration for the crop can be maintained even with stomatal closures. Vertical distribution of components influencing transpiration was evaluated by energy balance methods along with physiological response of the plant to diurnal changes in the environment in a crop of bullrush millet (Pennisetun typhoides S. et H). They found that transpiration from the upper leaves decreased at mid-day corresponding to stomatal closure, but that transpiration from lower leaves actually increased due to an increase in sensible heat transferred to the lower leaves by advection. Although the evaporation rate for the bullrush millet study was considerably higher than for the corn field study of Shinn and Lemon [8], they might be classified as being similar studies at different degrees of stress.

Two important considerations arise from the comparisons of these studies. First is the effectiveness of the stomata in controlling transpiration, as they respond to a decrease in water potential. Second is the response of growth processes, i.e., the photosynthetic mechanism, to decreases in water potential. The fact that transpiration continued to increase (Shinn and Lemon [8]) even though water potential decreased suggests that stomata may be insensitive to decreases in water potential until some critical water potential is reached. It might be concluded that in the work reported by Begg et al. [9] the water deficits were greater and the critical water potential was reached causing stomatal closure in the upper leaves and a corresponding reduction in transpiration. There is the added possibility that stomata still close gradually as water potential decreases, but that transpiration is insensitive to stomatal aperture until very small apertures are reached. The work by Bange [10] is frequently referred to (Slatyer and Gardner [11], Meidner [12]) as showing that unless the air is very still, which would not likely be the case in the work under discussion, transpiration is influenced over the complete range of stomatal apertures.

As reviewed by Miedner [12], the question of stomatal control of transpirational water loss has been studied for a number of years and particularly since the classical work of Brown and Escombe [13]. This early work led to some important misconceptions concerning the range of effectiveness of stomatal aperture in controlling transpiration because of the failure to recognize the resistance to diffusion of the layer of air surrounding the leaf. Until the effects of moving or still air were recognized, the opinion as to stomatal control ranged from "complete control" to "complete absence of control." This difference of opinion led to numerous theories concerning control by some other mechansim, the most prevalent being the incipient drying of the cell walls which would affect the delivery of water to the evaporating surfaces in the substomatal cavity. Although there is evidence of some incipient drying under certain conditions it has been generally concluded (Meidner [12], Slatyer [14]) that non-stomatal control of transpiration is unlikely under normal ranges of wilting and that only under extremely severe desiccation is direct control by non-stomatal mechanisms likely.

Based on the above considerations of stomatal control of transpiration over a wide range of apertures, the findings of Shinn and Lemon [8] suggest that stomatal closure does not follow the bimodal trend of leaf water potential. This suggestion is also based on the assumption that the upper leaves are the most actively contributing to the total evapotranspiration from the crop and that the lower leaves do not provide compensating transpiration because of lower radiation loads and the absence of additional sensible heat by advection. The lack of stomatal aperture measurements in this study leaves some questions unanswered and suggests a need to study the behavior of stomata under field conditions in response to diurnal changes in leaf water potential.

Before reviewing the response of stomata to environmental factors, consideration of the response of growth processes and the photosynthetic mechanism to decreases in water potential is in order. In the Shinn and Lemon work plant growth, as measured by stem length, stopped increasing with the onset of drought. The interruption of growth processes, but not transpiration, implies that the growth processes were being influenced by some mechanism other than restriction of the amount of CO_2 diffusion into the leaf.

Some controversy exists over the direct and indirect effects of decreased water potential on the photosynthetic mechanism. Crafts [15] has shown that water stress influences plant processes in many diverse ways. Explanations by one or two simple mechanisms become difficult. There is a danger in use of the term "water stress" because of the implication as an individual phenomenon. A specific definition of this term is the condition that the plant enters as the water potential falls below the zero mark and becomes increasingly negative. Plant processes react to the degree of this decline with the end result being an integration of all these effects on growth. When discussing the effects of water stress the distinction between effects on growth or the effects on some specific plant process must be kept in mind. The photosynthetic mechanism is of major concern because of its importance in the growth processes.

Since water vapor loss and CO_2 diffusion into the leaf occur mainly through the stomata, measuring photosynthesis and transpiration simultaneously is often done in evaluating the effects of water stress. This may be done on several different scales; short-term laboratory experiments or long-term field measurements. An example is the work by Brix [16] who studied photosynthesis, respiration, and transpiration of loblolly pine seedlings and tomato plants and found that transpiration and photosynthesis declined in phase as water stress developed. The correlation between the two processes suggests that both processes are controlled by stomatal closure. Idso [7] has presented a theoretical concept of separate effects of water stress on transpiration and photosynthesis and suggests that the photosynthetic mechanism is influenced directly by the free energy of water in the vicinity of the chloroplasts and that photosynthesis is influenced by a decline in water potential before the diffusional processes are influenced by stomatal closure. Idso [7] cites the work of Baker and Musgrave [17] and Denmead and Shaw [18] as evidence of decreases in assimilation of the plant early in the development of stress, while transpiration continued near the potential rate until more substantial stress levels developed. The implication is that photosynthesis was reduced long before any effects of stomatal aperture on transpiration or before any visible signs of wilting occur. Idso [7] recognizes the apparent contradiction the work of Brix [16] offers to his theory and explains that the young seedlings were grown in a sandy soil, and the moisture extraction curve of the sandy soil exhibits only small changes in soil moisture tension for some time until a point is reached where a rapid decrease in soil moisture tension occurs. At this point transpiration and photosynthesis would be expected to decline in phase.

The concept of different components of the total diffusion resistance pathway must be considered in light of the apparent controversy. The components of the resistance pathways for CO_2 and water vapor have been described by Gaastra [19]. The resistance to diffusion of CO_2 located between the mesophyll cell walls and the chloroplasts (commonly called the mesophyll resistance, r_m) results in an added resistance for CO_2 in the pathway of which the external boundary layer resistance, r_a, and the stomatal resistance, r_s, are common for water vapor. Gaastra evaluated the magnitude of these resistances and citing work of Pisek and Winkler [20] suggests that water deficits may cause an increase in the mesophyll resistance before the stomatal component is influenced, thus reducing photosynthesis before transpiration is reduced.

Gale, Kohl, and Hagan [21] used the same technique as Gaastra [19] in evaluating mesophyll and stomatal resistances by measuring leaf temperature, transpiration, and photosynthesis of bean leaves (Phaseolus vulgaris) in a chamber. A range of soil water potentials was established in potted plants. Leaf water potentials were not measured. Mesophyll resistance increased as vapor pressure difference (leaf to air) increased even when soil was wet, and also generally increased as soil water potential decreased. In addition, mesophyll resistance appeared to be independent of stomatal resistance, the latter being more or less constant with decreasing soil moisture. They concluded that the mesophyll resistance under conditions of water stress may constitute a significant portion of the overall resistance to photosynthesis.

Willis and Balasubramaniam [22] studied transpiration and photosynthesis of Pelargonium nortorum in a chamber that also included a detachable porometer. The porometer evaluated the stomatal resistances by measuring the change in viscous flow through the leaf as stomatal aperture changes. They found transpiration and photosynthesis to correspond closely with changes of stomatal resistance under different conditions of illumination and water stress. Although they did not evaluate mesophyll resistances, they concluded that the main differences were due to stomatal resistance.

More recently Troughton [23] reported on the effects of water status on the CO_2 exchange in cotton leaves and found that the mesophyll resistance was not influenced until quite severe stress developed and concluded that plant water status primarily affects CO_2 exchange by regulating stomatal aperture.

With the apparent discrepancies reported, the mechanism by which water stress influences gaseous exchange is unclear. The apparent conflict could have resulted from differences in techniques, chambers, flow rates, plant species, etc. The statement concerning the possibility of direct hydration effects on the photosynthetic mechanism is not discounted (Troughton [23]; Willis and Balasubramaniam [22]; Gale, et al [2]). Slavik [24] has studied the effects of decreasing water potential on the liverwort Conocephallum conicum in an attempt to eliminate the stomatal factor. He found photosynthesis to decrease almost linearly with decrease in osmotic potential. Although it is difficult to project this work to higher plants, the work illustrates that the exact mechanism is complex.

The complexity is apparent even within a single species. Heichel [25] examined the photosynthetic response of thirteen varieties of corn to leaf water potential using a regression model that estimated the main source of variability in the measurements of photosynthesis in leaves of the same physiological age. Included in the model were the water potential per se and the leaf temperature (as an index of stomatal activity). Some varieties showed photosynthesis to respond only to water potential while others responded to a combination of water potential and leaf temperature (stomatal closure) and still others responded only to changes in leaf temperature. Even in the varieties that responded only to water potential there was considerable difference in the sensitivity of photosynthesis to water stress. Heichel concluded that the decrease in water potential caused a decrease in the intracellular CO_2 transport (increase in mesophyll resistance). In addition a decrease in the intracellular utilization of CO_2 as shown by the increase in the CO_2 compensation point occurred under water stress. The direct and indirect response of photosynthesis of varieties within a single species to water stress emphasizes the complexity of the mechanisms involved and that a unique mechanism between species is not likely to be found.

The above review has pointed out some areas of research that are beyond the scope of this project and are discussed here only to illustrate important questions to consider in evaluating the influence of water stress on plant communities.

In view of the objective of this study, a review of the environmental factors influencing stomatal behavior and the interaction of these factors under field conditions is in order. The mechanism of stomatal action (namely the mechanism that initiates and maintains differences in turgor in the guard cells) has been studied for many years and it is not feasible in this review to present a discussion of all the diverse theories and experimental work that are in the literature. Several reviews covering this subject are available including Heath [26], Ketellapper [27], and more recently Zelitch [28]. In addition the recent book by Meidner and Mansfield [29] contains an up to date discussion and a nearly complete bibliography of mechanisms and interactions. Based on these reviews it can be concluded that the predominant environmental factors influencing stomatal behavior are light intensity, CO_2 concentration, water status of the plant, and temperature. This list of factors has evolved from studies of the effects of these factors singly while others were held constant. Separating the mechanism by which each factor operates becomes very difficult because the influence of one factor often consists of an interaction with another.

In general, stomatal aperture increases as light intensity increases. Meidner and Mansfield [30] discuss the theories behind the mechanism as linked to the photosynthetic production of substances in the guard cells that in turn cause water to be absorbed by the guard cells and thus inducing stomatal opening. The role of photosynthesis in stomatal behavior is immediately apparent and also illustrates the interaction involved, since the stomata generally open in response to a reduction in the carbon dioxide concentration. Conversely increases in carbon dioxide cause stomatal closure. The effect of light is generally thought to act by way of its influence on internal CO_2 concentration although some direct light effects, depending on the spectral quality have been reported (Meidner and Mansfield [29]; Raschke [31]). The temperature effect is also linked to the carbon dioxide concentration and under some conditions increased temperature induced closure due to an increase in respiratory CO_2 (Heath and Orchard [32]).

The interaction of water supply and other factors is of special importance because as stated by Meidner and Mansfield [29] "...ultimately, changes in the turgor relations between epidermal and guard cells determine the direction and rate of stomatal movements."

Interactions between water supply and the other environmental factors are occurring constantly in natural conditions. The assumption that stomatal aperture acts as a first order influence on photosynthesis and transpiration suggests an approach whereby the gross effects of changing water supply might be evaluated by simultaneous measurement of photosynthesis, transpiration, stomatal aperture, and soil and plant water status. An example of gross effects has been discussed earlier (Begg, et al. [9]; and Shinn and Lemon [8]) and some difference in the response of stomata is apparent. In one case mid-day closure of stomata and corresponding decrease in water potential caused reduction in photosynthesis and transpiration, while in the other, bimodal trends in water potential did not cause mid-day closure and corresponding decrease in transpiration. Both experiments were conducted under conditions of high illumination and with increasing water stress. With the high illumination the water potential of the plant and its diurnal change would be the predominant factor. The apparent inconsistency of these results suggests a more complex interaction between water potential and stomatal behavior.

As stated by Cowan and Milthorpe [33] there is a need for more measurements of the diurnal and spatial variation of stomatal diffusion resistance in field crops. Quantitative measurements of this plant parameter would also enhance the usefulness of various models involving the microclimate of the crop. The separation of the effects of illumination and water potential on stomatal diffusion resistance, as stated previously, is a next logical step for including the effects of water stress in various conceptual and descriptive models.

In recent years the development of a porometer for field use which measures the diffusion of vapor from the leaf has made possible more rapid measurements of stomatal diffusion. The porometer also has the advantage of integrating the diffusion resistance of a large number of stomata over a relatively large leaf surface. This technique is an improvement over visual observations under the microscope or of stomatal impressions which attempt to calculate resistance from the geometry and dimensions of the stomata. Two types of porometers have been described; the viscous-flow (Alvim [34]; Bierhuizen, Slatyer, and Rose [35]; Shimshi [36]) and the diffusion porometer (Wallihan [37]; Van Bavel, Nakayama, and Ehrler [38]; Slatyer [39]; Kanemasu, Thurtell, and Tanner [40]; Turner [41]). The viscous flow porometer measures the resistance of the two epiderma of the leaf in series and it is difficult although not impossible to calibrate in terms of diffusive resistance. It is restricted to amphistomatous leaves. The diffusion porometer measures the diffusion of water vapor for evaporating surfaces inside the leaf into a chamber of dry air. The rate of diffusion is evaluated and used as an indication of stomatal aperture. For quantitative expression the porometer has been calibrated in terms of diffusive resistance (Van Bavel, et al. [38]; Kanemasu, et al. [40]). Gale and Poljakoff-Mayber [42] compared measurements of viscous flow resistance and diffusive resistance on bean (Phaseolus vulgaris) and maize (Zea mays) leaves and concluded that porometers in which gas is made to pass through the leaves may give completely erroneous estimates of stomatal aperture and leaf resistance to CO_2 and water vapor exchange. They further suggest where evaluation of stomatal resistance alone is desired, the diffusion porometer appears to be the preferred instrument. This does not discount the pressure-drop type used by Alvim [34] and Shimshi [36] however, since this instrument measures the complete resistance through the leaf and hence may even be more sensitive as an indication of incipient internal stress.

Several authors have reported using porometers to evaluate stomatal resistance of various crops in field and greenhouse conditions. Turner

[41] measured profiles of relative stomatal resistance in corn (*Zea mays*), yellow-poplar (*Liriodendron tulipifera* L.), and flowering dogwood (*Cornus florida*) presumably under low water stress conditions and found illumination to be the most important factor influencing resistance values. Ehrler and Van Bavel [43] followed the diurnal fluctuation of stomatal resistance of sorghum (*Sorghum vulgare*, var RS-610) in a uniform, arid environment and found the minimum stomatal resistance to be influenced by the degree of water stress during a drying cycle. Burrows [44] measured stomatal resistance of potatoes and sugar beets and found similar results. Hurd [45] studied resistance of tomatoes in greenhouses in relation to leaf position and solar radiation. Ehrler and Van Bavel [46] established response curves of stomatal resistance to illumination of several crops by varying light intensity in an otherwise controlled environment.

These studies appear to substantiate the concept that under most field conditions light intensity and the leaf water potential are the primary factors influencing stomatal movement. A hyperbolic relationship between stomatal resistance and light intensity has been developed (Kuiper [47]; Gaastra [19]; Turner [41]; Ehrler and Van Bavel [46]). These relationships have been developed in controlled conditions or under conditions where water stress was unlikely.

In order to consider the effects of decreasing water potential, the relationship of leaf resistance and leaf water potential must be sought. Because stomata react to a number of conditions a perfect relationship between stomatal resistance and water potential may not always be found. Slatyer [1] and Barrs [48] suggest that stomata may not respond until some critical water potential has been reached. Kanemasu and Tanner [49] have examined this concept in snap beans (*Phaseolus vulgaris* L.) and found the critical water potential (critical water potential here defined as the water potential that must be reached by the leaf before a rise in stomatal resistance begins and with further decline in water potential a rapid rise in resistance occurs) for the abaxial surface to be -11 bars and for the adaxial surface to be -8 bars. Taking into consideration the diurnal change of leaf water potential the stomatal resistance may act as an on-off switch depending on the critical water potential.

It is the objective of this work to study the interaction of light intensity and leaf water balance for corn under field conditions. Quantitative expressions of these relationships are sought that can be used in developing models for linking the effects of water stress to other soil-plant-atmosphere models.

MATERIALS AND METHODS

Field Site

The experimental site for this study is the Ellis Hollow site near Ithaca, New York. During the summers of 1967 and 1968 a canopy density experiment in corn was undertaken. The stomatal diffusion and water balance experiments to be discussed are part of the larger experiment. The primary planting pattern for corn (Zea mays var. Cornell M-3) consisted of a 13-acre site planted in a hexagonal pattern in approximately 15-inch rows. This gave a plant density of approximately 26,000 plants per acre. One half of the field was subsequently thinned to establish contrasting plant densities.

The soil at this site is a Chenango silt loam which is a moderately well-drained soil with a layer of glacially deposited stones at a depth of two feet. The desorption characteristics and bulk density measurements have been described by Shinn, Brown, and West [50]. The desorption curve is shown in Figure 1. Field capacity in the upper 12 inches corresponds to approximately 0.1 bars soil moisture tension.

Soil moisture tension for the 1967 and 1968 experiments was measured by placing tensiometers (Model R Irrometer, Irrometer Co., Riverside, California) at three depths -- 12, 24, and 36 inches. Two tensiometers for each depth were located at each of four sites in the main sampling area. Two sites were located in the thinned and two in the unthinned portion of the field.

Leaf Resistance Measurements

Leaf resistance measurements were made using a porometer of the type described by Van Bavel, Nakayama, and Ehrler [38]. The construction of the porometer cup was essentially the same as described except the cup was modified to allow easy introduction of additional tube lengths for calibration purposes. The humidity sensor used in the porometer is a narrow range element #4-4817 manufactured by Hygrodynamics, Inc., Silver Spring, Maryland. The AC resistance meter used was the same as described by Van Bavel, et al. [38].

The principle of the porometer consists of enclosing a small portion of a leaf surface in a chamber that includes a sensor with a hygroscopic surface. The spatial arrangement of the sensor with respect to the leaf surface is constant. The air in the chamber is dried to a constant value prior to each measurement, and the change in humidity in the chamber resulting from evaporation from the leaf is detected by the sensor. The rate of change of the humidity is determined by timing the movement of the meter indicator between two fixed positions. The meter monitors

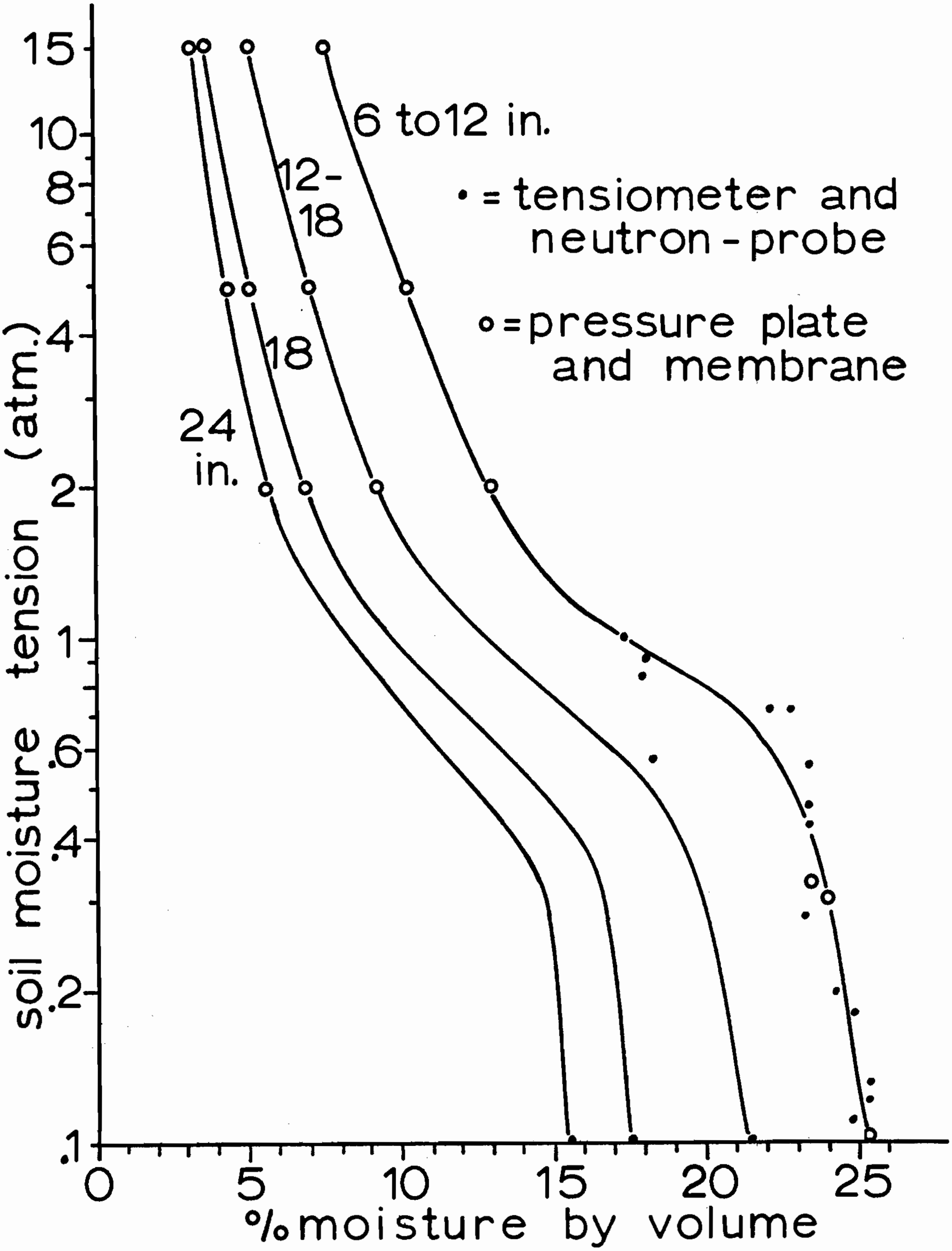


Figure I. Desorption curve of Chenango channey silt loam fan phase (from Shinn, Brown and West [50]).

the change in electrical resistance of the lithium chloride-impregnated resistor as water vapor is absorbed on the hygroscopic surface. The time change in electrical resistance is related to the diffusion resistance of the water vapor from the evaporating surface in the leaf.

Kanemasu, Thurtell, and Tanner [40] have shown that the tube-type porometer described by Van Bavel et al. [38] does not give a true linear relationship between the transit time and the resistance. They compared the tube-type calibration against the pore-type porometer that they describe, and found the tube-type to underestimate the resistance value when resistance is large. According to their calibration a resistance of 20 sec/cm given by the tube-type corresponds to a resistance of 27 sec/cm by the pore-type. This is a 35% underestimation by the tube [% error = $((r_{pore} - r_{tube})/r_{tube}) \times 100$]. The percent underestimation increases as the resistances increase, i.e., 66% error with a tube-type resistance of 24 sec/cm. However, below a resistance of 12 sec/cm, the magnitude of the error is smaller and in the opposite direction. A tube value of 6 sec/cm corresponds to a pore-type value of 5 sec/cm which is a 16% overestimation by the tube porometer. Although the percent error at the low resistances may be larger, the actual difference between the resistance values below the 12 sec/cm level is not greater than 1 sec/cm.

The resistance measurements in this study are in the low range for the greater part of the day. The error in the resistance values resulting from use of the tube-type porometer are not serious in the low range. Large errors would more likely occur at very high resistances either before sunrise or after sundown.

Porometer Calibration

The porometer was calibrated in terms of diffusive resistance according to the method outlined by Van Bavel, et al. [38]. Wet blotter paper was substituted for the leaf, and the diffusion path length, L, was varied by interposing cylinders of the same internal diameter as the cup but of different lengths. The cup dimensions as used in the subsequent leaf measurements were taken as the zero length. Transit times, Δt, with the wet blotter paper in the cup were determined by timing the movement of the meter needle between 0.20 and 0.60 full scale. Prior to inserting the wet blotter the air in the chamber was dried by pumping in air that had passed through a drying compound. This procedure was repeated for a series of temperatures. The calibration was conducted in a controlled temperature room where a range of temperatures comparable to outdoor conditions could be established. The temperature of the blotter paper was measured by a thermocouple mounted inside the porometer cup in a manner such that the thermocouple was in contact with the blotter paper while the transit time was being measured. The blotter temperature was maintained to 1 to 2 °C of the air temperature in the room. From 6 to 8 transit times for each path length were obtained.

The stomatal diffusion resistance or "leaf" resistance is obtained from:

$$r_\ell = \frac{S\Delta t}{D} - \frac{L_o}{D} \qquad (1)$$

where r_ℓ is leaf resistance in sec/cm; S is an instrument factor in cm/sec called the sensitivity; L_o is a diffusion length in cm and assumed constant for the porometer; Δt is the transit time in seconds, and D is the molecular diffusivity of water vapor in air in cm^2/sec. Use of blotter paper in the calibration assumes no stomatal resistance, and the effective resistance in this case is related to the path length:

$$r_\ell = \frac{L}{D} \qquad (2)$$

where L is the interposed path length. Substituting (2) in (1) gives:

$$L = S\Delta t - L_o. \qquad (3)$$

Both S and L_o are obtained from the plot of Δt versus L. Once S has been determined at different temperatures, D evaluated at different temperatures (see List [51]; p. 395), and the constant L_o determined, the leaf resistances can be calculated from equation (1) by measuring transit times and the temperature inside of the porometer cup. This relationship assumes thermal equilibrium of the system, steady state evaporation, and only small change in relative humidity.

Different humidity sensors and slightly modified cups were used in 1967 than in 1968. The calibration curve for 1967 is shown in Figure 2 and for 1968 in Figure 3. A linear regression was calculated for each temperature and the sensitivity (S) evaluated as the inverse of the regression coefficient. The cup factor (L_o) was evaluated from equation (3) with L = 0 and the average Δt when L = 0. Sensitivity (S) and the diffusivity of water vapor in air (D) in relation to temperature are shown in Figure 4.

<u>Field Measurements</u> -- leaf resistance 1967

The 1967 season was mainly used to develop sampling procedures and evaluating the leaf resistance -- light intensity relationships.

Figure 2. Porometer calibration curve -- 1967.

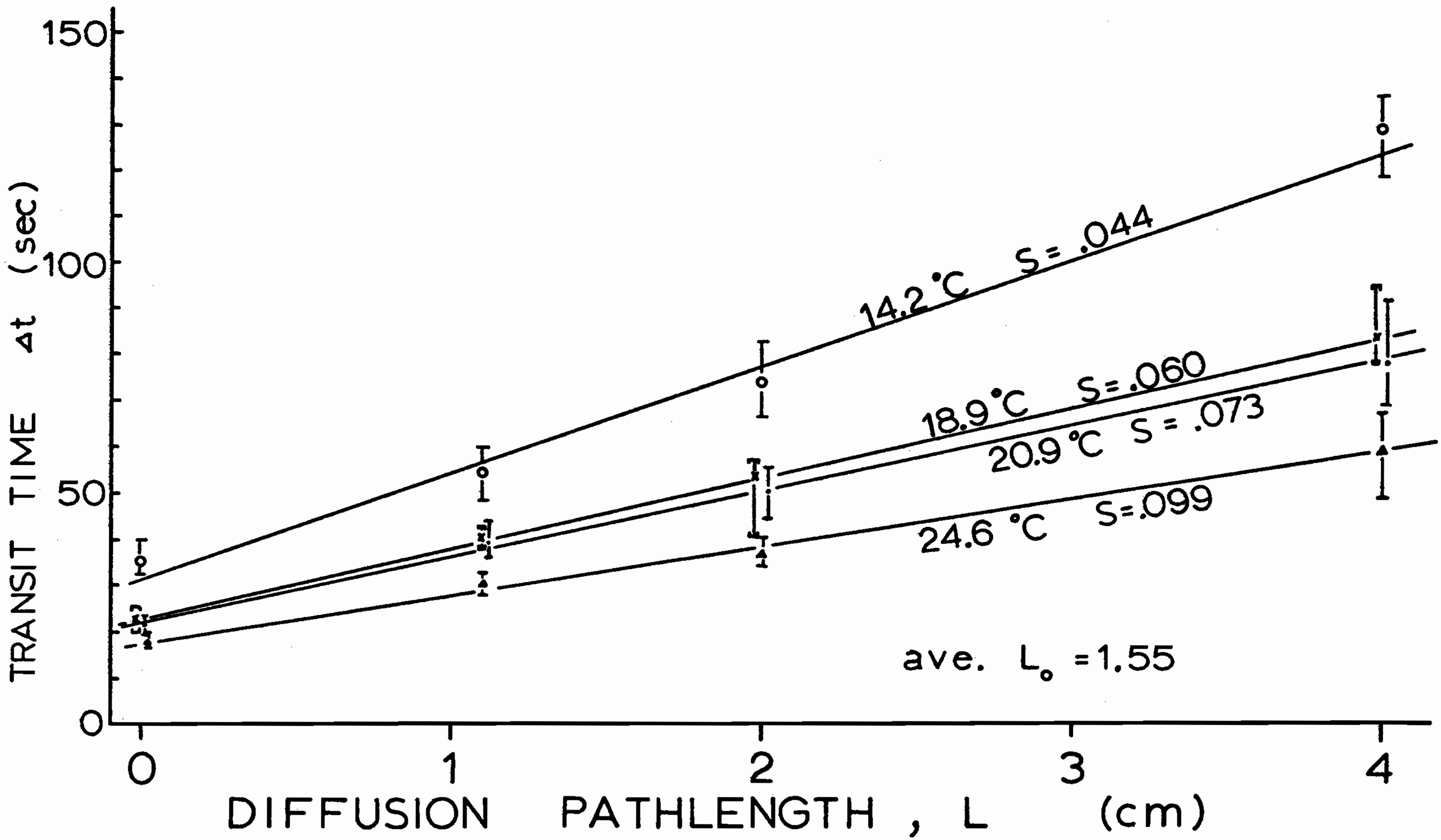


Figure 3. Porometer calibration curve -- 1968.

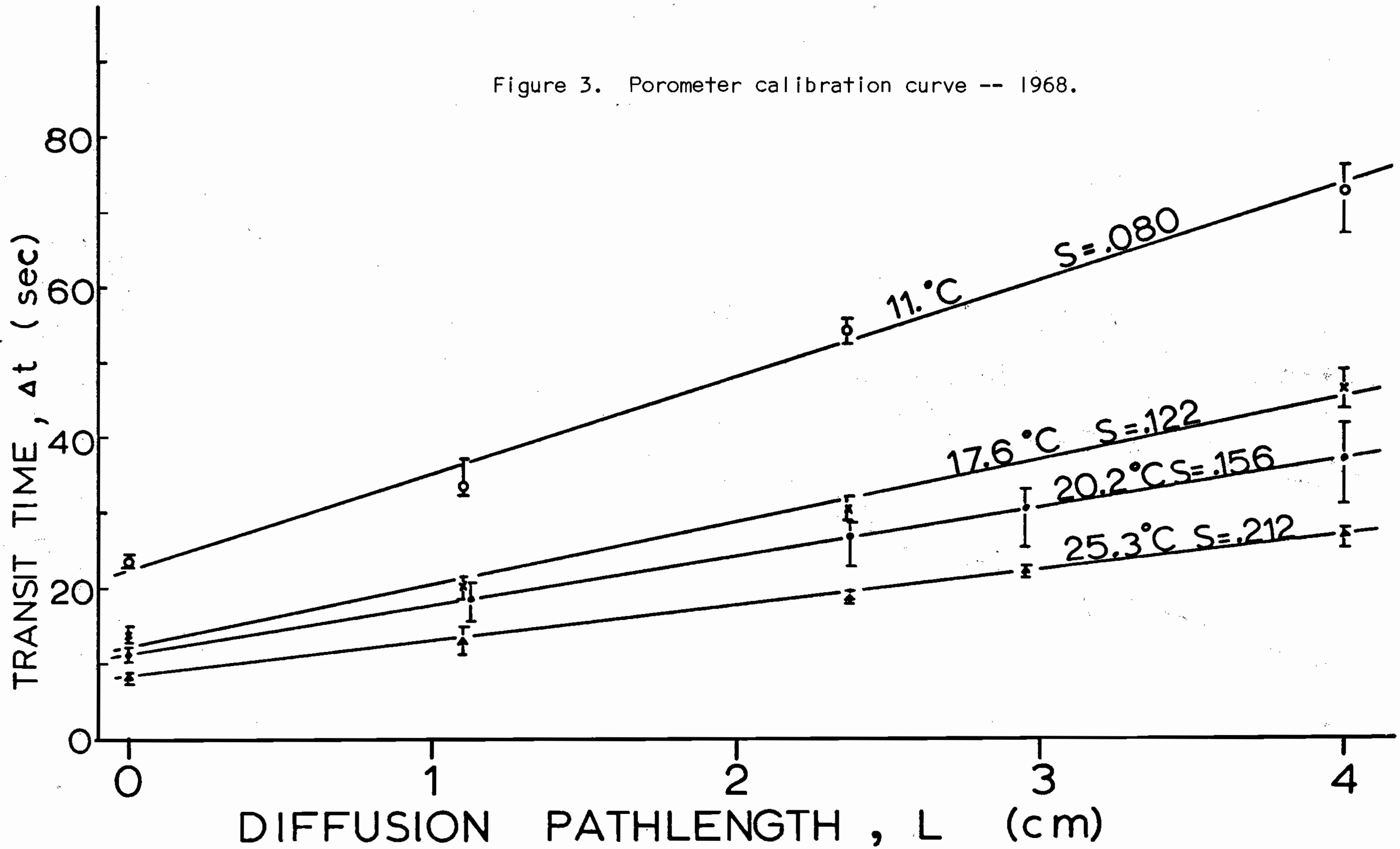
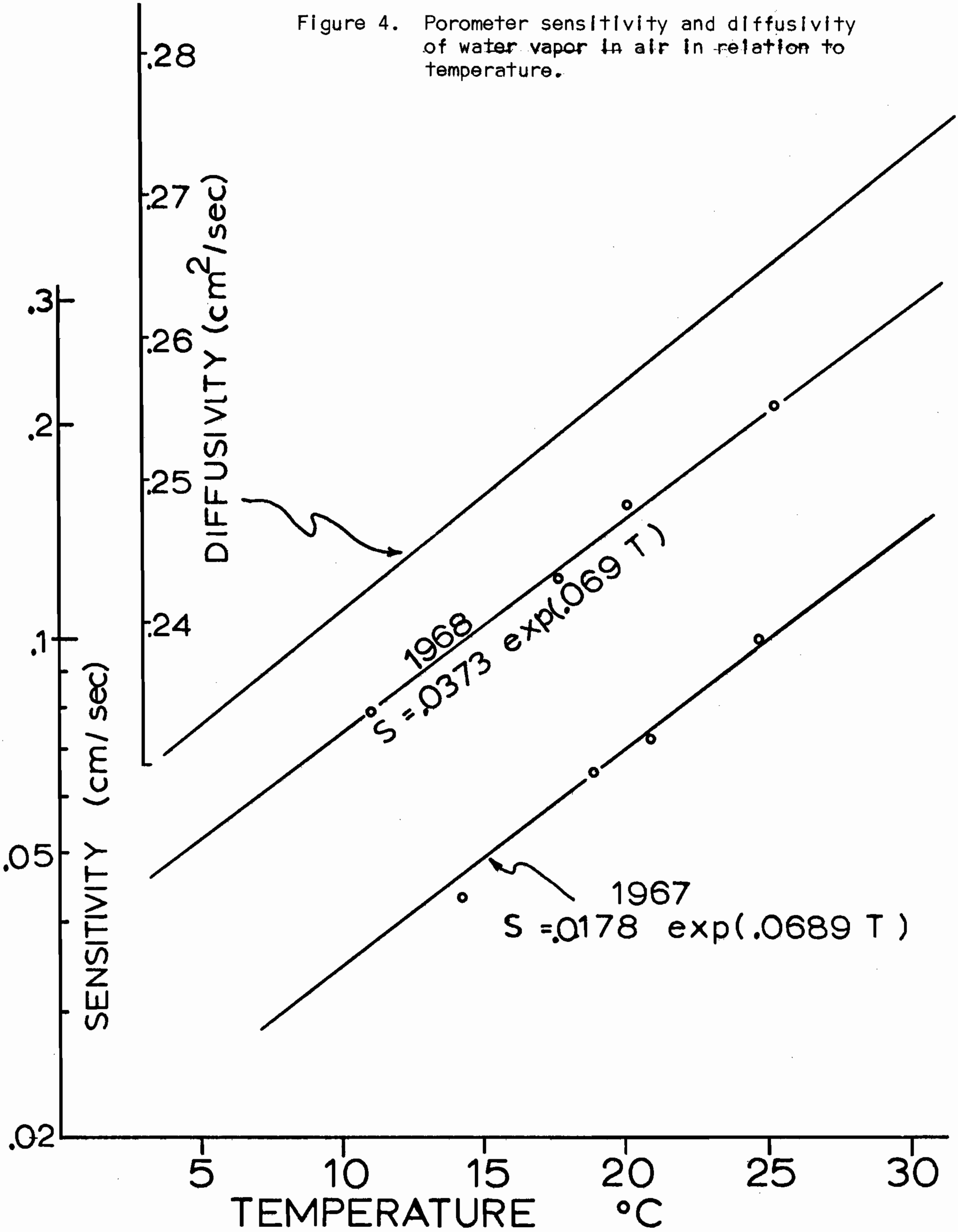


Figure 4. Porometer sensitivity and diffusivity of water vapor in air in relation to temperature.



The variation with depth in the canopy and the diurnal trends in leaf resistance were evaluated by dividing the plant canopy into three layers designated as upper, middle, and lower. The corn crop was approximately nine feet tall to tassels. Leaves sampled from the upper layer were roughly from the seven to nine foot level and were fully exposed to sunlight. Middle leaves corresponded to the three to five foot level and were intermittently exposed to direct sunlight. Lower leaves corresponded to the zero to two foot level and would generally be shaded. Leaves were sampled at random from these levels at regular intervals through the day.

To obtain a representative sample of the resistance values at a given time interval, it is necessary to sample as many leaves as possible. Only a small number of leaves could be sampled by carrying all the instrumentation necessary for a measurement to the leaf. Comparisons were made with detached and intact leaves, and no differences in transit times could be detected before and after the leaves were severed within several minutes after the leaves were severed. Severing the leaf does influence the turgor of the cells. Raschke [52] has shown that the subsidiary cells of maize leaves react instantaneously to a change in water supply. The response of the stomata is a transient, passive opening due to the release of the pressure of the subsidiary cells on the guard cells. Ultimately the stomata adjust to the prevailing water potential. Apparently the porometer of the type used in this study is not sensitive enough to detect the rapid change. The instantaneous change is on the order of tenths of seconds. With the porometer used in this study it appears that the errors introduced in measuring resistance on severed leaves as soon as possible after severing is less than the errors between individual leaves. The procedure followed was to cut a leaf from one of the three layers, take the leaf immediately to the instrument set-up and measure transit times on the adaxial (upper) and abaxial (lower) surfaces. Four to six leaves could be measured from the same level in a 15-minute period. A complete set of measurements, i.e., upper, middle, and lower layers, could be completed in roughly 45 minutes.

Leaves were sampled at random and without noting whether they were in the sun or shade. The sensing element covered an area of 2.85 cm^2 usually mid-way between the mid-vein and the edge of the leaf. The mean stomatal component of the overall epidermal resistance on a total leaf surface basis (leaf surface = 2 x leaf area) is calculated from the following:

$$\frac{1}{r_s} = \frac{1}{r_{ad}} + \frac{1}{r_{ab}} \qquad (4)$$

where r_s is the mean (sometimes called the total) stomatal resistance for the leaf, and the subscripts referring to adaxial and abaxial surfaces. All values are in units of sec/cm. Equation (4) accounts only for the stomatal component of the epidermal resistances of the leaf. This should not be confused with the total transpiration resistance which includes the resistance of the air boundary layer surrounding the leaf as well as the stomatal component. Moreshet, Koller, and Stanhill [53] and Kanemasu et al. [40] discuss the correct equation for the total transpiration resistance. They emphasize that the total transpiration resistance is composed of the stomatal component alone, only when the cuticular component of the epidermal resistance is very large, and the boundary layer resistance is very small. The porometer evaluates only the epidermal resistance. Equation (4) is the correct general formula for the stomatal component (Moreshet, et al. [53]) with larger cuticular resistances assumed (Slatyer [1]).

Light Intensity -- Leaf Resistance Relationship

The light intensity -- leaf resistance relationship was determined on intact corn leaves in the field on three clear days, September 2, 4, and 7, 1967. Instrumentation for measuring leaf temperature, light intensity, and leaf resistance was located in the corn canopy. Light intensity measurements were made using a selenium cell mounted under a cosine correcting head and on 85c Wratten filter as described by Stewart [54]. Leaf temperatures were measured using an infrared thermometer (Barnes Engineering Company, Model IT-3). Both leaf temperature and light intensity were recorded on a millivolt strip-chart recorder. The selenium cell was held in the same position and angle as the leaf. Leaves were selected from all levels in the canopy and included both exposed and shaded leaves in order to obtain a range in light intensities.

Field Measurements -- Leaf Resistance 1968

Based on the findings in the previous year and the need for more frequent sampling, the procedure was changed slightly. The canopy was divided into two layers. Upper, fully exposed leaves and lower, shaded leaves were sampled on continual basis through the day on parts of eleven different days in August and September. These measurements were taken in conjunction with other intensive measurements that will be discussed in succeeding sections.

The measuring procedure was the same as described. Approximately six leaves, three each from the upper layer and the lower layer and both adaxial and abaxial surfaces could be measured in a 20 to 30 minute period. Alternate sets for the thinned and unthinned portions of the experiment were made beginning shortly before sunrise and continuing until after sundown on the intensive sampling days.

Relative Water Content Measurements

During both years the relative water content of the leaves was measured according to the procedure described by Weatherley [55] and more recently discussed by Barrs [48]. Relative water content (RWC) is defined as:

$$RWC = \frac{\text{fresh wt.} - \text{dry wt.}}{\text{turgid wt.} - \text{dry wt.}} \times 100. \tag{5}$$

Duplicate samples of 20 leaf discs each were punched from corn leaves. The discs were ejected from the leaf punch into tared, stoppered bottles. The bottles were taken to a trailer parked in the field. After fresh weights were determined the discs were floated in water in closed petri dishes for four hours under relatively low illumination. Temperature in the trailer during flotation time was constant, and flotation temperatures did not differ greatly from temperature of the leaf at the time of sampling. Upon removal from the flotation the discs were blotted between sheets of filter paper under a 500 gram weight for one minute. Discs were then weighed to obtain the turgid weight and then dried in an oven at 75 °C.

In 1967 leaves from three levels in the crop were sampled and in 1968 two levels were sampled every hour during the intensive sampling days and at less frequent intervals on other days. The desire for numerous samples for evaluating the degree of water stress through the day led to the adoption of this technique over a direct measurement of water potential. The RWC values can be converted to water potential using the relationship reported by Shinn and Lemon [8] for corn grown under similar conditions. This calibration is used as an approximation for expressing the energy status of the water in the plant. Barrs [48] has reviewed the question of the energy status or the water content being more important as a measure of water stress. He concludes that both can be used as measures of water deficits.

RESULTS AND DISCUSSION

Soil Moisture and Rainfall -- 1967 and 1968

The climatic conditions during the summer months of 1967 and 1968 were quite different. The soil moisture tension at three depths and the rainfall records[1] for the duration of the experimental period are shown in

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[1]Monthly Meteorological Summaries, Division of Meteorology, Department of Agronomy, Cornell University, Ithaca, New York, 1967 and 1968.

Figures 5 and 6 for 1967 and 1968. The 1967 season was extremely wet with approximately 6.5 inches of rainfall during the month of August. This was approximately 2.8 inches above the average rainfall for the month, and the accumulated excess for the year was 0.55 inches. The soil moisture tension remained between 0.1 and 0.2 bars for most of the two month experimental period except for a rain free period from August 10 to 18. Soil moisture tension in the 12 inch level approached the limit for measurement with the tensiometers, 0.85 bars, only during this period. In general the moisture in the soil remained at a constant, high level for the period, and no severe plant water deficits were observed.

In contrast, the 1968 season was much drier. Rainfall during August was 3.00 inches which is 0.57 inches below normal for the month. Severe drought conditions prevailed throughout the year, and the accumulated deficit for the year was 4.20 inches through the month of August. Soil moisture tension for all depths was generally higher (more negative) than in 1967 and approached the limit of the tensiometers on several days. The field was irrigated in mid-July which alleviated drought conditions temporarily; however, the corn plants showed visible signs of stress on occasion. An obvious manifestation of the drought effect between the two years was the crop height which was approximately 300 cm in 1967 and 215 cm in 1968 for the same planting density.

Leaf Resistance -- 1967

Changes in leaf resistance and relative water content through the day were measured on August 23, 24, 29 and September 12 and 14, 1967 by the sampling system described earlier. The same general trends occurred each day. The results for August 29 are shown in Figures 7, 8, and 9. This day was chosen as representative because it was more completely cloud free than on August 23 and 24, and leaves had suffered some frost damage by September 12. The mean stomatal resistance values for both surfaces of the leaf, r_s, for the different layers of the crop (Figure 7) show that the uppermost, exposed leaves have the lowest resistance values with the middle leaves intermediate between lower and upper leaves. The trend through the day is from high resistance in the early morning hours to a minimum resistance near midday followed by a rise to higher resistance values toward late afternoon. These trends are consistent with the expected behavior of stomata in response to light intensity changes due to sun angle and to light attenuation within the crop canopy. The variability in measurements as shown by the range of the individual measurements for a given time interval is the same order of magnitude throughout the day for each layer. The range in individual measurements during midday was smaller than the range early or late in the day. A statistical analysis showed significant differences between time of day and between layer in the canopy; however, more

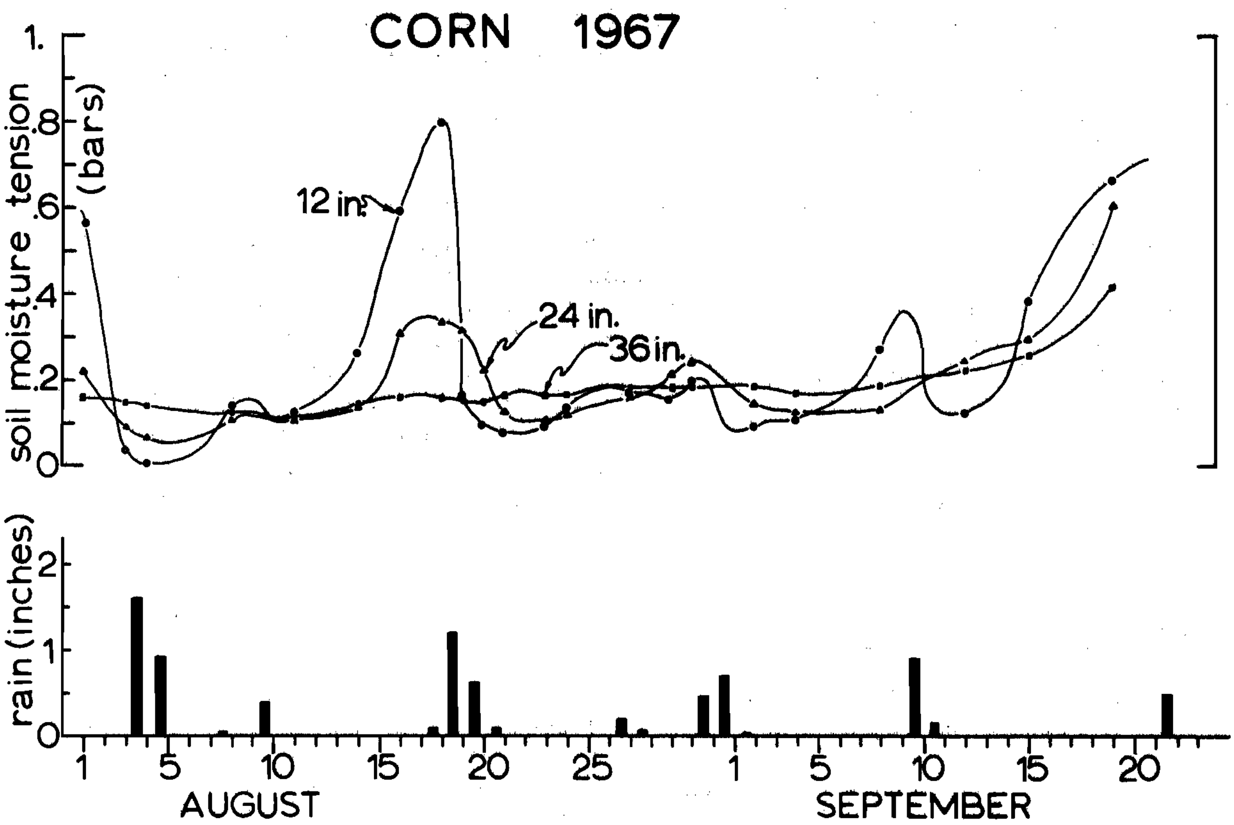


Figure 5. Rainfall and Soil Moisture Tension -- August and September 1967.

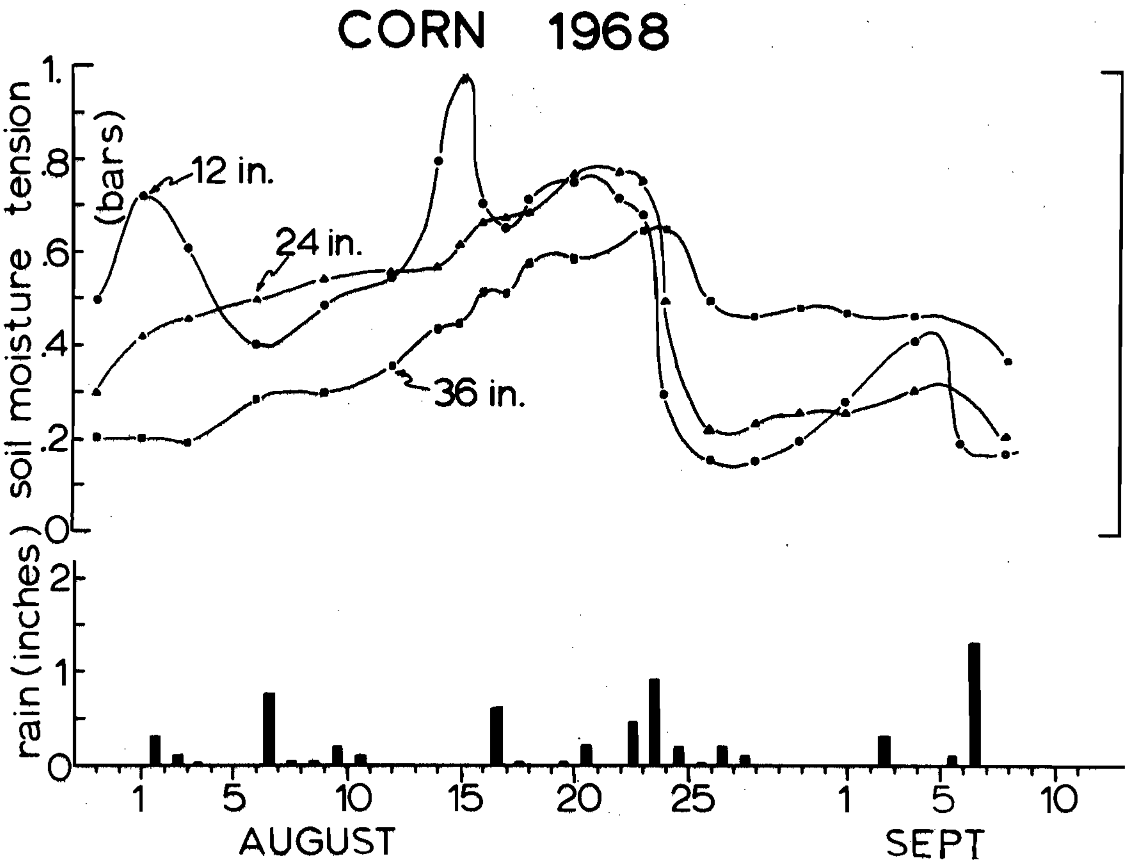


Figure 6. Rainfall and Soil Moisture Tension -- August and September 1968.

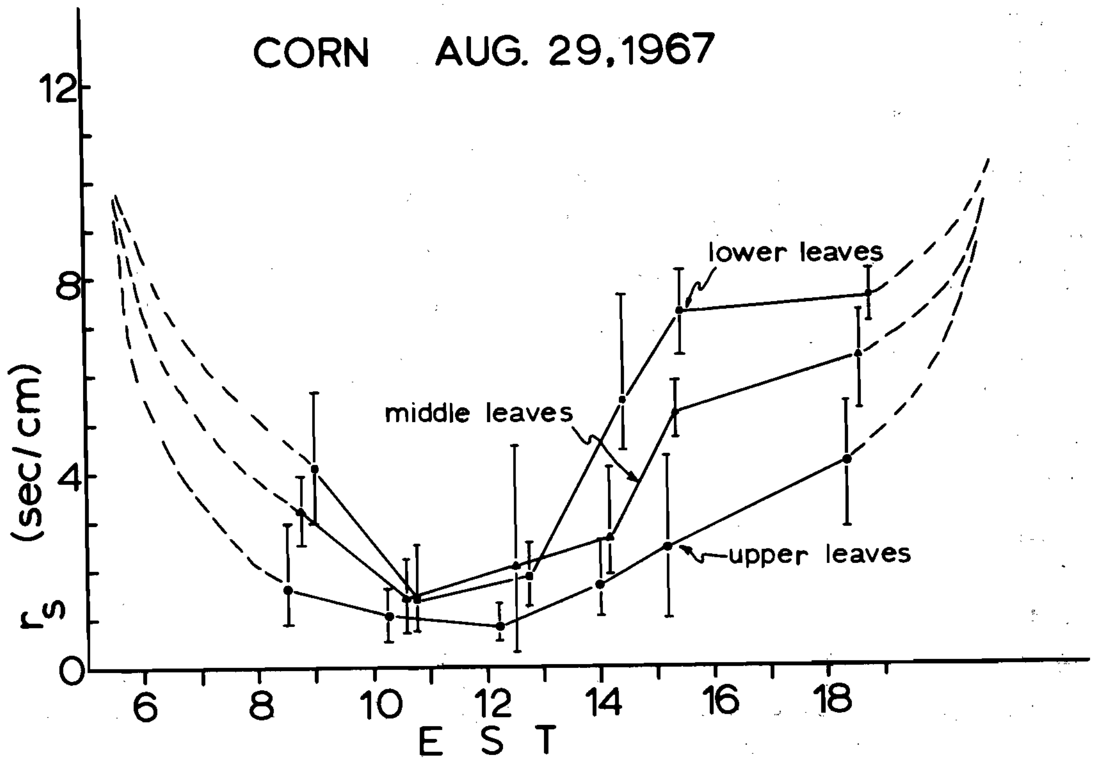


Figure 7. Stomatal resistance measurements, August 29, 1967.

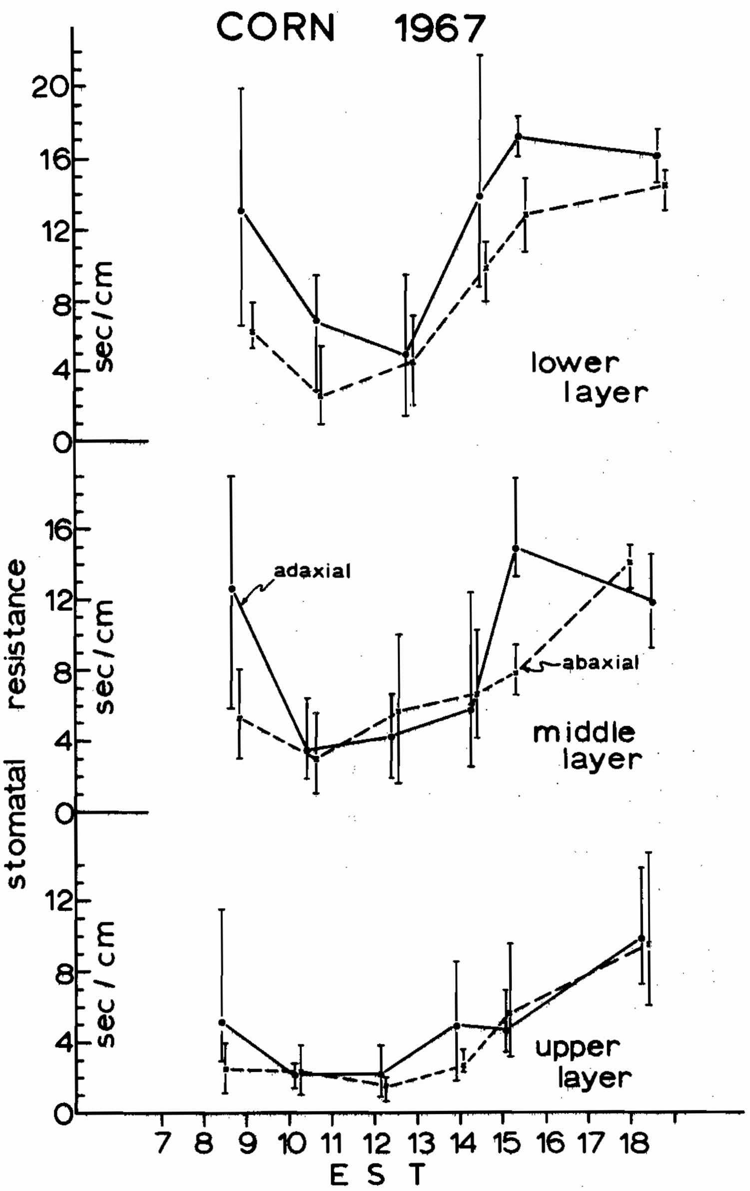
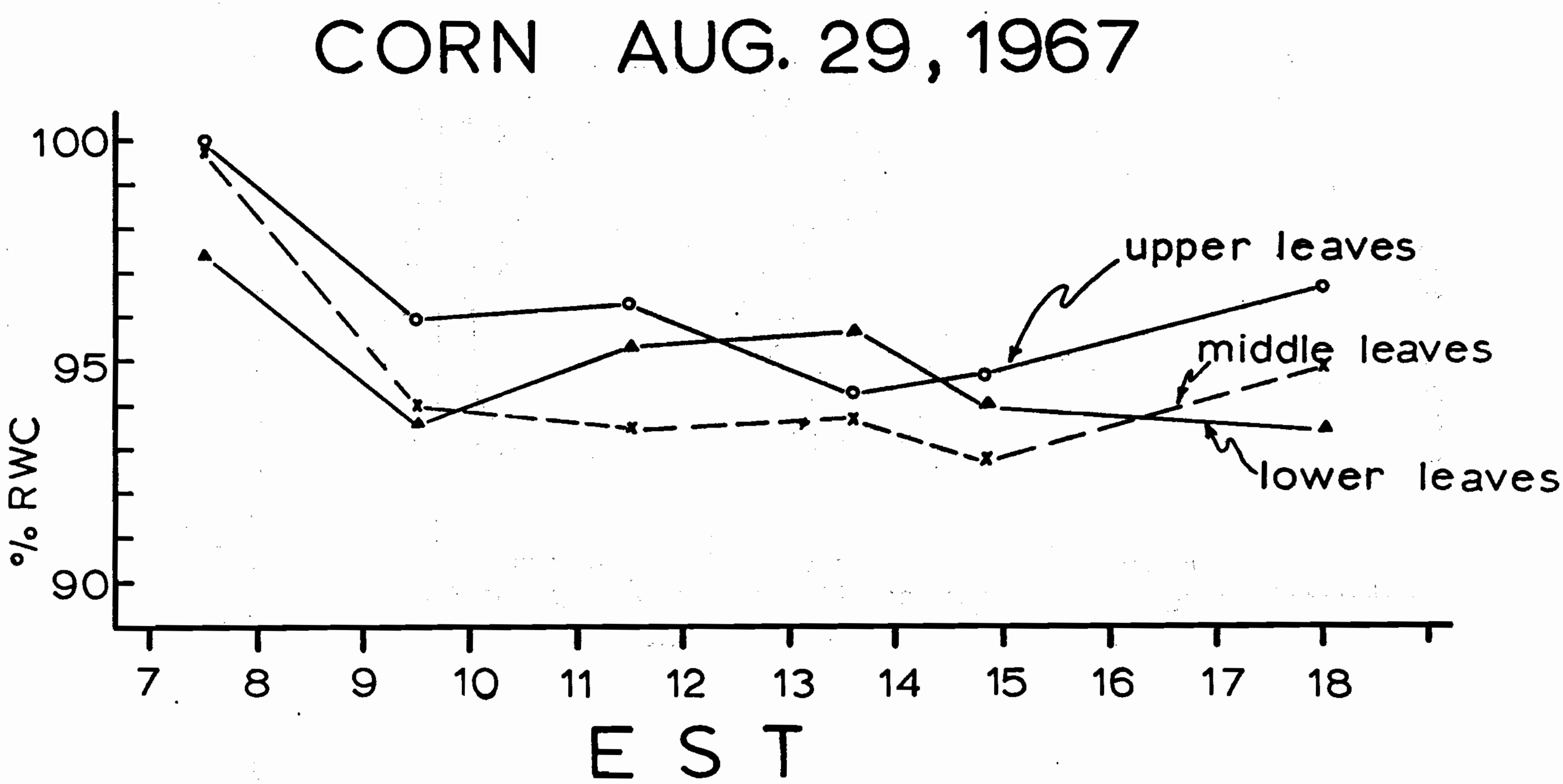


Figure 8. Comparison of resistances on adaxial and abaxial surfaces, August 29, 1967.

Figure 9. Relative water content measurements, August 29, 1967.



significant was the suggestion of an interaction between layers and time of day. Resistance values do not change at the same rate in each layer as shown by the more rapid increase in the resistance values in the middle and lower layers in the afternoon.

Minimum resistance values for the days measures between 0.5 and 2.5 sec/cm and usually occurred in the period between 1000 and 1400 hours.

Comparison of the resistances between adaxial and abaxial surfaces is shown in Figure 8. Based on the average values, there is little difference between the two surfaces of the leaf particularly in the upper layer of the canopy. Tha adaxial (upper) surface is generally higher than the abaxial surface although the range in measurements is large for both surfaces and may preclude any significant difference. Based on an analysis described by Snedecor [56], it would take a sample size of 5 to set a 95% confidence limit using an allowable error in the sample means of $\pm$ 2.0 sec/cm for a range of 4.5 sec/cm. The range in values is sometimes larger than this and overlaps between surfaces, and since the means of the two surfaces both fall within the allowable error it is assumed that there is little difference between the resistances of the two surfaces. Turner [41] reported similar results although for younger leaves the adaxial resistance was higher than the abaxial surface. These results were for leaves under high light intensity. Ehrler and Van Bavel [46] reported large differences between adaxial and abaxial surfaces at low light intensities, and the difference diminished as light intensities increased. The mean values shown in Figure 8 express similar results. The difference between the two surfaces would largely be due to differences in stomatal number. No measurements of size or number of stomata were made. However, corn generally has an adaxial to abaxial ratio of about 0.75 (Spector [57]).

Relative water content of the leaves taken from layers corresponding to the leaf resistance measurements is shown in Figure 9. Only small differences between layers and in a single layer were detected. The minimum RWC observed was 93% for the middle layer at 1500 hours. Values for all layers ranged between 96% and 93% and gradients from lower leaves to upper leaves were indefinite. The high RWC values reflect the high soil moisture conditions that prevailed throughout the season. It was not possible to measure response of leaf resistance to large changes in leaf water content under the prevailing moisture conditions during the 1967 season.

The diurnal trend in leaf resistance for the different layers largely reflects responses to changes in light intensity with time of day and with depth in the canopy. With the high moisture conditions prevailing during this experiment, the influence of water deficits would be minimal. Under adequate soil moisture conditions a direct relationship between leaf resistance and light intensity could be used to estimate diffusion resistances for different layers in the canopy. Advantage of the relatively constant moisture supply was taken to obtain a relationship between light intensity and leaf resistance.

Leaf Resistance -- Light Intensity Relationship

The leaf resistance -- light intensity relationship is shown in Figure 10. The light intensity is expressed in units of μEinsteins/cm^2 sec, which expresses the visible radiation in terms of photons, and also in energy units (cal/cm^2 min) for radiation between 0.4 and 0.7 microns wavelength. The light sensor was calibrated against two Eppley pyranometers on clear days as described by Stewart [54], and visible radiation can be expressed in energy units and converted to μEinsteins/cm^2 using the spectral distribution of sun and sky radiation measured by Federer and Tanner [58]. Both units are used in Figure 10 for convenience. Full sunlight is approximately 0.23 μEinsteins/cm^2 sec and 0.7 cal/cm^2 min in the visible radiation band. The measured values are from intact leaves at various positions in the canopy, and at various times of the day. Both shaded and unshaded leaves were measured to obtain resistances at a large range of light intensities. The resitance values are the mean, total resistance from measurements of the adaxial and abaxial surfaces. A hyperbolic equation was fitted to the data points in order to obtain a mathematical expression of the relationship. The general equation for this relationship is:

$$r_s = \gamma_o + \frac{\beta_o}{I} \qquad (6)$$

where γ_o and β_o are constants having the units of sec/cm and μEinsteins/cm^2, and I is the light flux density in μEinsteins/cm^2 sec. The values of γ_o and β_o were found to be 0.97 and 0.0269. The shape of the curve agrees well with similar measurements on beans by Kuiper [47] and for corn by Turner [41] and Ehrler and Van Bavel [46]. Although the absolute units for light intensity are not the same and conversion to corresponding units is only an approximation, the resistance values in Figure 10 are close to the values reported by Ehrler and Van Bavel for comparable light flux densities. Turner has expressed the units of resistance in seconds and not directly comparable to the units used here. However, the light intensity curve has the same hyperbolic relationship, and the light intensity where a rapid increase in resistance occurs compares closely with the same value in Figure 10.

Relative water content measurements at various intervals through the day on the same day as the light-resistance measurements were above 94% RWC for all layers sampled, and lend confidence to the assumption that the water deficits did not interfere with the leaf resistance measurements.

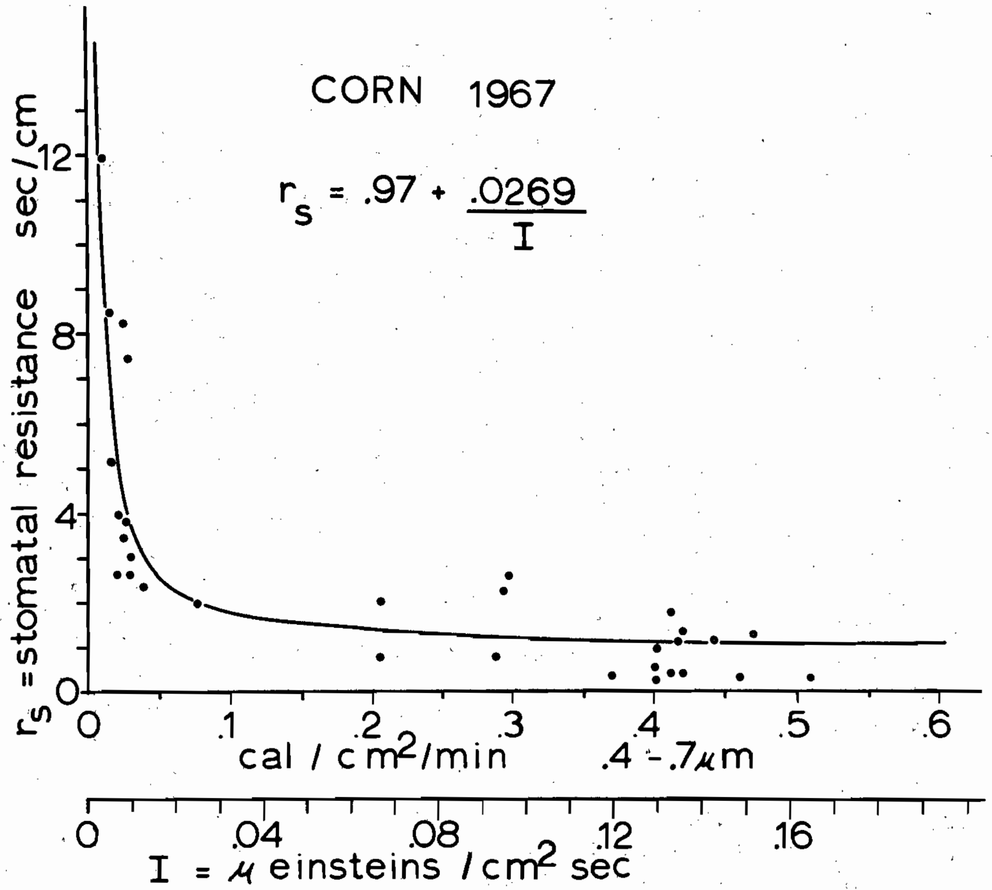


Figure 10. Light intensity -- stomatal resistance relationship.

The main feature of this relationship is that over a large range of light intensity up to full sunlight, the leaf resistance changes very little. Assuming this same relationship holds for all active leaves in the canopy, light intensities at lower layers in the canopy would have to be at low levels to cause stomatal closure. This does not include chlorotic or senescent leaves.

The leaf resistance -- light intensity relationship can be checked by comparing the leaf resistance value predicted using equation (6), (Figure 10), and light intensity values determined from the percent transmission into the plant canopy. Light measurements in the canopy and percent transmission in the canopy were made by Stewart [54] in the same crop and at approximately the same time as the resistance measurements. In 1967 the cumulative leaf area index from the top of the crop to ground level was 5.2 (Stewart's Figure 11). Taking the relationship of percent transmission and cumulative leaf area index at a sun angle near 1200 hours (Stewart's Figure 14) and assuming a visible radiation intensity at the top of the crop of 0.7 cal/cm^2 min, the horizontal light intensity at various depths in the canopy, corresponding to the layers given for the August 29, 1967 data shown in Figure 7, can be determined. Taking the leaves from the lower layer as being from approximately 50 cm from the ground, the percent transmission to this depth is 4.5%, which gives a visible light intensity of 0.02 cal/cm^2 min. The corresponding resistance value from Figure 10 is 3.7 sec/cm. This is slightly higher than the mean value for 1200 hours in the lower layer as shown in Figure 7. However, the value is within the range and is reasonable considering the approximations used in the calculation.

Probably a more significant check is that the light intensities at the lower layers in the canopy fall in the range where the leaf resistance -- light intensity relationship shows rapidly increasing resistance values. This could explain the reason for the more rapid rise in resistances in the lower and middle layers of the canopy in late afternoon as compared to the upper layer. The exact light intensity values at the top of the crop for the day shown in Figure 7 are not available, and the visible radiation intensity is estimated from similar, clear days when measurements were taken near the same time of the month and should be reasonable estimates for these calculations.

The relationship of equation (6), (Figure 10), is concluded to be a reasonable approximation for determining the response of stomata of corn under field conditions to change in light intensity and under conditions free from water deficits. This relationship will subsequently be used in the development of a model that includes the effects of water deficits.

Leaf Resistance -- 1968

The contrast in soil moisture conditions between the two seasons has already been illustrated (Figures 5 and 6). The 1968 season was much drier and plant water deficits were more likely to occur. Examination of Figure 6 shows that a wide range in moisture conditions prevailed through the month of August. The intensive sampling days included this wide range in moisture conditions and provided an opportunity to evaluate the influence of water deficits on stomatal diffusion resistance and the light intensity -- water deficit interaction. The intensive sampling days for leaf resistance and relative water content and the time interval of sampling for each day are given in Table 1.

The results for all days sampled were similar depending on the degree of water deficit prevailing for the day. The data for three days with contrasting moisture conditions is presented for detailed consideration. Leaf resistance measurements through the day for August 15, 18, and 28 are shown in Figures 11, 12, and 13, and the relative water content values for the same days are shown in Figure 14. Both upper, exposed leaves and lower, shaded leaves are given. These results are separated into three categories of stress conditions based on the soil moisture tension and the relative water content of the leaves. The categories are: high stress, August 15; moderate stress, August 18; and low stress, August 28. These particular days were chosen for detailed analysis because energy balance measurements are the most complete.

The visible radiation intensity at the top of the crop for each day is shown in Figure 15. The data points are the mean values for a 30-minute scan at a scan rate of 1 reading per second. Points are plotted at the mid-point of the 30-minute interval. The visible radiation was determined from two Eppley pyranometers measuring total and infrared radiation, and after the proper corrections the visible (0.4--0.7 microns) is obtained from the difference between the two Eppleys (Stewart [54]). All three days have the same general shape, although the peak intensity for August 18 was 0.7 cal/cm^2 min compared to approximately 0.6 cal/cm^2 min for the other days. There is evidence of intermittent clouds on August 28 as shown by the dips in the curve at 1000 and 1400 hours.

The contrast in water deficit is apparent in the relative water content of the leaves. On both the moderate and low stress days the RWC remains above 90% for the upper leaves with the lower leaves showing slightly higher values. The RWC on the high stress day was below 90% most of the day with a minimum RWC in the upper leaves near 87%. The average RWC between 0900 and 1700 hours is 91.5% and 91.2% for August 28 and August 18 while the average for August 15 is 88.5%. Visible curling of leaves in the afternoon of August 15 corresponded to the low RWC values. In terms of water potential, 90% RWC corresponds to a water potential of approximately -6.0 bars and 87% RWC to about -8.0

TABLE I

LOG OF SAMPLING DAYS AND TIME INTERVAL OF SAMPLING -- 1968

Date	Leaf Resistance	% RWC
July 30		0700-1600
Aug. 8	1100-1830	0700-1800
Aug. 11	0600-1900	0600-1900
Aug. 12	0600-1900	0600-1900
Aug. 15	0600-1900	0600-1900
Aug. 18	0530-1830	0530-1900
Aug. 21	0530-1800	0530-1830
Aug. 22	0600-1400	0600-1400
Aug. 27	1000-1830	1000-1700
Aug. 28	0630-1830	0630-1830
Sept. 8	0630-1730	0630-1700

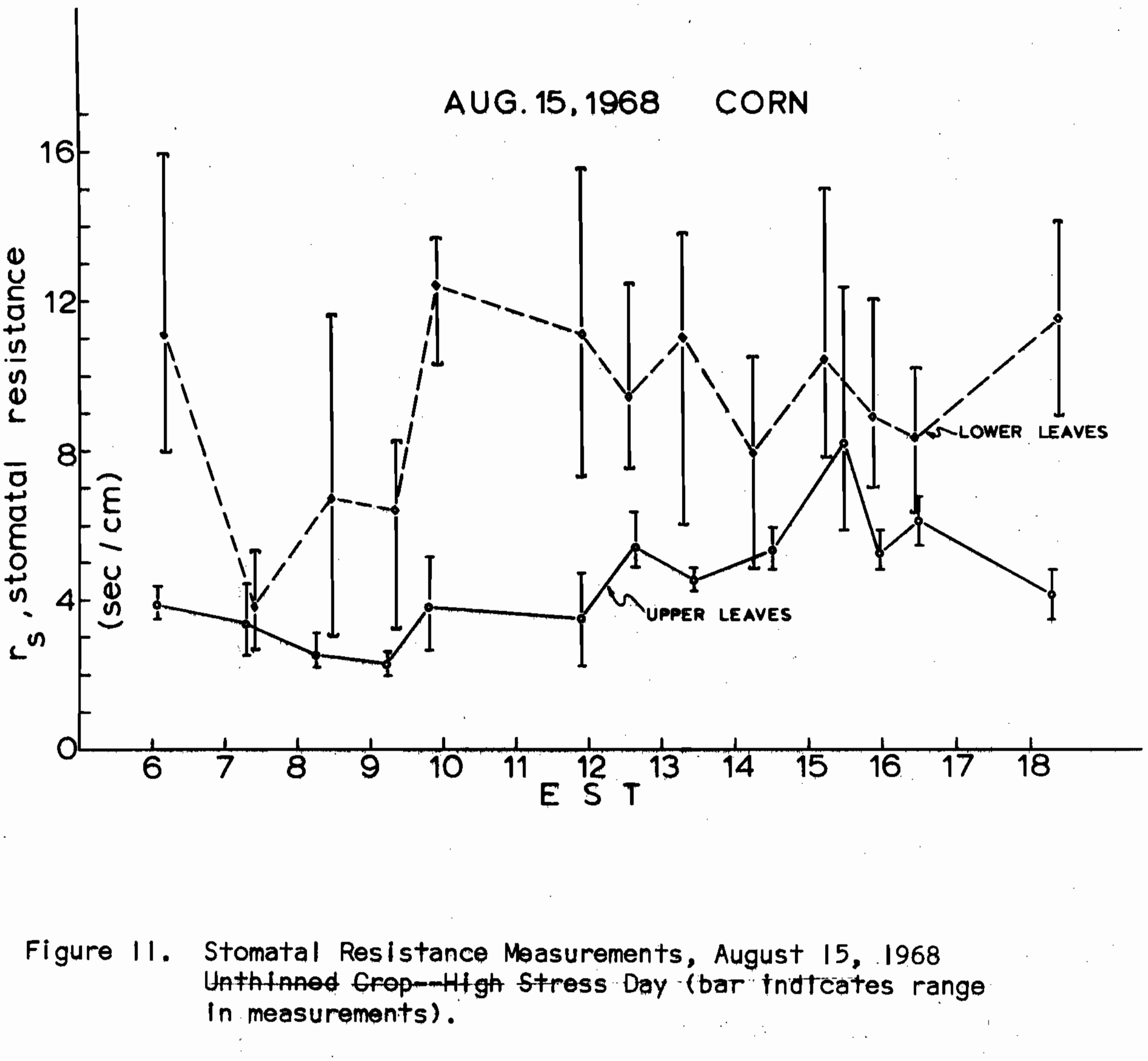


Figure 11. Stomatal Resistance Measurements, August 15, 1968 ~~Unthinned Crop--High Stress~~ Day (bar indicates range in measurements).

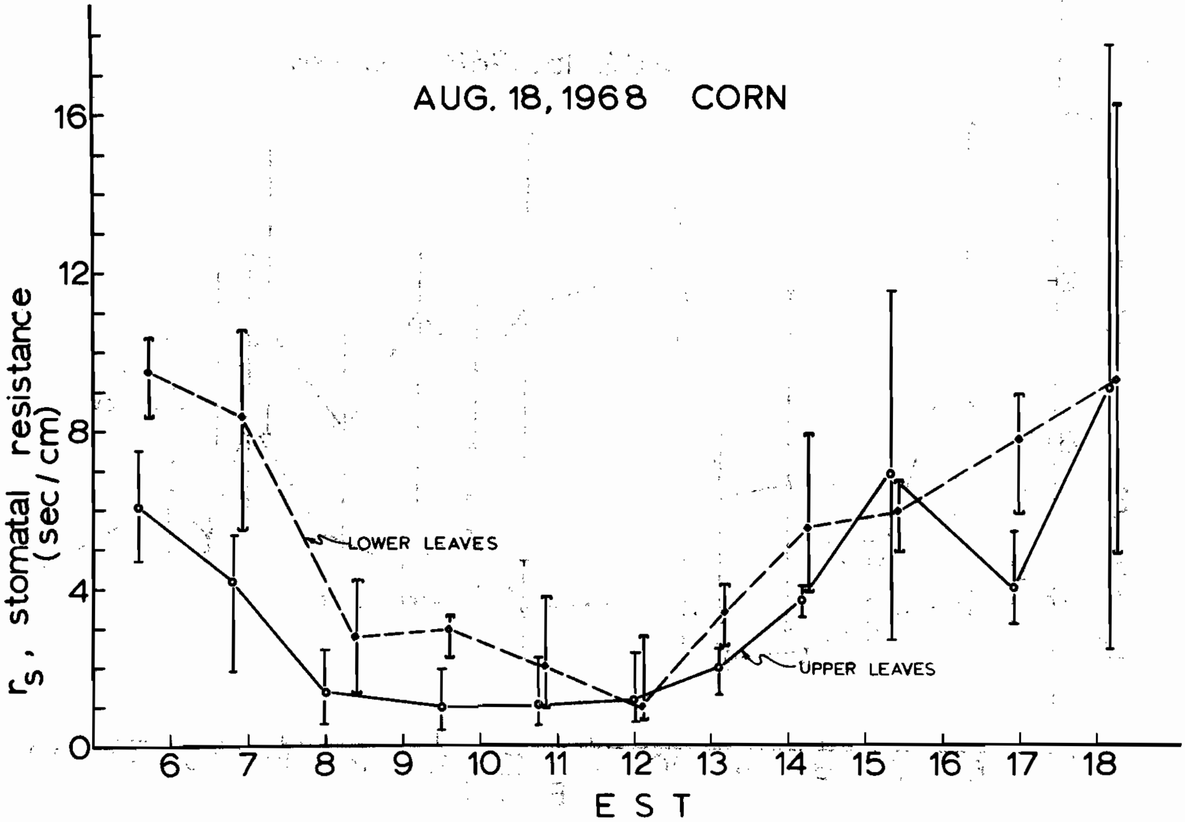


Figure 12. Stomatal Resistance Measurements, August 18, 1968 Unthinned Crop--Moderate Stress Day (bar indicates range in measurements).

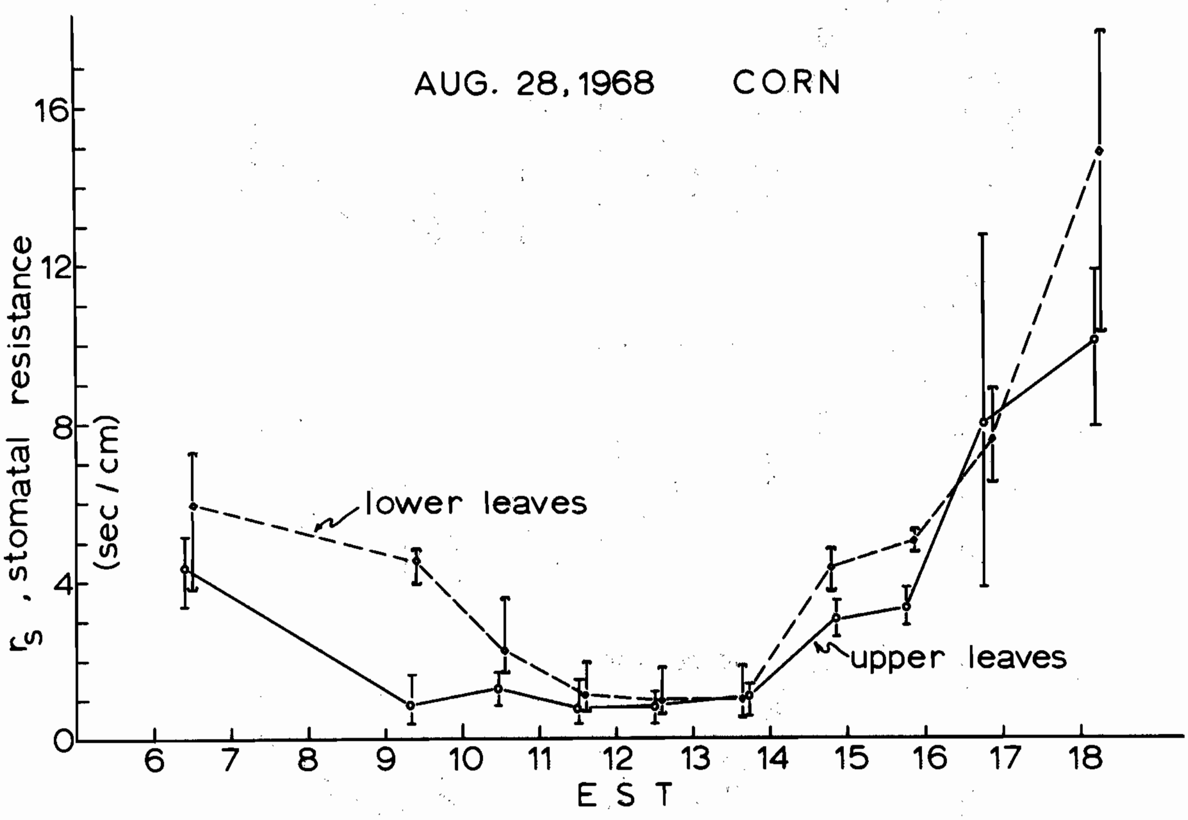


Figure 13. Stomatal Resistance Measurements, August 28, 1968 Unthinned Crop--Low Stress Day (bar indicates range in measurements).

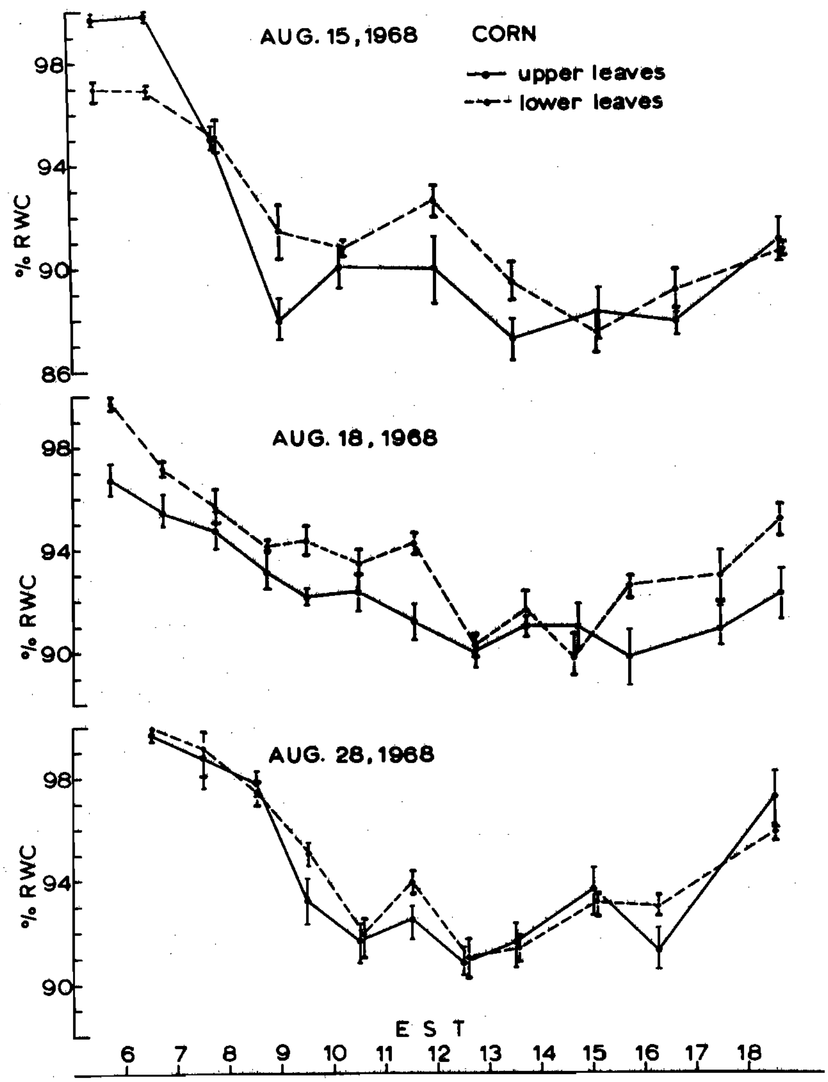


Figure 14. Relative water content measurements on high, moderate, and low stress days.

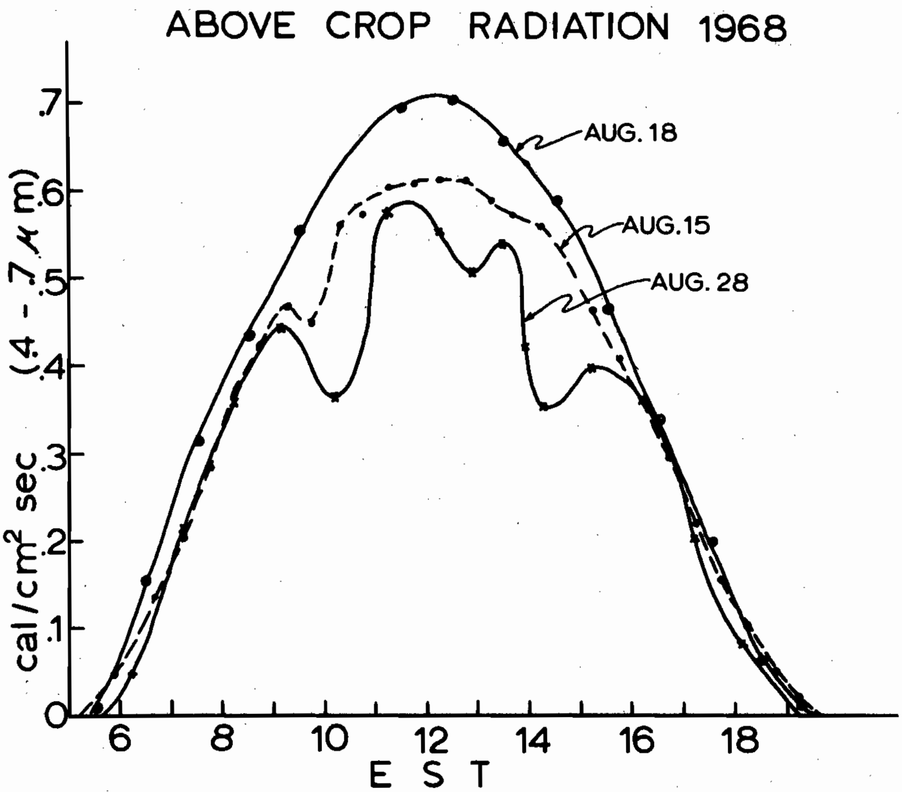


Figure 15. Visible radiation intensity at top of crop on high, moderate, and low stress days.

bars. The minimum RWC for the moderate and high stress days does not occur until after 1200 hours while a low RWC, close to the minimum, occurs near 0900 on the high stress day. There is some evidence of a bimodal trend in RWC and seems to be more pronounced on the high stress day. The gradient in water potential is consistently in the direction from lower to upper leaves (ψupper <ψlower, where less than means more negative). However, there is a tendency for decreasing gradient, and in mid-afternoon on the high and moderate stress days the gradient appears to be reversed (ψlower <ψupper). This is in contrast to the measurements in 1967 under very low stress conditions where gradients were reversed and not well defined. Differences between upper leaves and lower leaves were significant (analysis of variance, F test significant at 1% level) on August 18 and 15, but not significant on the low stress day, August 28. Differences between hours of the day were significant on all three days. An estimate of the errors in sampling can be inferred from the range in the duplicate samples. Each sample is a composite of 20 leaf discs from several leaves in a particular layer.

The mean stomatal resistance values, r_s, in Figures 11, 12, and 13 are the mean values of 3 to 4 readings plotted at the mid-point of the time interval. The bar indicates the range in the measurements, and as discussed earlier the sample size and magnitude of the range allow confidence of no less than $\pm$ 1.5 sec/cm.

The resistances of the leaves from the lower layer are higher than the upper, exposed layer, and are similar to the response to light intensity as discussed earlier. The difference between layers is greater during periods when sun angle is low. Near mid-day the differences between upper and lower layers are nil. The resistances generally decrease from high, early morning values in response to light intensity and reach some minimum value after a threshold light intensity is obtained.

Notable exception to the above is observed on the high stress day, August 15 (Figure 11). The resistances of the lower leaves are considerably higher than the upper leaves, and the diurnal trend is in contrast to the low and moderate stress days. The resistances in the upper leaves decrease from early morning readings and reach a minimum r_s about 0900 EST, from this point on there is a steady increase in r_s for both upper and lower leaves. This rise in resistance corresponds to the low %RWC at the same hour. There appears to be an over-riding influence of water deficit in reducing the response to increasing light intensity. Comparison of the minimum r_s values between the three stress categories shows that a minimum of 2.3 sec/cm near 0900 hours is higher than the minimum of 1.0 sec/cm on the lower stress days. Furthermore, the minimum value on the lower stress days is maintained for some hours. These results are similar to those reported by Ehrler and Van Bavel [43] with sorghum. They measured a minimum resistance of near 5.0 sec/cm near 1000 hours with a gradual increase in resistance thereafter with a dry soil, and with a wet soil the minimum resistance was near 1.0 sec/cm and was maintained from 0900 until after sundown. The response of the stomata under the wet soil conditions appears to be solely due to the light regime. Indeed this response would be predicted by the light intensity -- leaf resistance relationship discussed earlier under low stress conditions.

Although the moderate and low stress conditions follow the light response pattern for the most part of the day, the resistance values rise sharply at certain points, i.e., 1230 hours on August 18 and 1400 hours on August 28. The %RWC values for these two days indicate that response to water deficits would be unlikely. If this is true then some other mechanism would be responsible for the rapid closure. This aspect will be considered later. Another feature of the resistance curves is the difference in the time of day where the sharp rise in resistance occurs. There is a relationship with this point and the degree of stress. This critical point occurs later in the day as the severity of water stress decreases.

As mentioned in the review, the concept of a critical water potential for stomatal closure has been reported. The critical water potential is defined here as the water potential at which stomata begin to close (resistance begins to rise) rather than the water potential at which stomata are closed that is sometimes referred to as the critical point. Because stomata respond to many factors the correlation between leaf resistance and water balance is not always perfect, but the critical water potential concept seems consistent although varying with species. Ehlig and Gardner [59] found stomata not commencing to close until leaf water potentials of -5 to -12 bars were obtained depending on species. Kanemasu and Tanner [49] found the critical water potential to be -8 and -11 bars for the adaxial and abaxial surfaces of snap beans. Dale [60] found that the critical %RWC (synonymous with critical water potential) of cotton was 85% RWC or about -12 bars.

No attempt is made to plot a correlation between %RWC and r_s for the observations made here because leaf resistance was not measured on the same leaves as the %RWC was measured. The critical %RWC or water potential can only be inferred from the comparison of the diurnal trends of leaf resistance and %RWC. Based on these trends, once some critical potential is reached, there is a closing mechanism that is initiated and resistances continue to rise even though some improvement in the water status might occur. From the data on the three stress categories the critical %RWC for the corn in this study is about 90% or about -6 bars water potential.

At this point in the discussion two concepts have emerged and are summarized. One, stomata of corn open in accord with the well known response to increasing light intensity in the morning hours. The aperture continues to increase until some maximum aperture is obtained. This maximum aperture (or minimum resistance) is related to the degree of water stress prevailing for any particular day, and that the minimum resistance decreases upon relief of the stress condition. Second, there is little effect of decreasing (more negative) water potential on stomata until some critical water potential is reached. Once this critical potential is reached there is a sharp increase in the resistance value even though there is an improvement in the water balance of the plant. The over-riding influence of the water potential over the light response can occur even under relatively adequate soil moisture conditions. Thus far, little has been said about the possible mechanisms involved in these responses. This study is not designed to investigate in detail the mechanisms of stomatal movement, but to consider some of the relationships under field conditions in light of the documented mechanisms. The general results as summarized above will be used in the development of a simple model that can be used in describing the interaction of light intensity and water potential. The model is developed as a systematic approach for inclusion into larger photosynthesis and transpiration models. A discussion of the possible mechanisms involved will be deferred until after the development and testing of the simple stomatal model.

Stomatal Model Development

Assuming no stress conditions, consider the light intensity -- leaf resistance relationship given in equation (6) as the "ideal" no-stress case:

$$r_s = \gamma_o + \frac{\beta_o}{I} \qquad (6)$$

where γ_o and β_o are considered constants for the ideal case. In order to have r_s remain finite at some very low light intensity ($I \to 0$), a minimum light intensity, I_o, which is very small compared to I is introduced that corresponds to some maximum, finite resistance, r_c. This resistance is taken to be a constant and can be thought of as the cuticular resistance or some maximum resistance when the stomata are closed. Expressing this similarly to equation (6) gives:

$$r_c = \gamma_o + \frac{\beta_o}{I_o} \simeq r_s \ . \qquad (7)$$

With r_c as a constant, I_o can be calculated from (8):

$$I_o = \frac{\beta_o}{r_c - \gamma_o} \ . \qquad (8)$$

From the ideal case in equation (6) the minimum r_s for the day, r_{min}, approaches γ_o at high light intensities. Following the suggestion from experimental measurements, imposing a water stress condition will cause the minimum resistance, r_{min}, to increase. One could think of a family of curves of the general shape as the ideal case, but with changing γ and β as stress increases. A schematic representation of this is given in Figure 16. Then for some stress condition, i.e., %RWC decreasing or ψ becoming more negative,

$$r_c = \gamma + \frac{\beta}{I_o} , \tag{9}$$

$$r_s = \gamma + \frac{\beta}{I + I_o} . \tag{10}$$

Note that I_o is added to I in the denominator of (10) to maintain r_s at some finite value at very low light intensities. Equation (9) can be solved for β:

$$\beta = I_o(r_c - \gamma). \tag{11}$$

Substitution of (11) into (10) and rearranging gives:

$$r_s = \frac{I\ \gamma + I_o\ r_c}{I + I_o} . \tag{12}$$

Equation (12) includes the light intensity influence, and the water stress influence by considering γ = f (water stress). Some quantitative expression of γ as a function of a particular degree of stress is needed.

Recalling that γ is similar to the r_{min} and considering the concept of the critical water potential as discussed earlier, a relationship shown schematically in Figure 17 is deduced. Here γ is some single value for a day, and for low stress levels (high minimum RWC) the γ would be close to γ_o for the ideal case. When the stress level approaches the critical point, γ would increase above that of the ideal case and lead to the family of curves depicted by the model in Figure 16.

The relationship between γ and minimum RWC is deduced by analogy with the concept of a critical water potential on the stomatal behavior for any single day. For a single diurnal trend in RWC, resistance is not influenced until some critical RWC is reached. The model assumes the same type of relationship for some mean stress level for the day, and more simply stated says that the minimum resistance obtained after light intensities reach a certain threshold value in the morning hours is

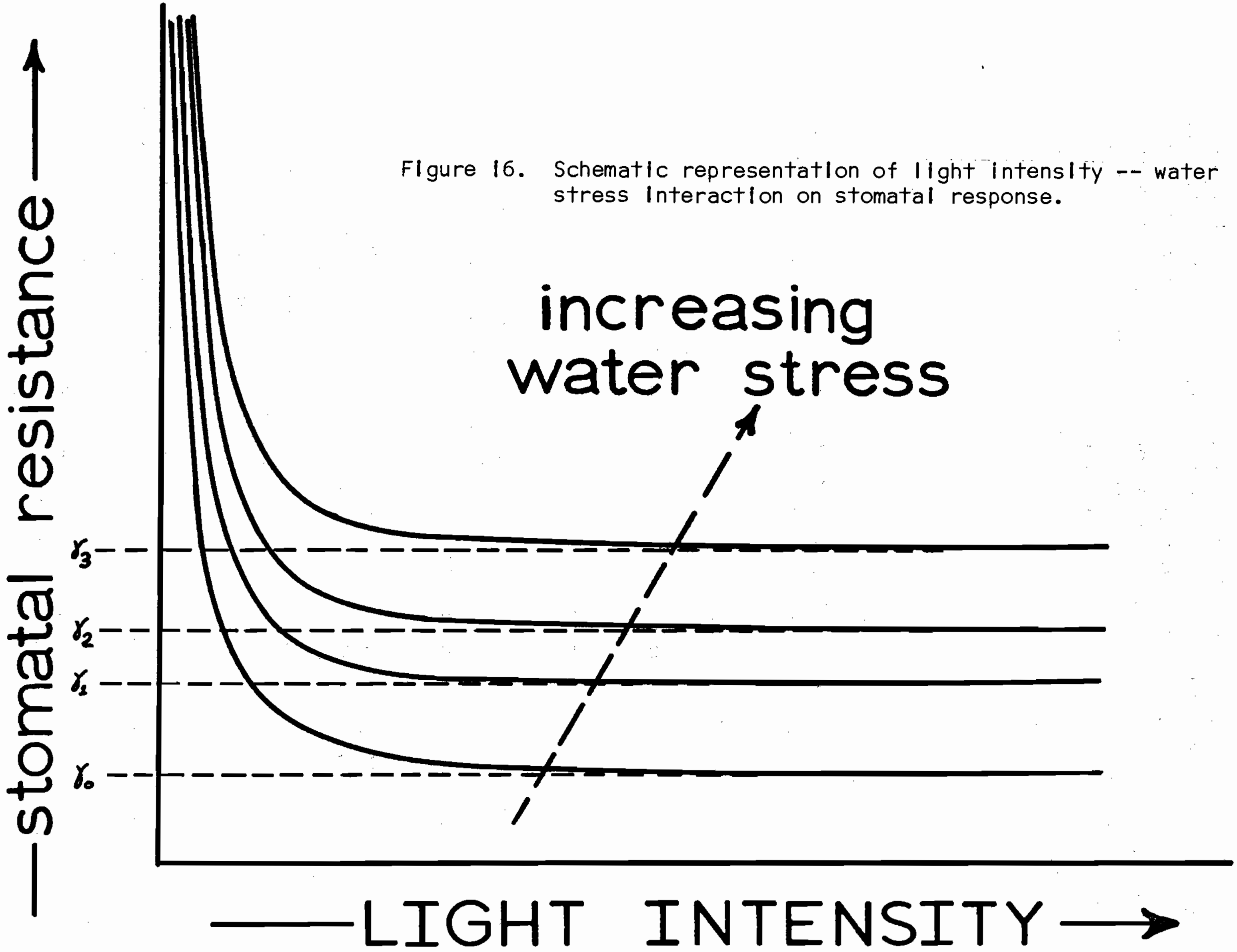


Figure 16. Schematic representation of light intensity -- water stress interaction on stomatal response.

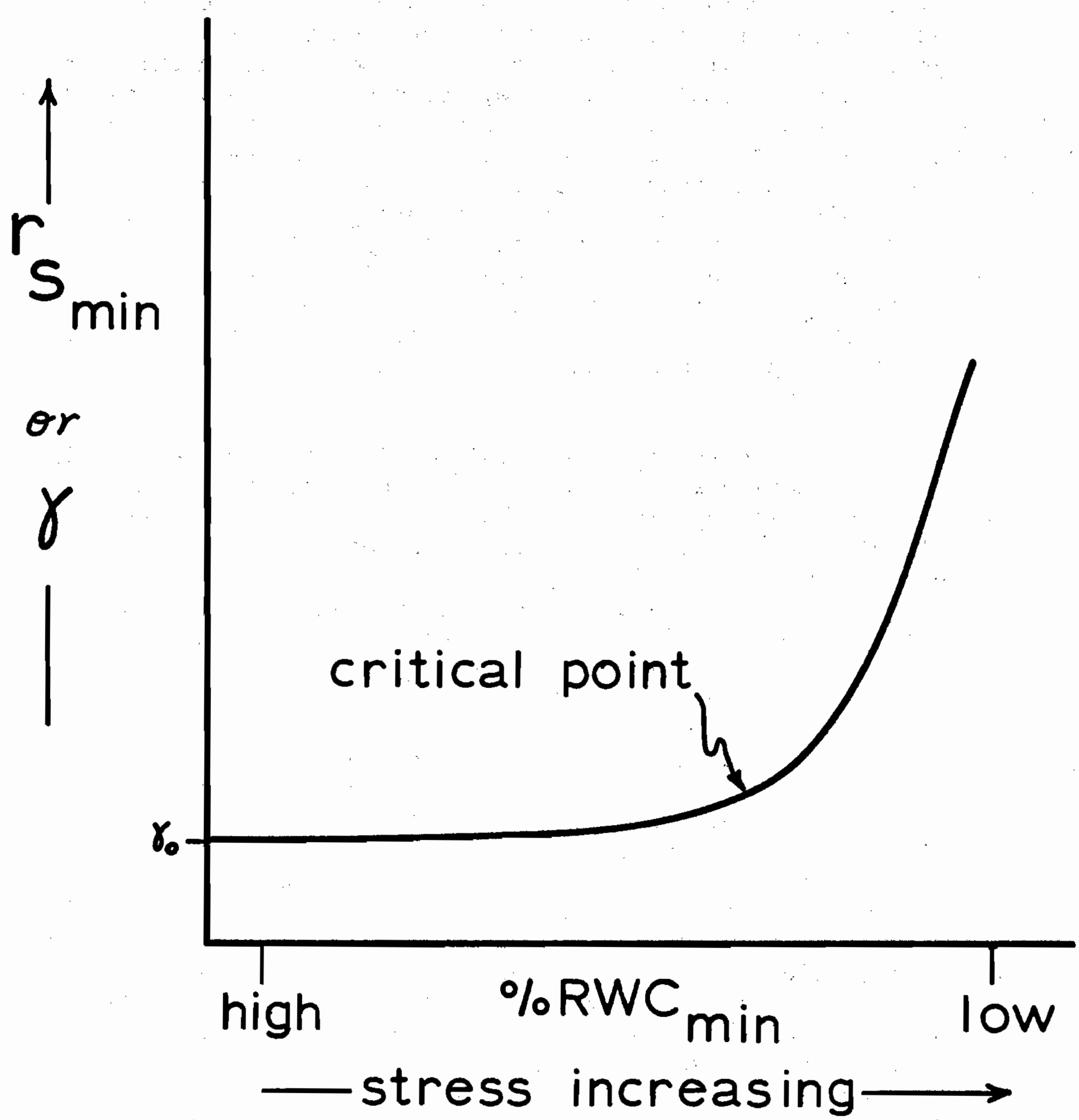


Figure 17. Schematic representation of relationship between minimum stomatal resistance and increasing water stress.

nearly the same as the ideal no-stress case until some critical stress level is reached.

The next step is to evaluate the relationship of γ and stress level. As depicted in Figure 17, the theoretical curve says that as drying or wetting cycles occur γ will change along the same curve. A unique relationship would over simplify the case, but several observations indicate that this would not likely be the case. After-effects of drought on stomatal movement have been shown. Glover [61] observed stomata of maize to close during a drought cycle, and the stomata took several days to return to their normal sensitivity after drought was alleviated. If the drought was severe and extended, the after effects were permanent and stomata became nonfunctional. Slatyer and Bierhuizen [62] found stomata of cotton leaves to remain closed and become nonfunctional after water stress. The combination of after-effects and ageing of the leaves indicates that a single, unique curve depicting the response of γ to changes in stress is unlikely.

To approximate the γ versus min RWC relationship, the γ value and min RWC for all days sampled were estimated from the measured minimum resistances and RWC's through the day. The values for each day are plotted in Figure 18 along with theoretical curve bracketing the estimated values. Considering the errors in estimating the γ and min RWC values, and the complexity of the after-effects and ageing, the curves depict the model as a first approximation. This aspect is probably the weakest point of the model, and a more definitive experiment is needed to evaluate the complexities involved here.

The model is tested by using equation (12) and the γ versus min RWC relationship and calculating r_s values for different light intensities. The value for r_c is assumed at 20 sec/cm. The calculated r_s values, plotted against light intensity, are shown as the solid lines in Figures 19-24 which also include measured values for upper leaves taken from the plots of the measured r_s versus time (Figures 11-13) and light intensity versus time (Figure 15). The calculated resistances are based on a range of γ values, and there is general agreement between calculated and measured values. For any given γ, r_s values should follow the calculated curve both in the morning and in the afternoon. Measured values correspond to calculated values both in morning and afternoon on August 8 and 11 (Figures 19 and 20) with a deviation from the calculated occurring in late afternoon. Notable exceptions are shown on August 15, 18, and 28, which show agreement between calculated and measured during morning hours but a sharp disagreement at some point. The deviation of measured from calculated is related to the degree of stress. On August 15 (Figure 21), a high stress day, the deviation occurs before the peak light intensity, while on August 18 (Figure 22) the deviation corresponds to the peak light intensity and on August 28 (Figure 24) the deviation is sometime after the peak light intensity. The stomata

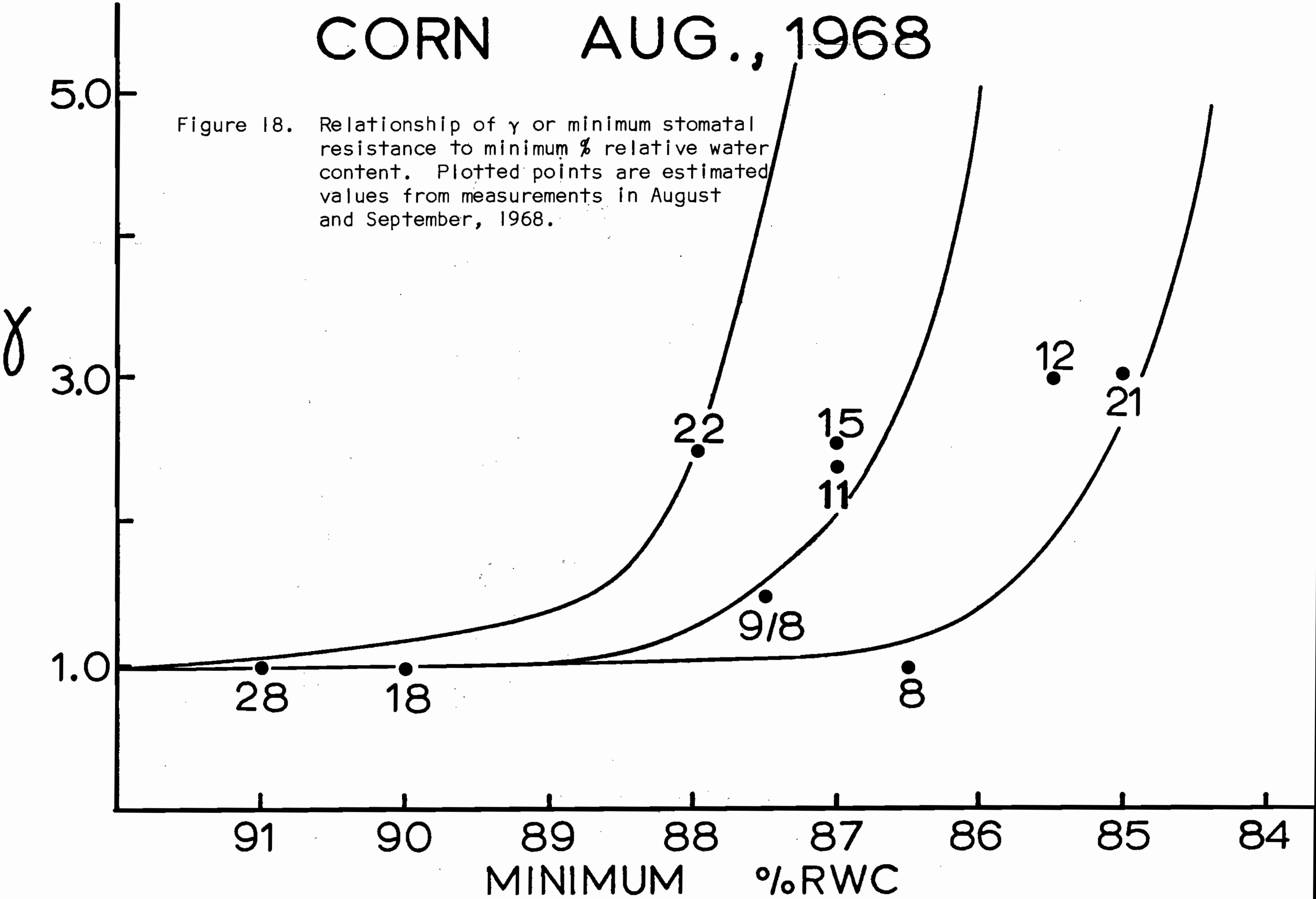


Figure 18. Relationship of γ or minimum stomatal resistance to minimum % relative water content. Plotted points are estimated values from measurements in August and September, 1968.

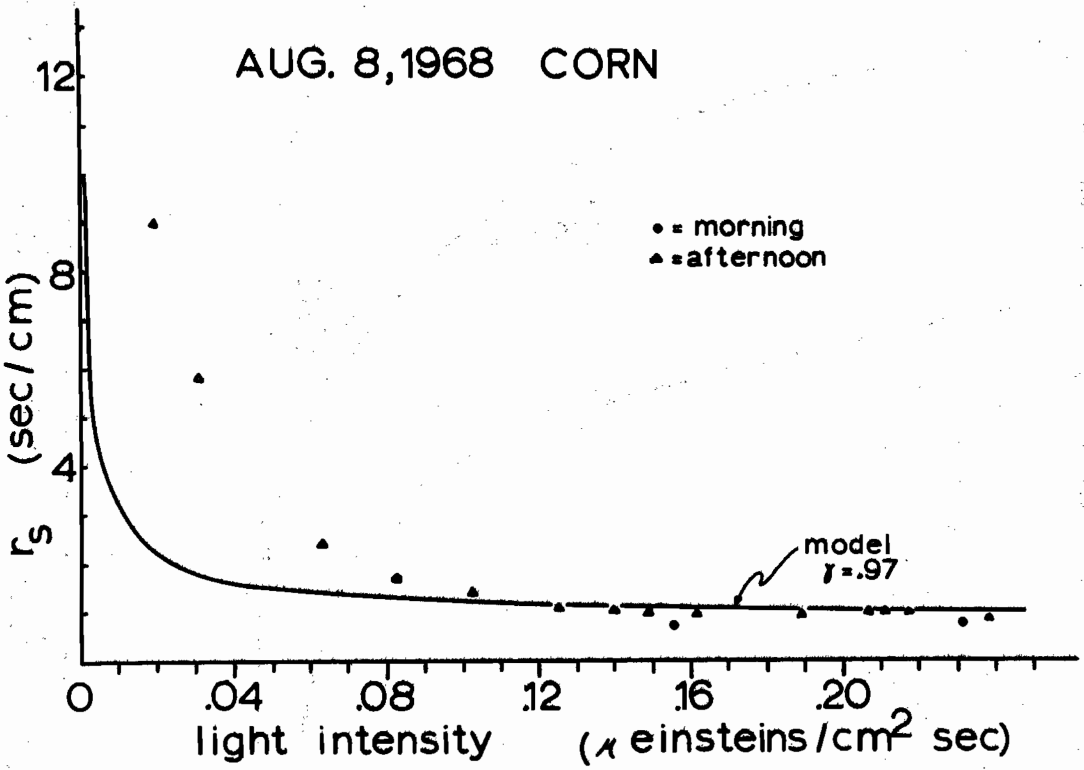


Figure 19. Comparison of stomatal model resistance with measured resistance, August 8, 1968 unthinned crop.

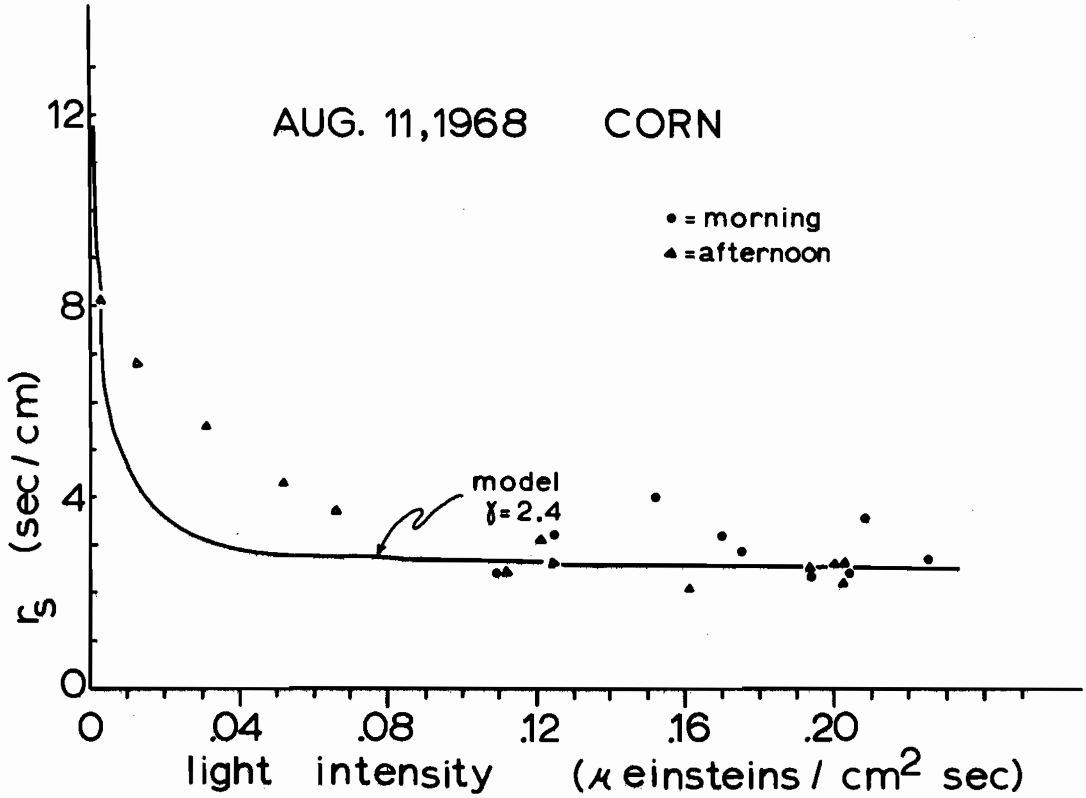


Figure 20. Comparison of stomatal model resistances with measured resistances, August 11, 1968, unthinned crop.

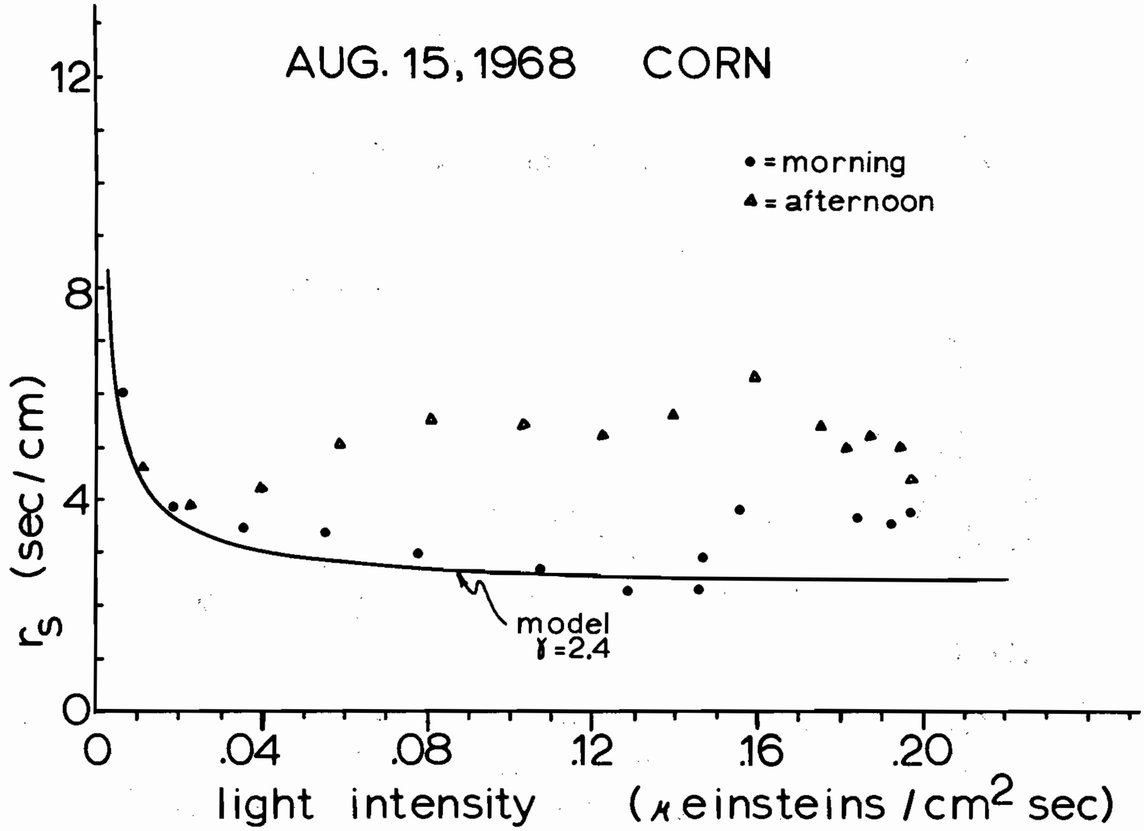


Figure 21. Comparison of stomatal model resistances with measured resistances, August 15, 1968 unthinned crop.

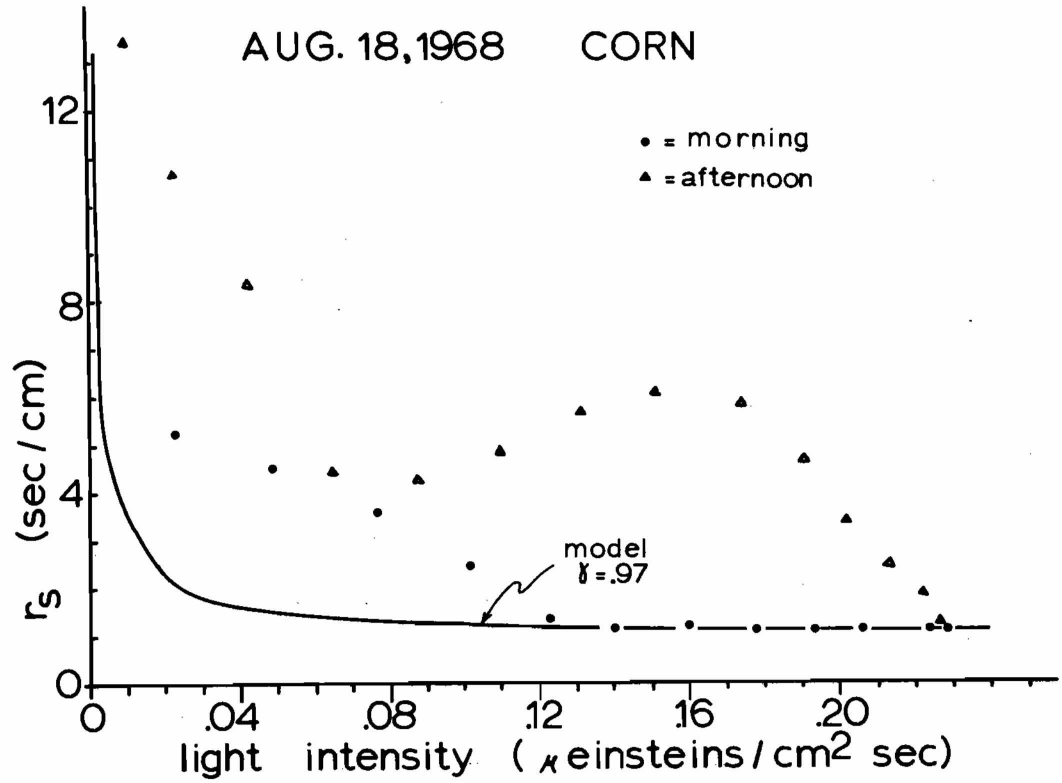


Figure 22. Comparison of stomatal model resistances with measured resistances, August 18, 1968 unthinned crop.

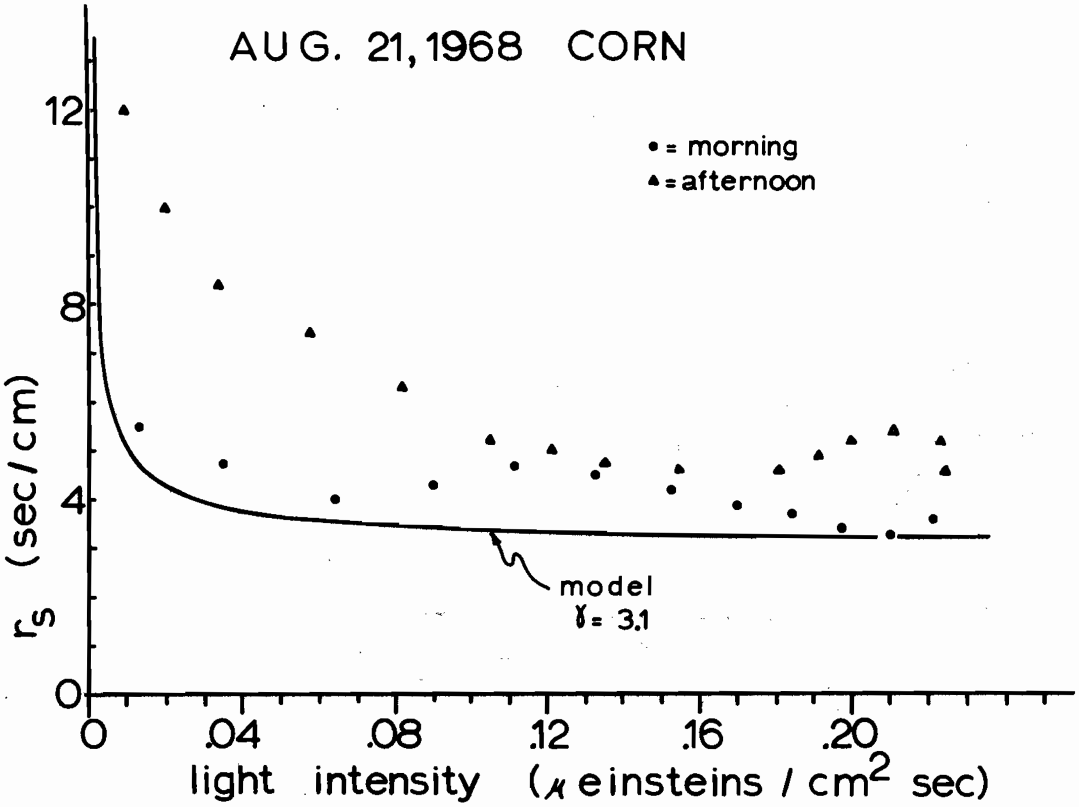


Figure 23. Comparison of stomatal model resistances with measured resistances, August 21, 1968 unthinned crop.

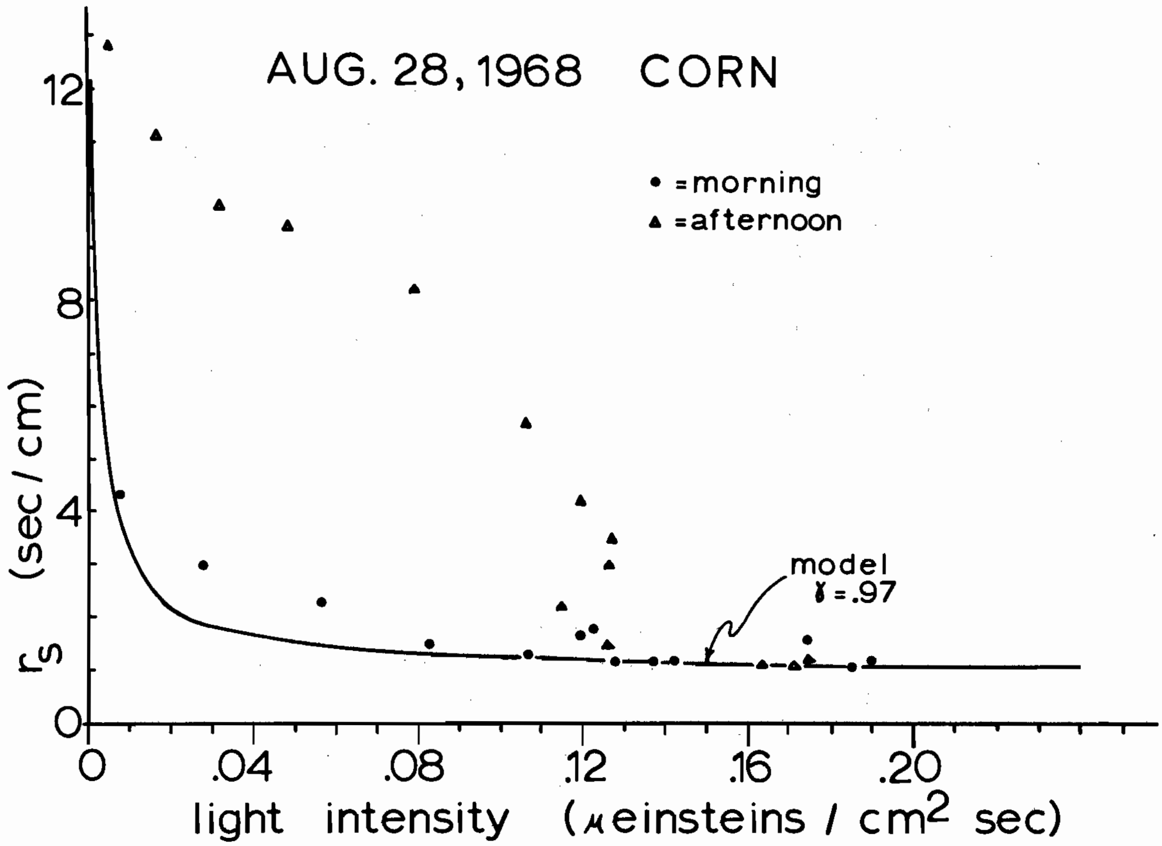


Figure 24. Comparison of stomatal model resistances with measured resistances, August 28, 1968 unthinned crop.

are not exhibiting the same response to light intensity in the afternoon as they did in the morning. This appears to be the case even for days where stress conditions are not likely to occur, i.e., August 28.

A possible mechanism for the change in sensitivity of the stomata and the nature of the after-effects of drought is the response to an increase in the carbondioxide concentration inside of the leaf. Stomata close in response to an increase in internal CO_2 (Meidner and Mansfield [30]). Furthermore there appears to be an increased sensitivity to internal CO_2 after water deficits have developed (Heath and Mansfield [63]; Kuiper [47]; Meidner and Mansfield [29]; Willis and Balasubramaniam [22]). The change in the response of the stomata indicated in the August 15, 18 and 28 data after a reasonably severe stress condition on the 15th agrees with this mechanism. Even at the relatively high RWC values on August 18 and 28, the results of the earlier stress could have made the guard cells more sensitive to increased CO_2. The increase in internal CO_2 could arise from an increase in respiratory CO_2 resulting from increased leaf temperatures or a possible reduction in the photosynthesis due to direct effect of stress on the photosynthetic apparatus.

Summary

The study described here is an attempt to separate the effects of light intensity and water stress on stomatal behavior under field conditions. A simple model has been developed as a means of systematically approaching the problem. The model is based on measurements of leaf resistance and relative water content through the day for a range of different stress conditions. The results of the model indicate that after-effects of stress must be considered and that a more complete model must include the effects of internal CO_2 concentration.

The model appears to hold during the morning hours before critical water potentials are reached. The concept of the minimum resistance for the day as a function of a stress condition is based on the actual measurements, and the model can be used as a means of introducing the effects of water stress, as it may be operative through the stomatal resistance, into larger, more complex models for photosynthesis, latent and sensible heat transfer of plant communities. This will be the subject of the next chapter.

CHAPTER II

TESTING CHANGES IN STOMATAL RESISTANCE USING A PLANT COMMUNITY MODEL

Review of Literature

Mathematical modeling of the plant community is becoming popular as more information about various responses of the plant community is documented. Modeling tries to fit all the available information that can be described mathematically into a system of equations for simulation of processes in the plant community. The inputs of the model should include all possible interactions between the physiological processes of the plant and the microclimate. Obviously all the interactions are not known or at least the laws governing these relationships are not defined to the extent that they can be included in the simulation model. The next step is to begin with simplified assumptions and then increase the sophistication of the model as more information becomes available. As testing of the model indicates that some factors are more or less important, the model will need to be changed accordingly.

Microclimatic models are involved with the calculation of the exchange of energy within and above the plant community and with the calculation of the vertical profiles of humidity, temperature, wind, radiation, and carbon dioxide concentration in the canopy. Models of this type with variations as to emphasis and assumptions have been developed (Philip [64]; Denmead [65]; Cowan [66]; Waggoner and Reifsnyder [67]; Waggoner, Furnival, and Reifsnyder [68]). These models are similar in that they need as inputs 1) the distribution in the canopy of net radiation, leaf area, and diffusivity; 2) temperature, humidity, wind velocity both above and within the canopy; 3) distribution of leaf characteristics, i.e., resistances, H_2O vapor concentration of the leaves in the canopy; and 4) properties determining fluxes at the soil surfaces.

One of the main differences in the models has been in the treatment of the leaf properties. Philip [64] assumed a uniform resistance in the canopy and that stomata are open thus no leaf resistance to evaporation. Brown and Covey [69] evaluated the energy budget and the transfer processes in a corn crop. They defined a leaf wetness parameter which has the physiological interpretation similar to the stomatal aperture. This parameter was shown to take part in the regulation of the transpiration rate. The introduction of this parameter in microclimatic models was an improvement over Philip's model. Waggoner and Reifsnyder [67] included a relationship of stomatal resistance and light intensity. They varied the stomatal resistance in the model which included inputs for a barley crop and found that with a decrease in the minimal stomatal resistance (r_s at high light intensity) from 1 sec/cm to 0.5 sec/cm, evaporation increased from 0.6 - 1.6 mly/sec. When the minimum resistance was increased from 1 to 2 sec/cm, the calculated evaporation for the day, the 50% decrease in minimum stomatal resistance in the model produced a 30% increase in total evaporation. The same percentage decrease in total evaporation was calculated by doubling the resistance. These results were compared to a field experiment described by Montieth, Szeicz, and Waggoner [70] and showed very close agreement. It was concluded that the usefulness of the model was demonstrated by the way a single factor could be varied and the effect on the canopy synthesized.

Cowan [66] similarly uses an energy balance to calculate fluxes but uses a momentum balance approach for determining the ventilation characteristics of the canopy. Heat and vapor transfer are calculated with leaf resistances taken constant with height. There is no difficulty in obtaining solutions for arbitrary distributions of resistances in this model. Cowan deferred extensive testing of stomatal resistance in his model until more understanding of the interactions between leaf turgidity, stomatal resistance, and the energy balance is obtained as well as more knowledge of the diurnal and spatial variation (Cowan and Milthorpe [33]).

Waggoner, et al. [68] used the same basic model described above and applied it to simulate the microclimate of a forest. Changes in stomatal resistance corresponding to measured values were included in the model. Based on the calculated change in evaporation the model appeared to agree with measured values.

The models described above deal only with the exchange of sensible and latent heat and further refinements are needed for any attempt at simulating a plant community. Including photosynthesis and respiration in the model is necessary because these are also energy-utilizing processes and must be considered as part of the energy balance. Lemon [71,72] has discussed the exchange of CO_2 between the atmosphere and the plant canopy and shows how the gain or loss of photochemical energy must be included in the energy balance. A model for testing the effects of stomata should include photosynthesis and respiration.

One approach for building a complete model is to use the microclimate models in conjunction with radiation models. The latter models have traditionally dealt only with the light regime in the canopy, but have recently been developed in a more realistic sense to include direct and diffuse light, leaf angle distributions, light scattering, and solar elevation (DeWit [73]; Duncan, et al. [74]).

A third type of model that is necessary if photosynthesis and respiration are to be included is a model for leaf assimilation and respiration of CO_2 which must include effects of light, temperature, CO_2 concentration, resistances to diffusion through the boundary layer, stomata, and mesophyll. Waggoner [5] describes such a model. He included the relationship of stomatal resistance to concentration of CO_2 in mid-stoma and to light intensity. Changes in the sensitivity of the stomata to changes in irradiance and CO_2 concentration appeared to have minor effects on the net photosynthesis. Reasonable changes in the minimum value of the stomatal resistance did seem effective in changing net photosynthesis.

Finally Waggoner [75] summarizes how the photosynthesis-respiration models can be coupled with microclimatic models to act as a crop simulator and predict profiles of temperature, vapor pressure, and CO_2. By manipulating the stomata the model indicated that photosynthesis would be decreased relatively less than evaporation.

Stewart [54] has compiled a model that included characteristics of all the models discussed. The model combines the microclimatic models, the photosynthesis-respiration models of leaves, and uses a radiation model that considers the leaf area density, leaf angle, solar angle, and light scattering in the canopy. The radiation model is an improvement over previous models in that no extinction coefficients had to be assumed for penetration of visible and net radiation. The visible radiation model was extended to include the distribution of near infrared radiation. By also including a treatment of the thermal radiation the net radiation could be calculated. Properties of the soil surface influencing the temperature, water vapor and CO_2 concentrations are also included.

Various portions of the model were tested by direct measurements. Measurements of mean values of visible radiation in the canopy were made using selenium cells. The model agrees reasonably well with the measurements except that penetration at low levels in the canopy was underestimated. The leaf model compared favorably with leaf chamber measurements of net photosynthesis of corn leaves made by Dr. R. B. Musgrave.

Preliminary tests of the complete simulation were made by comparing the calculated air temperature, CO_2, and water vapor profiles to measured profiles and by comparison of the simulated fluxes of CO_2 and sensible and latent heat to the measured values determined from the energy balance technique. The calculated profiles of CO_2 and water vapor agreed quite closely to the measured profiles. The largest difference was between the temperature profiles where the calculated temperature was as much as two degrees lower than the measured.

The model underestimated the sensible heat and overestimated the latent heat exchange for the three test periods (August 15, 1200 hours; August 18, 0900 hours; August 18, 1200 hours). The model did show a good agreement with the measured net photosynthesis with only a small tendency for overestimation of the model.

The model includes the relationship of stomatal resistance to light intensity, and preliminary testing by Stewart indicates that the model is sensitive to changes in stomatal resistance. The theoretical treatment of the soil surface is difficult because of the problem of estimating temperature and vapor pressure at the immediate soil surface. More testing is needed to determine the sensitivity of the model to factors at the soil surfaces. The model calculated values of sensible and latent heat that agreed more closely to the measured values when a more realistic minimum stomatal resistance was included.

Although the model is in the initial stage, the preliminary testing indicates that it is a useful tool in studying the interrelationships of physiological processes and the environment.

The models discussed thus far in this review have seriously neglected any inputs concerned with water stress. In view of the complexity of the models it is not unreasonable that this factor be left out. However, for realistic simulation of the crop environment the importance of water stress must be considered. The simple model developed in Chapter I describes a relationship between water stress and stomatal resistance. The model described by Stewart [54] includes the treatment of the stomatal resistance. The objective of this chapter is to attempt a linkage between the simplified stomatal-water stress model and the larger plant community model.

The precedent for model testing of this nature has been reviewed. However, the model testing to be described has the advantage over previous attempts in that all inputs for the plant community model, the stomatal model, and the measured fluxes were taken over the same crop and at common time periods. A single species was used for the physiological data. In addition, an experiment where the architecture of the plant community was altered provides an opportunity for testing the models to see if they can be used as tools for increasing the understanding of the plant community architecture on exhange processes.

MATERIALS AND METHODS

In Chapter I the light intensity -- resistance relationship was derived from measured resistances and light intensities as shown in equation (10). Stewart [54] included this relationship in the plant community model as a means of estimating the resistance at various levels in the canopy once the light flux density at leaf surfaces of different leaf angles was calculated. It has been shown in Chapter I how the value of γ in equation (10) changes with increasing water stress.

Gamma (γ) is similar to the minimum stomatal resistance at high light flux densities since in the hyperbolic relationship (equation 10) $r_s \to \gamma$

when I becomes large. In Chapter I γ is expressed as a single value for a day with a certain mean stress level. In order to vary the stomatal resistance in the computer program of the model, the concept of γ as a single value for a day must be slightly modified. The model takes various inputs that are mean values for one half hour periods and subsequently calculates profiles and energy flux values for this half hour. The approximate minimum stomatal resistance, γ, for this half hour period must be included as an input for each half hour. In order to vary systematically the stomatal resistance in the model a family of curves similar to Figure 16 was calculated using equation (10) and different values of γ. The appropriate γ value is estimated by first determining the r_s value for a time period from curves shown in Figures 11-13. The light intensity for the same time period is estimated from Figure 15. The value of γ is then determined by choosing the proper curve from the family of curves that passes through the plotted r_s versus light intensity point. For a period later in the afternoon when measured resistances are higher, the same procedure was used. The γ value as an input for any half hour period to be tested sets limits on the minimum resistance value at the highest light intensity for the time period. The vertical distribution of the resistances in the canopy will be determined by the same light intensity -- resistance relationship and will depend on the light attenuation in the canopy. If several half-hour time periods through the day are chosen for testing, the γ value may change according to the measured resistance values. For example, the ideal "no-stress" case discussed in Chapter I would imply that the γ value would be the same for all periods through the day and also be the minimum γ value, i.e., γ_o.

The approach used for testing the model was to select five half-hour periods for a given day; 0800, 1000, 1200, 1400 and 1600 hours. The input data for these periods as outlined by Stewart were obtained from measurements in the field for corresponding time periods. The inputs are summarized briefly here and for complete description of inputs consult Stewart [54]. For any time period tested, values of air temperature, CO_2 and water vapor concentration, and wind velocity at a reference height above the crop are needed as well as net radiation, direct and diffuse visible, and total solar radiation at the top of the crop. The soil surface characteristics that may also vary with time of day are soil heat flux and soil moisture tension at the immediate soil surface. Additional inputs that might be considered constant for a single day but may vary with stage of growth and with plant density are the displacement height, D, roughness length, z_o, and the adjusted crop height. The individual leaf characteristic and the leaf area density, cumulative leaf area index, and the leaf angle distribution are also included.

The days chosen for testing, August 15, August 18, and August 28 are the high, moderate, and low stress days discussed in Chapter I. Both the unthinned and the thinned portions of the experiment are tested. The three days tested for the thinned portion include a range of cumulative LAI's since this spans the three thinning operations. The LAI for the unthinned portion was 3.60 and assumed to be constant for the time period tested. The LAI's for the thinned portion were 2.60, August 15; 1.44, August 18; and 0.80, August 28.

The model generates profiles of various components, but preliminary testing indicated the differences between measured profiles and calculated profiles are small. Comparison of measured profiles between thinned and unthinned as shown in Figure 25 also shows small differences. However, calculation of total fluxes of sensible and latent heat and photochemical energy flux showed larger differences and would appear to be a more sensitive test of the model.

There is a need for an independent check of the model. This may best be obtained by accurate experimental measurements of similar values generated by the model. Included in the field study at the Ellis Hollow site were measurements needed for calculating fluxes of CO_2, sensible and latent heat by the energy balance technique. The energy balance technique has been described by Lemon [71] and examples of flux calculations are shown by Brown and Covey [69] and Begg, et al. [9]. The details of the sampling apparatus and the procedure for measuring profiles are described by Lemon, et al. [76].

In order to use the energy balance technique as a standard for comparison with the model, an estimate of the error in the flux values measured by the energy balance method is needed. Svend E. Jensen (personal communication, 1970, Ithaca, New York) used a modified Bowen ratio-energy balance technique for calculating the total flux components from the crop. The Bowen ratio, $B = k\ \Delta T/\Delta e$, where k is the psychrometric constant and ΔT and Δe are the differences in temperature and absolute humidity over the same height interval, was determined by ploting measured values of T against e and taking the slope of a regression line for points immediately above the crop. The slope of the T--e curve can be used to determine B above the crop since the flux above the crop is constant and T and e are linearly correlated. Once the Bowen ratio is known the total flux components can be calculated using the energy balance relationship and the assumption that the diffusivities of heat, water vapor, and carbon dioxide are equal. The energy flux values are used as a standard for comparison with the model.

The probable error of each flux calculation is estimated by an error analysis described by T. R. Sinclair (personal communication, 1970, Ithaca, New York) that considers the absolute errors in measurements, $\delta(\ )$, of various components of the energy balance. In this analysis the absolute errors were taken as follows: $\delta T = 0.02$ °C, $\delta e = 0.05$ gm/m^3, $\delta C = 0.1$ ppm, $\delta Rn = 0.05$ cal/cm^2 min, $\delta G = 0.005$ cal/cm^2 min,

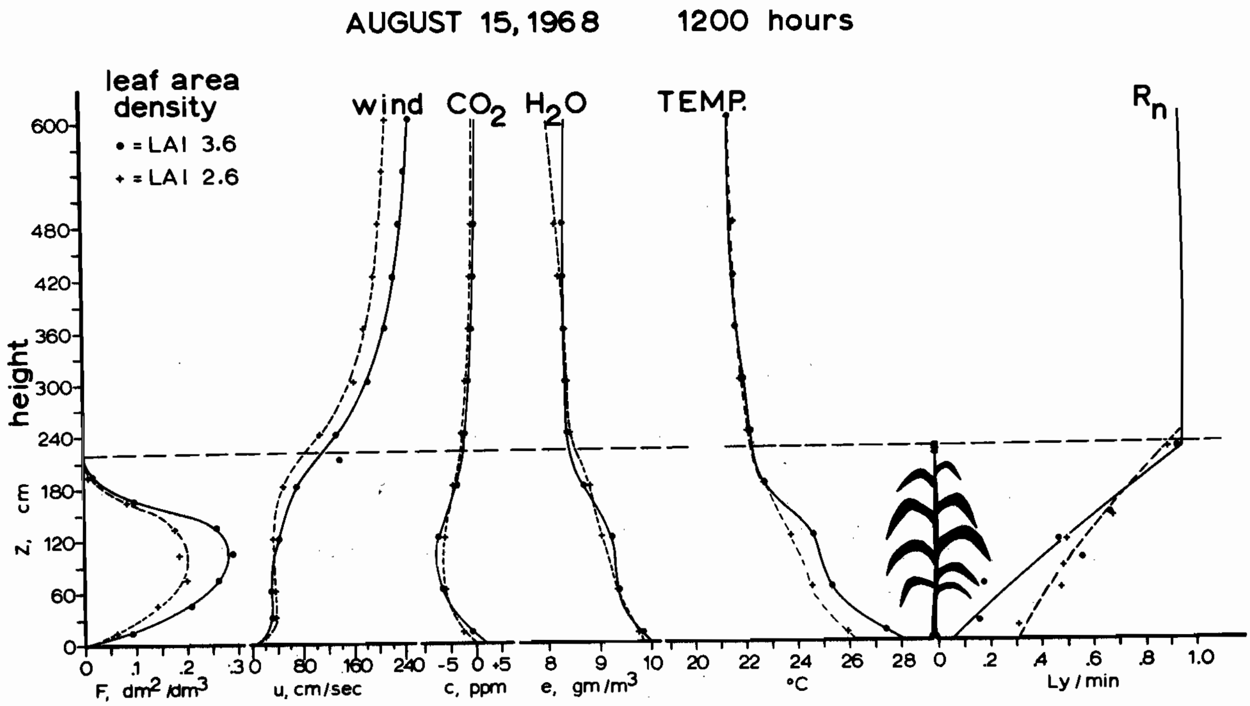


Figure 25. Profiles of crop climatic elements in the thinned and unthinned crop.

where, T, e, C, Rn, and G stand for temperature, water vapor concentration, CO_2 concentration, net radiation, and soil heat flux, respectively. The calculated probable error in the flux value, based on these absolute errors is shown as an error bar in subsequent figures, i.e., LH $\pm$ δLH.

All computing for data reduction and for running the models was done on an IBM 360/65 computer operated by Cornell University.

The inputs to the models, the programming and the field measurements represent the efforts of a team of researchers under the direction of Dr. E. R. Lemon. The author was directly involved in the water relations and stomatal resistance measurements as well as the data reduction and data analysis.

RESULTS AND DISCUSSION

Testing of the model indicated that both the stomatal resistance and the soil moisture tension have significant effects on the calculated flux values. In order to show how the model behaves with each variable, the results will be discussed on the following order: 1) the effect of changing the minimum stomatal resistance and assuming the same minimum resistance at each hour at a constant surface soil moisture tension; 2) the effects of changing soil moisture tension at the immediate soil surface; 3) comparison of measured fluxes with calculated fluxes for the unthinned crop using measured resistance values; and 4) effect of changing crop architecture by comparing flux values from the thinned portion of the experiment.

A summary of the input data (field measurement) for the five hours tested in the model for August 15, 18, and 28, 1968, and for both the unthinned and thinned portions of the experiment is given in Tables II thru IX. The above-crop radiation values are nearly the same for each day with the exception of August 28. Some intermittent clouds on the 28th reduced the radiation levels below the values for August 15 and 18, particularly at 1000 and 1400 hours (see Figure 15, Chapter I). Temperature and water vapor concentration at the reference heights are comparable although the temperature on the 28th is from one to two degrees lower. The wind speed on the 28th is higher than on the 15th and 18th. The inputs for the thinned side on the same days (Tables V thru VII) are similar. The same above-crop radiation values as the unthinned side are used with the exception of the net radiation. Above-crop net radiation measured on the thinned side was slightly lower than the unthinned. Soil heat flux was greater on the thinned portion and slightly greater on the drier days.

Leaf angle distribution was supplied by D. W. Stewart for the thinned and unthinned portions. The cumulative leaf area indices and the leaf

TABLE II

INPUT DATA FOR AUGUST 15, 1968 UNTHINNED

	ABOVE-CROP RADIATION					REFERENCE HEIGHT (600cm)*			
Time	Direct Visible $\frac{\mu Einsteins}{cm^2\ sec}$	Diffuse Visible $\frac{\mu Einsteins}{cm^2\ sec}$	Direct Solar $cal/cm^2 min$	Diffuse Solar $cal/cm^2 min$	Net Radiation $cal/cm^2 min$	Wind Speed cm/sec	Temperature C	H_2O Vapor mb	Soil Heat Flux $cal/cm^2 min$
0800	0.1155	0.0225	0.7018	0.0983	0.49	218.0	15.8	11.52	0.0082
1000	0.1825	0.0253	1.1255	0.1230	0.83	230.7	18.5	10.75	0.0354
1200	0.1979	0.0258	1.2417	0.1303	0.94	252.6	21.1	11.19	0.0388
1400	0.1808	0.0212	1.1119	0.1176	0.79	279.1	22.2	11.37	0.0374
1600	0.1148	0.0183	0.6938	0.0799	0.40	243.7	22.5	10.34	0.0247

*CO_2 constant for all hours at 315 ppm.

TABLE III

INPUT DATA FOR AUGUST 18, 1968 UNTHINNED

	ABOVE-CROP RADIATION					REFERENCE HEIGHT (600cm)*			
	Direct Visible	Diffuse Visible	Direct Solar	Diffuse Solar	Net Radiation	Wind Speed	Tempera-ture	H_2O Vapor	Soil Heat Flux
Time	$\frac{\mu Einsteins}{cm^2\ sec}$	$\frac{\mu Einsteins}{cm^2\ sec}$	$cal/cm^2 min$	$cal/cm^2 min$	$cal/cm^2 min$	cm/sec	C	mb	$cal/cm^2 min$
0800	0.1214	0.0197	0.6634	0.0839	0.41	227.2	15.4	11.93	-0.0030
1000	0.1980	0.0223	1.0900	0.0991	0.79	278.0	17.4	11.88	0.0091
1200	0.2268	0.0211	1.2770	0.0944	0.96	276.5	20.4	11.39	0.0137
1400	0.2020	0.0208	1.1500	0.0872	0.82	275.2	22.4	10.53	0.0150
1600	0.1290	0.0172	0.7400	0.0853	0.45	269.0	22.3	9.69	0.0050

*CO_2 constant for all hours at 315 ppm.

TABLE IV

INPUT DATA FOR AUGUST 28, 1968, UNTHINNED

Time	ABOVE-CROP RADIATION: Direct Visible (µEinsteins/cm² sec)	Diffuse Visible (µEinsteins/cm² sec)	Direct Solar (cal/cm²min)	Diffuse Solar (cal/cm²min)	Net Radiation (cal/cm²min)	REFERENCE HEIGHT (600cm)*: Wind Speed (cm/sec)	Temperature (C)	H_2O Vapor (mb)	Soil Heat Flux (cal/cm²min)
0800	0.1161	0.0099	0.6546	0.0883	0.46	217.6	14.11	12.60	0.0104
1000	0.1206	0.0192	0.6658	0.3339	0.47	298.4	17.8	11.89	0.0217
1200	0.1787	0.0207	0.9958	0.3695	0.74	347.9	19.4	10.53	0.0245
1400	0.1135	0.0174	0.6197	0.2688	0.39	355.1	19.5	10.48	0.0077
1600	0.1151	0.0101	0.6325	0.0988	0.35	332.0	19.8	9.18	0.0067

*CO_2 constant for all hours at 315 ppm.

TABLE V

INPUT DATA FOR AUGUST 15, 1968 THINNED

	Above Crop Radiation*	Reference Height (600cm)**			
Time	Net Radiation cal/cm^2min	Wind Speed cm/sec	Temperature C	H_2O Vapor mb	Soil Heat Flux cal/cm^2min
0800	0.43	197.5	15.8	11.49	0.0148
1000	0.78	240.2	18.0	10.60	0.0326
1200	0.87	215.5	19.4	11.00	0.0475
1400	0.75	266.6	19.5	11.28	0.0421
1600	0.38	233.4	19.4	10.33	0.0311

*Visible and solar radiation above crop same as unthinned
**CO_2 constant for all hours at 315 ppm.

TABLE VI

INPUT DATA FOR AUGUST 18, 1968 THINNED

	Above Crop Radiation*	Reference Height (600cm)**			
Time	Net Radiation cal/cm^2min	Wind Speed cm/sec	Temperature C	H_2O Vapor mb	Soil Heat Flux cal/cm^2min
0800	0.42	216.1	15.4	9.20	0.0034
1000	0.78	282.2	17.4	11.57	0.0380
1200	0.92	291.3	20.4	10.86	0.0419
1400	0.79	277.3	22.4	10.22	0.0211
1600	0.41	256.8	22.0	9.52	0.0029

*Visible and solar radiation above crop same as unthinned.
**CO_2 constant for all hours at 315 ppm.

TABLE VII

INPUT DATA FOR AUGUST 28, 1968 THINNED

	Above Crop Radiation*	Reference Height (600cm)**			
Time	Net Radiation $cal/cm^2 min$	Wind Speed cm/sec	Temperature C	H_2O Vapor mb	Soil Heat Flux $cal/cm^2 min$
0800	0.42	210.7	14.1	12.53	0.0241
1000	0.46	302.3	17.8	11.69	0.0379
1200	0.73	367.3	19.4	10.27	0.0545
1400	0.40	322.0	19.7	10.19	0.0077
1600	0.34	274.0	18.6	9.18	0.0025

*Visible and solar radiation above crop same as unthinned.
**CO_2 constant for all hours at 315 ppm.

TABLE VIII

MEASURED RESISTANCES THROUGH THE DAY

Time	Mean Resistance - Upper Leaves (sec/cm) Unthinned	Thinned
August 15, 1968		
0600	3.9	4.0*
0700	3.4	3.8
0800	2.6	2.4
0900	2.3	3.0
1000	3.7	3.2
1100	3.4	3.4
1200	5.4	3.2
1300	4.6	3.7
1400	5.3	4.3
1500	8.2	6.1
1600	6.1	5.3
1700	6.5	6.4
August 18, 1968		
0530	6.1	7.8
0600	5.4	6.0
0700	3.7	3.5
0800	1.4	2.0
0900	1.1	1.4
1000	1.0	0.8
1100	1.1	0.7
1200	1.1	1.3
1300	1.9	1.6
1400	3.4	2.6
1500	5.9	4.4
1600	5.7	5.9
1700	4.0	5.9
August 28, 1968		
0600	5.0	4.1
0700	3.7	2.4
0800	2.5	2.0
0900	1.3	1.8
1000	1.1	1.5
1100	1.0	0.8
1200	0.8	0.8
1300	0.9	0.7
1400	1.5	0.7
1500	3.1	2.0
1600	4.4	2.3
1700	8.0	4.0

*Values for August 15, 1968 estimated from spot checks and from values on unthinned side.

TABLE IX

AVERAGE SOIL MOISTURE TENSION* (BARS)

	Unthinned	Thinned
August 15, 1968		
12 inches	1.00	1.00
24 inches	0.62	0.66
36 inches	0.45	0.65
August 18, 1968		
12 inches	0.73	0.70
24 inches	0.69	0.76
36 inches	0.58	0.60
August 28, 1968		
12 inches	0.18	0.16
24 inches	0.24	0.20
36 inches	0.47	0.50

*Readings taken each day near 0730 hours EST.

area densities for the unthinned and the three stages of thinning are shown in Figures 26 and 27 (Figure 26 from Stewart [54]).

Variation of Minimum r_s -- Surface SM Constant

Two test periods with data from August 18 using a γ of 0.97 (γ approximates the minimum stomatal resistance) and a surface soil moisture tension of -600 bars were reported by Stewart [54]. This same day was chosen for more testing by varying the γ value as well as using the same γ for each hour. Again the surface soil moisture tension (called SM from here on) was held constant at -600 bars. The reasons for choosing this value will be discussed in the next section. Two different γ's were used, γ = 0.97 and 5.2. The γ of 0.97 corresponds to the ideal "no-stress" case discussed in Chapter I.

The γ value of 0.97, taken at each hour through the day, simulates a condition where stomata are open throughout the day. The calculated flux values are compared to energy balance values in Figure 28. With this condition the latent heat flux calculated by the model was much larger than the energy balance value, and the sensible heat flux was much less. The photochemical energy flux as determined by the energy balance method shows an increase in the morning hours, but declines sharply in the afternoon. The model, with γ = 0.97, calculates photosynthesis values that were close to the energy balance values in the morning, but overestimated photosynthesis in the afternoon. When γ was increased to 5.2 sec/cm the latent and sensible heat flux values calculated by the model agreed more closely with the energy balance method. However, the calculated photosynthesis with γ = 5.2 was considerably below the energy balance value except at points late in the afternoon.

Although this increase in the minimum stomatal resistance produced more comparable estimates of LH and SH, the reduction in the calculated PH suggests the interaction of some other factor. The calculated values of PH using high stomatal resistances are compared to measured PH values in the afternoon and show a correspondence with an increase in measured stomatal resistance values in the afternoon. The results of this portion of the testing led to the consideration of the influence of the surface soil moisture tension on the calculated flux value.

Variation of Surface Soil Moisture Tension, SM, with a Constant Value of γ

The model treats the soil surface as one of the boundaries in the soil-plant-atmosphere model. The approach used by Stewart [54] follows that of Owen and Thompson [77] and Chamberlain [78] for the mass and heat exchange between the soil surface and air stream immediately above the surface. For this treatment, values of the soil heat flux and the sur-

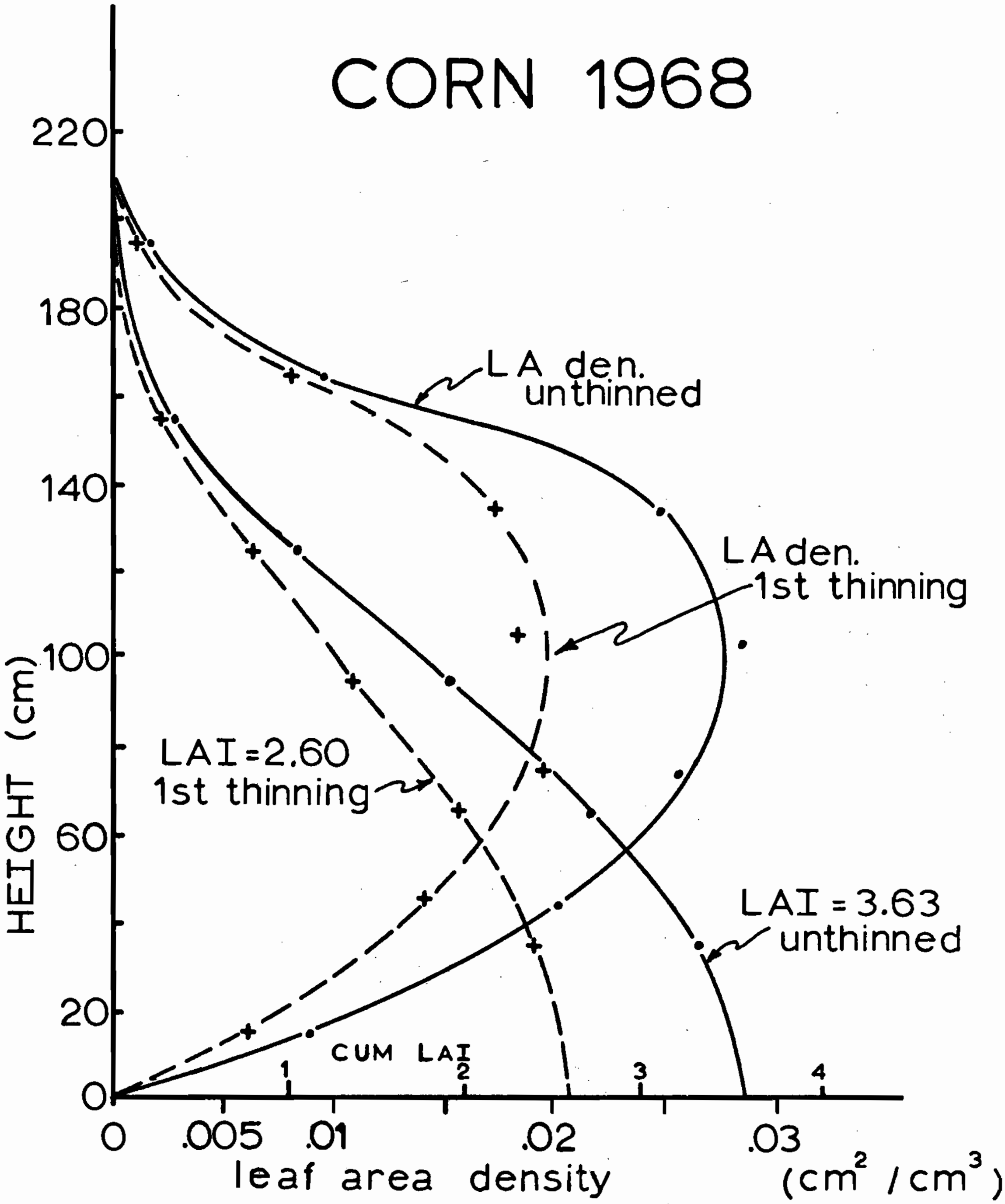


Figure 26. Leaf area density and cumulative leaf area index for unthinned and first thinning, August 15, 1968 (from Stewart [54]).

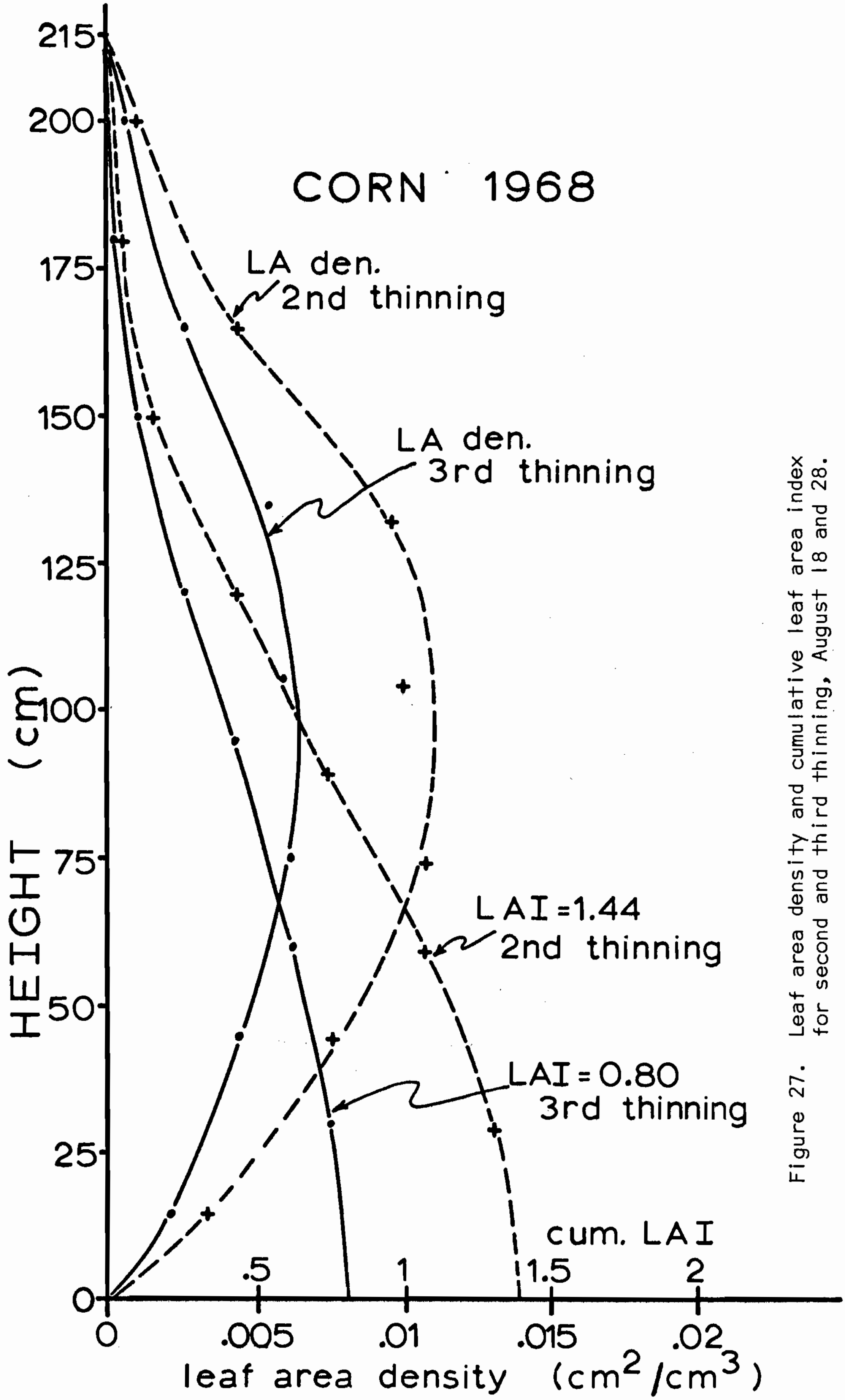


Figure 27. Leaf area density and cumulative leaf area index for second and third thinning, August 18 and 28.

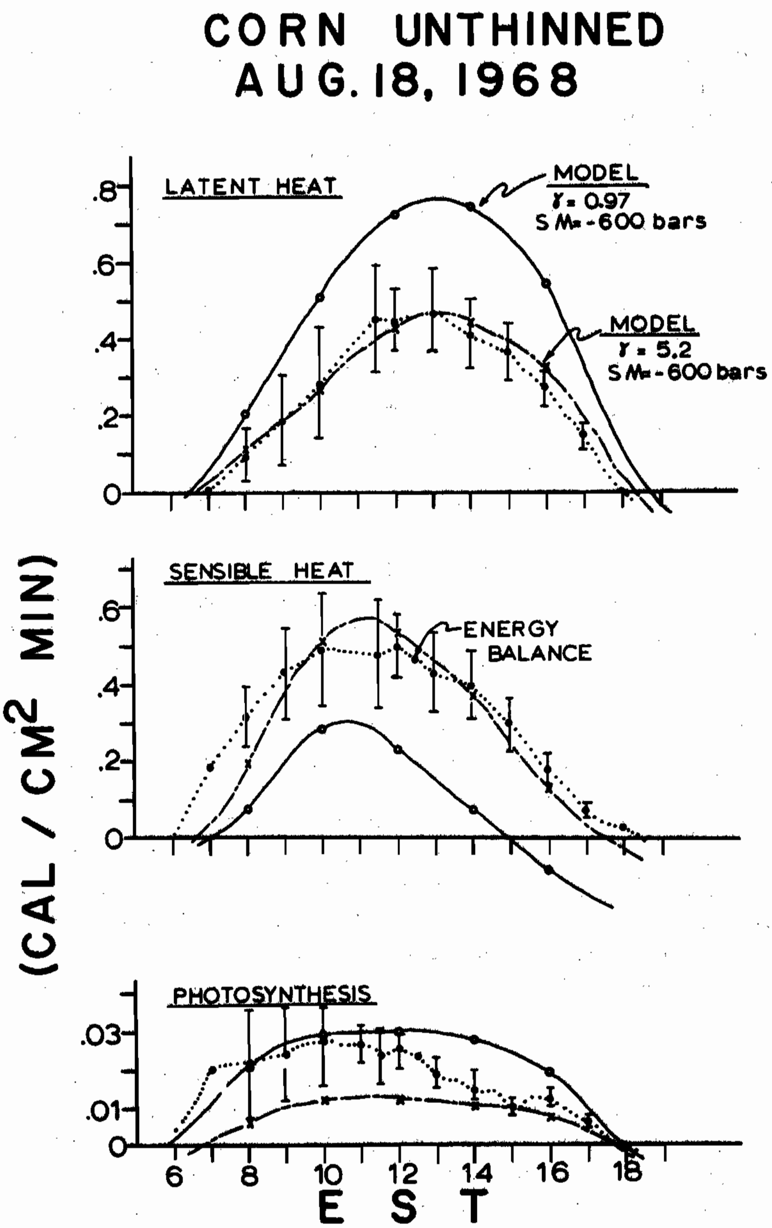


Figure 28. Latent heat flux, sensible heat flux, and photosynthesis determined by energy balance method and calculated by model ~~with values of γ taken the same~~ at each hour and with a constant surface soil moisture tension = -600 bars.

face soil moisture tension are needed. From the surface soil moisture tension the model calculates the vapor pressure and the soil surface temperature and subsequently the fluxes of latent and sensible heat from the soil surface. A problem arises in the exact estimation of SM from measurements of tension at some depth below the soil surface. The difficulty in predicting a mean or effective surface soil water tension is apparent if the relationship between soil water tension and percent soil water is examined. For the soil in Ellis Hollow, the soil water characteristic curves show that the soil water potential changes from near -50 bars at 6% water by volume to less than -10,000 bars at 3.5%. The soil at the immediate surface was in the percentage range where the soil water tension changes drastically with a small change in the water content. The large soil water tensions used as inputs in the model should not be confused with the effective soil water tension in the root zone which will be in the range for plant growth.

In the preliminary testing by Stewart, an SM value was assumed that gave approximately equal values of sensible and latent heat flux from the soil. This led to an underestimation of the soil surface temperature and large differences between measured and calculated flux values.

Two surface soil moisture tensions were assumed as inputs to the model: -600 bars as the "wet" surface and -8000 bars as the "dry" surface. The -600 bar tension results in a vapor pressure of 20.5 mb at 25°C and 63.7 mb at 45°C. The -8000 bar tension corresponds to an extremely dry surface with vapor pressure values of 0.1 and 0.4 at the corresponding surface temperatures. The surface soil in the experimental field contains over 50% by volume of large, flat stones. Although the -8000 bar tension leads to low vapor pressure values, it is not unrealistic when the high percentage of the surface consisting of dry, flat stones is considered.

The results of changing the surface soil moisture tension are shown in Figure 29 where two soil moisture tensions were used, each with γ = 0.97 held constant through the day. The calculated flux values with SM = -8000 bars were in closer agreement with the energy balance than with SM = -600 bars. There was still an overestimation of latent heat flux and photosynthesis and an underestimation of sensible heat flux by the model as compared to the values determined by the energy balance method in the afternoon hours.

The effect of varying both γ and SM in the model is summarized in Figure 30. Sensible, latent, and photochemical energy flux values are shown in relation to surface soil moisture tension with three values of γ for the 1200 hour period on August 18. The corresponding energy balance value with its probable error is also shown. Changing the surface soil moisture tension has considerable influence on the sensible and latent heat calculated by the model, but has little influence on the calculated

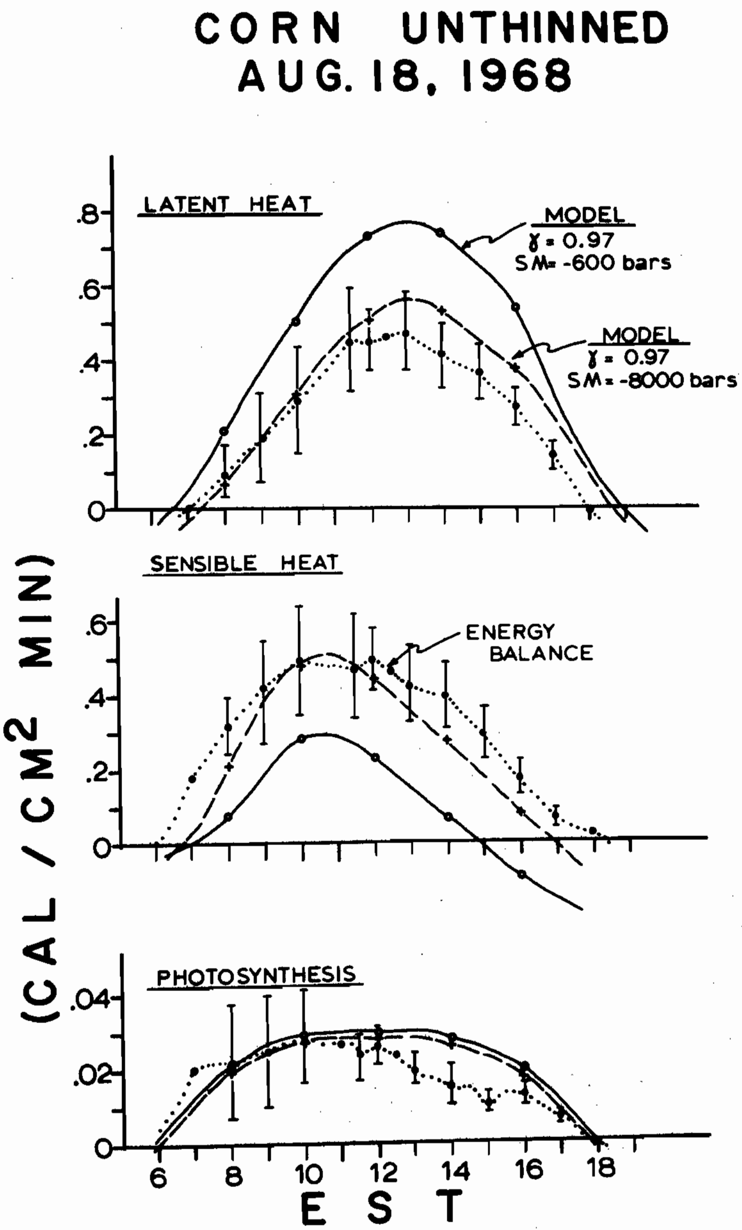


Figure 29. Latent heat flux, sensible heat flux, and photosynthesis determined by energy balance method and calculated by model with one value of γ and two surface SM values.

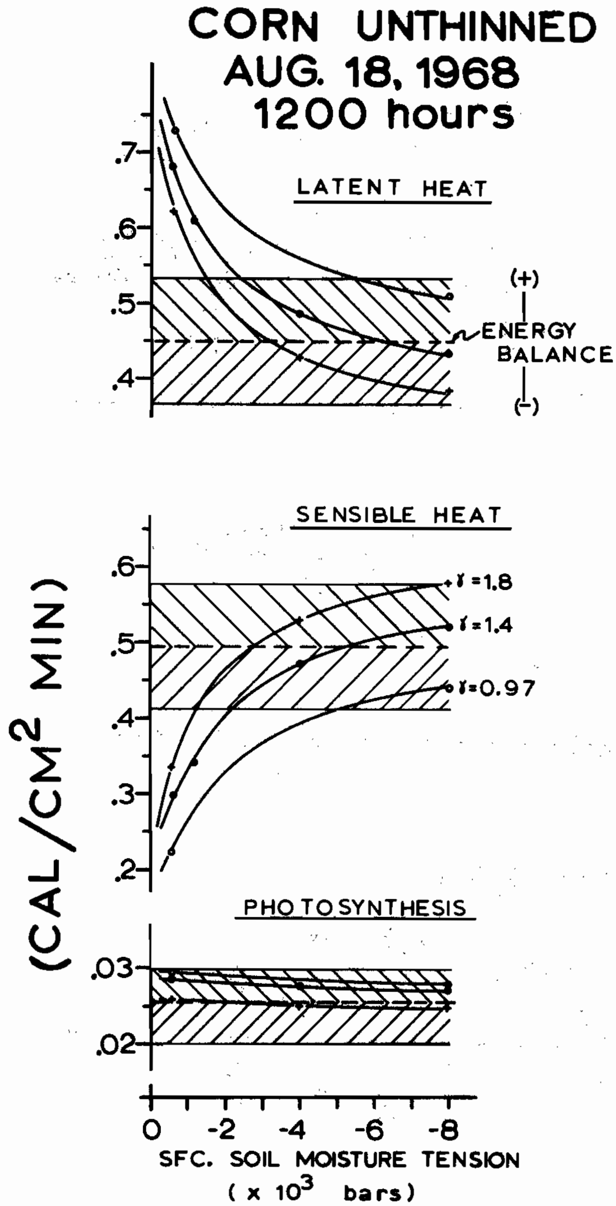


Figure 30. Summary of calculated flux values with changing surface soil moisture tension.

photosynthesis. The calculated flux values approach the energy balance value when low (more negative) SM values are used as inputs although they do fall within the probable error at SM values closer to zero bars.

Obviously there is some combination of stomatal resistance and surface soil water tension that predicts values close to the energy balance values. There is no point in adjusting the two input parameters unless there is some criterion for evaluating their change during the day. Surface soil water tensions were the most difficult to evaluate, and the values used as input parameters were assumed values and were held constant through the day. However, the changes in stomatal resistance have been evaluated and form a basis for further testing.

Model Test with Measured Stomatal Resistance -- Unthinned Crop Stand

In this model test, γ values arrived at from measured r_s values are used for three days of decreasing moisture stress in the unthinned crop. SM was assumed constant at -8000 bars. Comparisons of the flux values for three days with decreasing moisture stress are shown in Figures 31, 32, and 33. The flux values measured by the energy balance reflect the prevailing moisture conditions for each day. The sensible heat flux on the high (August 15) and moderate (August 18) stress days is larger than the latent heat flux. Although the plant moisture characteristics and the stomatal resistance values for the two days (Figures 11, 12, and 14) show considerable contrast, the flux values are nearly identical. Reasons for this phenomenon are not clear. There is a strong source of sensible heat in the crop, even with stomata opening on the 18th.

The energy balance measurement of photosynthesis shows a characteristic decline in the afternoon. Measured resistance on August 15 began increasing around 0900 hours, and this corresponds to the decline in photosynthesis. The same correspondence is observed on August 18 at 1200 hours, and on August 28 at 1400 hours.

The August 28 sensible and latent heat values are generally lower than the earlier days. However, the radiation load was somewhat lower due to intermittent clouds. Even though moisture conditions were improved and water was available for evaporation, the sensible heat component was the same order of magnitude as the latent heat flux.

The flux values calculated by the model are also shown in Figures 31, 32, and 33. The γ value used for each test hour for each day was determined from measured stomatal resistances (γ implies r_{min} for upper, exposed leaves). The agreement between the measured (energy balance value) and the calculated values is reasonably close. The calculated PH is in quite close agreement with the measured values and falls within the probable error of the energy balance value on nearly all periods tested. On August 15 the calculated latent heat is below and the cal-

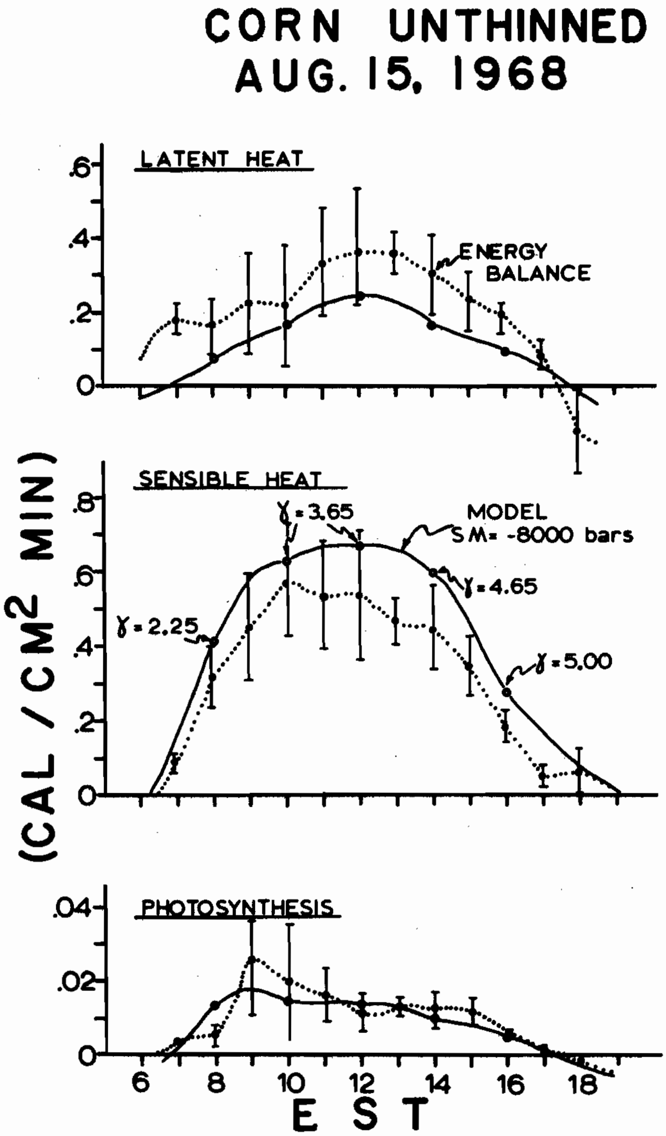


Figure 31. Comparison of calculated flux values, using γ values determined from measured resistances, with energy balance values, August 15 unthinned.

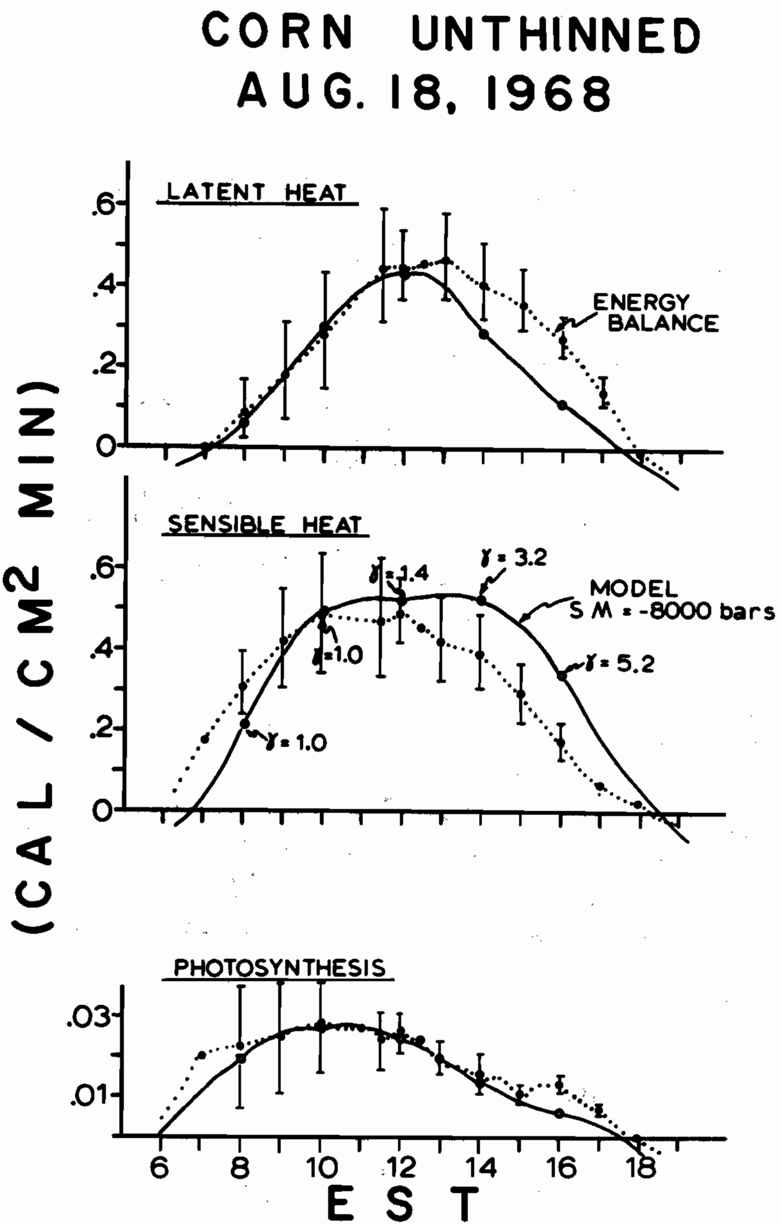


Figure 32. Comparison of calculated flux values, using γ values determined from measured resistances, with energy balance values -- August 18, unthinned.

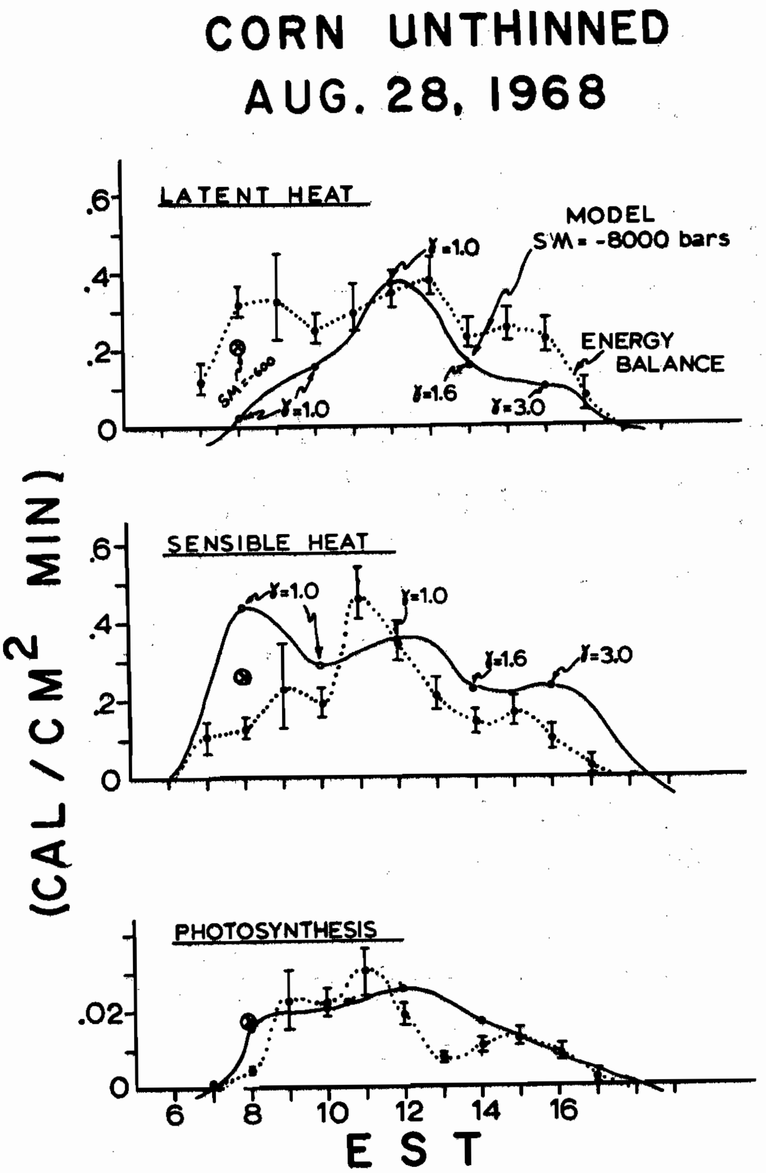


Figure 33. Comparison of calculated flux values, using γ values determined from measured resistances, with energy balance flux values -- August 28, unthinned.

culated sensible heat is above the measured flux value. This is also the case during the afternoon hours of August 18.

The use of the measured stomatal resistance values as inputs, in general, led to closer agreement between calculated and measured flux values and is more realistic than holding the stomatal resistance constant throughout the day. This is particularly true where water stress is likely. The difference between the calculated and measured flux values when measured resistances were used can be attributed to two things; 1) the resistance values near midday and afternoon were higher than the actual stomatal resistances, or 2) holding SM constant over the entire day was unrealistic. The SM value used in the test is a more likely reason for the discrepancy since it was an "assumed" value. The SM value would also change during the day as the surface (soil and stones) dried. Further evidence of this possibility is shown in Figure 33, August 28. This was a day falling shortly after substantial rains, and the SM early in the day would be nearer the zero bar potential. The flux values calculated at 0800 hours are considerably different than the measured. An additional point is shown for 0800 hours where an SM of -600 bars was used in the calculation. Although flux values are still low (LH) and high (SH) when compared to the measured values, they are closer to the energy balance values. This illustrates a need for a more accurate estimate of SM and its diurnal fluctuation.

A significant feature of these results is the apparent strong source of sensible heat. Sensible heat flux of this magnitude appears to be high for this humid area. A high SH would be expected during severe stress periods. However, the strong source of sensible heat is still apparent on the wetter day, August 28. Brown and Covey [69] report LH and SH that were 59 and 32 percent of the net radiation for the day with midday values of LH and SH from the crop 0.59 and 0.38 cal/cm^2 min, respectively. These values were determined Sept. 12, 1962 in the same field and are comparable to the values for August 15, 18, and 28, 1968.

<u>Model Test with Measured Stomatal Resistance -- Thinned Crop Stand</u>

The thinning experiment provides an opportunity to test the influence of the crop architecture. The three test days correspond to three different thinnings. The calculated fluxes and the energy balance measurements are shown in Figures 34, 35, and 36. The stomatal resistance measurements on the thinned portion showed the same trends as on the unthinned, although the lower leaves in the thinned crop generally showed lower resistances in response to increased light intensities deeper in the canopy. Surface soil moisture tensions were estimated on the basis of previous model testing. Since more testing of SM was made on August 18 on the unthinned crop, initial "bracketing" of SM was first tried on the August 18 crop. Then single "guessed" values were made for August 15 and August 28.

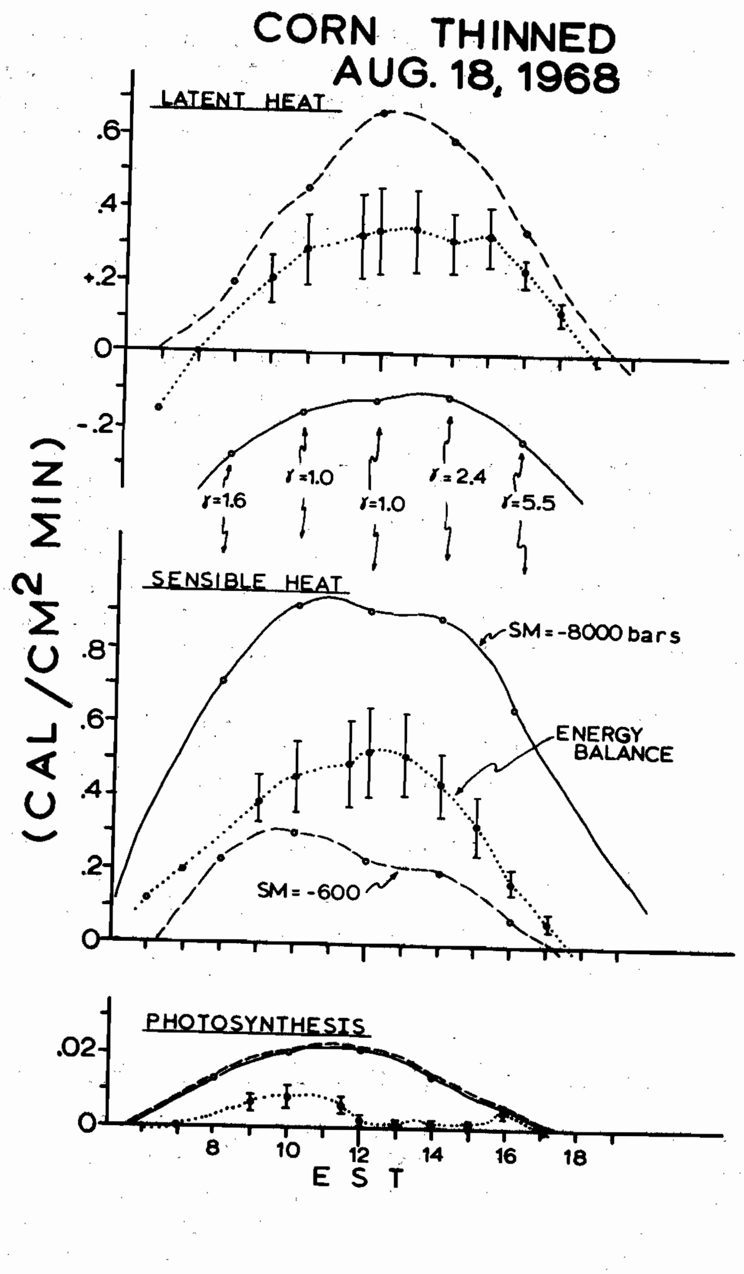


Figure 34. Comparison of calculated fluxes with energy balance fluxes using γ values determined from measured resistances -- August 18, thinned crop; SM = -600 and -8000 bars.

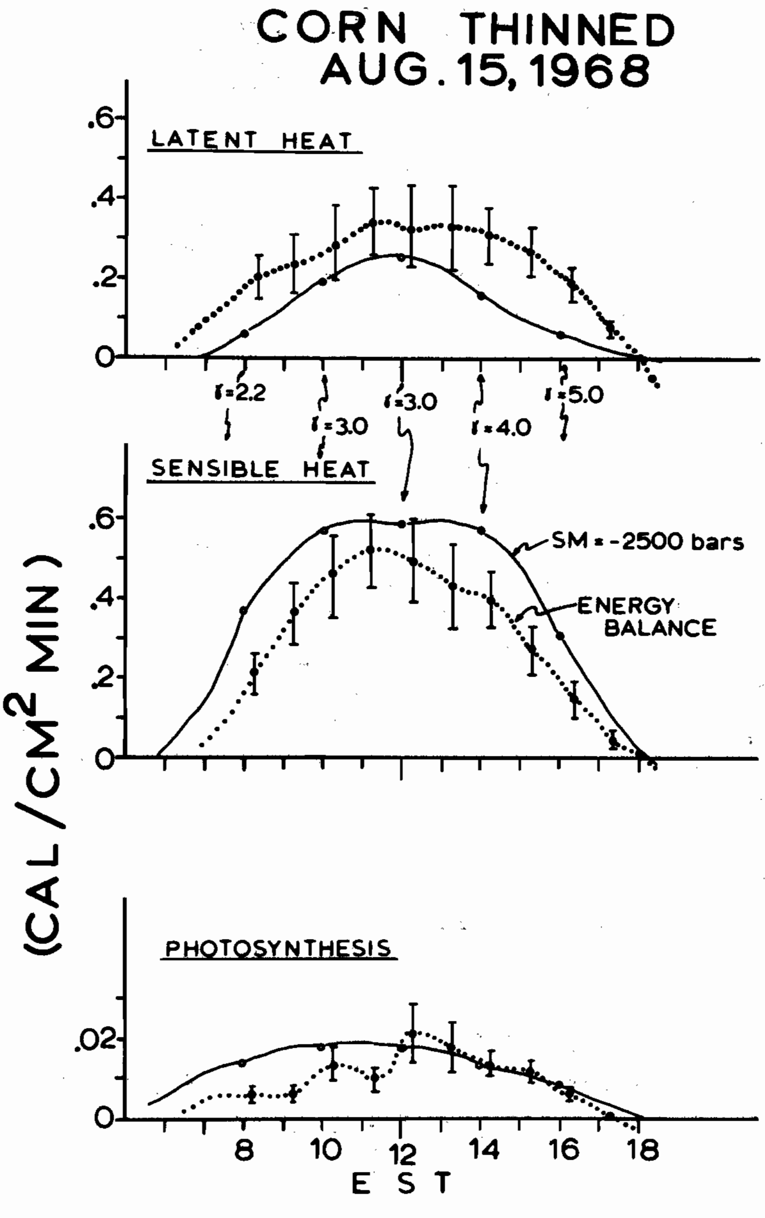


Figure 35. Comparison of calculated fluxes with energy balance fluxes using ɣ values determined from measured resistances -- August 15, thinned crop; SM = -2500 bars.

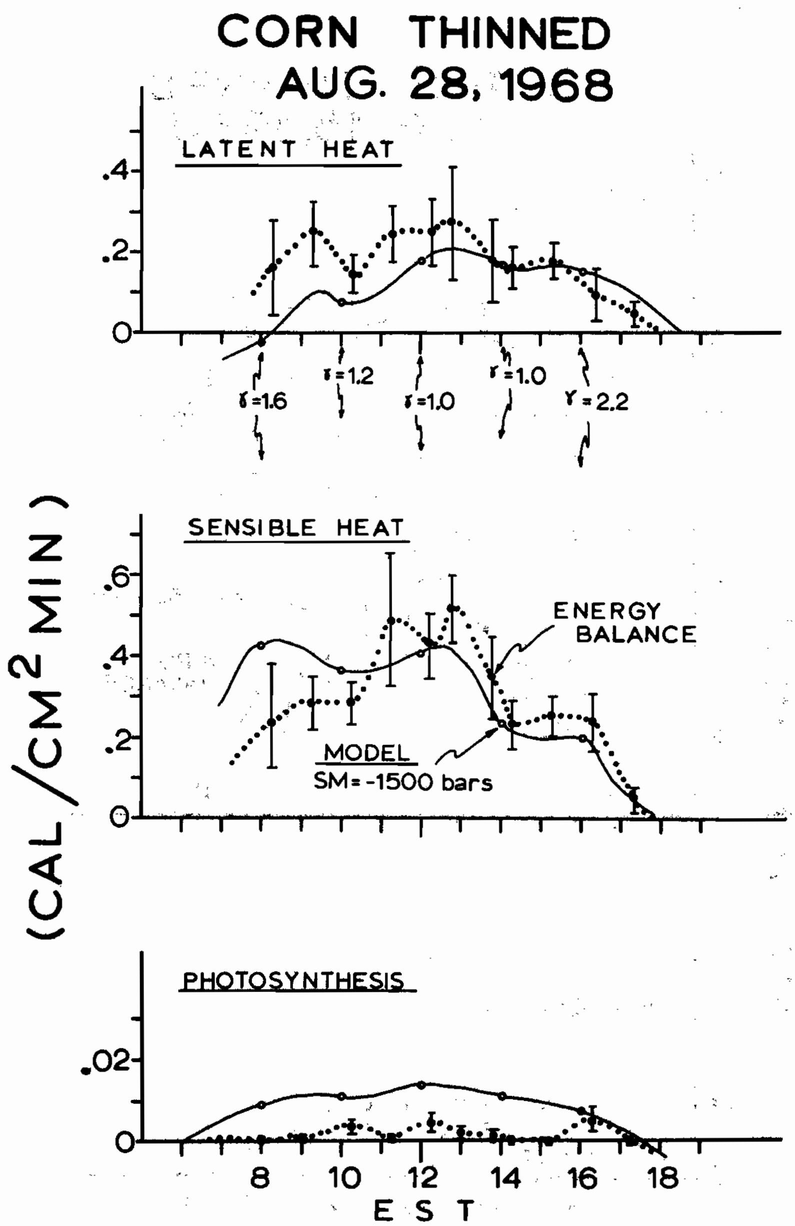


Figure 36. Comparison of calculated fluxes with energy balance fluxes using γ values determined from measured resistances -- August 28, thinned crop; SM = -1500 bars.

The energy balance values are of the same order of magnitude as the unthinned. The large source of sensible heat is still apparent. Relative water content of leaves for each day was similar to the unthinned. RWC's on August 28, remained above 91% and fell below 90% on August 15 and 18. The August 18 RWC's for the thinned were slightly lower than for the unthinned.

The energy balance measurements show notable reductions in photosynthesis with decreasing LAI. This would normally be expected with a decrease in the amount of leaf area for assimilation. Puckridge [79] reported similar results where defoliation of a wheat crop reduced the photosynthesis of the plant community by 25-28% and still further defoliation produced an additional 24-30% reduction. Extremely high values of sensible heat and negative latent heat fluxes were obtained with SM = -8000 bars on August 18. A subsequent test using -600 bars and the same resistances was made, and these values now overestimate LH and underestimate sensible heat. Adjusting SM between this range would give values close to the energy balance, e.g., see Figure 30.

Photosynthesis was overestimated by the model regardless of the SM used. Either the measured stomatal resistances used in this test were too high or the radiation sub-model is predicting greater light absorbtion by the crop than actually occurs due to the increase in nonrandom gaps in the canopy structure.

Testing the thinned portion on the other days is shown in Figures 35 and 36. Intermediate SM values were guessed at, and measured stomatal resistances were used as inputs. Closer agreement between calculated and measured was obtained using a "wetter" surface soil for the thinned planting, which is in contrast to the unthinned side where closer agreement was obtained using a "drier" surface. There would be a higher radiation load at the soil surface on the thinned side which would lead to increased soil temperatures. While the actual soil moisture tension might decrease (more negative), the increase in soil temperature raises the effective vapor pressure. The increase in the vapor pressure gives the effect of increasing (less negative) SM, thus the thinned side appears to behave as the "wetter" surface.

Summary of Model Testing

Comparison of the model testing between the thinned and unthinned crops particularly on August 18, shows that there is some inconsistency in the calculated versus the measured flux values. For the unthinned crop the model calculates values reasonably close to the energy balance using γ's corresponding to measured stomatal resistances and an SM of -8000 bars. The same procedure was used in testing the thinned portion.

Considering that soil moisture tension measurements and the prevailing moisture conditions on thinned crop and unthinned crop are esentially the same, the same SM was used. However, when the thinned crop data were used in the model, extremely high sensible heat and a negative latent heat flux were calculated. The predicted values were considerably different than the energy balance values. Subsequently an SM of -600 bars was used with the same γ value. In this case the calculated fluxes were now in closer agreement with the energy balance, but the predictions were slightly over compensated in the opposite direction, i.e., sensible heat was now underestimated, latent heat was overestimated. Photosynthesis with both values of SM was the same, but considerably above the energy balance.

This test shows that the surface soil on the thinned side is effectively wetter than the unthinned side even if the soil moisture tension on the two sides is about the same. As implied in the previous section, the radiation load at the surface would have considerable influence on the apparent wetness at the soil surface.

The results of the model testing illustrate one of the most useful aspects of the simulation model, in that it helps to focus attention on variables that are important and that need further investigation. The general agreement between the measured and calculated flux values, when measured stomatal resistances were included, indicates that this is an important crop parameter, and information as to the diurnal change of stomatal resistance in response to various environmental factors needs to be delineated. The simplified sub-model for stomatal response to water deficits is an attempt to delineate this response.

The inconsistencies in the calculated flux values between crop stands as a result of using "guessed" values of surface soil moisture tension emphasize the need for more information as to the change in SM through the day. The contrast between the thinned and unthinned crops also emphasizes the need for more information about the effective wetness of the soil surface in relation to sub-surface water tension, surface temperature, and radiation load at the surface.

The calculated and measured photosynthesis agree quite well when the full, unthinned canopy is tested. The model overestimates photosynthesis of the thinned canopies. In Stewart's preliminary testing of the model he states that approximately 7-10% more radiation penetrates to the soil surface than is predicted by the model and this implies that the model is calculating more light absorbed by the crop than is actually occurring. Stewart also stated that the photosynthesis sub-model tends to overestimate photosynthesis at intermediate light flux densities and this could account for the overestimation of photosynthesis at the lower LAI's.

CONCLUSIONS

Testing of the changes in stomatal resistance in response to changes in leaf water relations, as discussed in Chapter I, shows how the effects of water stress can be included as a sub-model in the larger plant community model. The agreement between the energy balance measurements and the model calculations using the measured resistances strengthens the confidence in the approach.

Comparison of the total flux values for the crop appears to be a good test of the model and illustrates how small differences in profiles can influence the overall exchange processes.

The modeling approach has been discussed as an example of how the plant parameters and meteorological parameters can be combined in a systematic way to evaluate the plant response to a change of a large number of factors. The model can be manipulated to arrive at "answers," but this is a dangerous procedure. The value of the exercise lies in the fact that it forces us to systematize our approach and helps identify areas where more precise information is needed. For example, the model showed the need for more information on the effective vapor pressure and effective water tension at the soil surface.

The value of the model in formulating a systematic approach to a complex problem has been demonstrated.

CHAPTER III

SUGGESTED FUTURE WORK

As in nearly every experiment the results often lead to more unanswered questions than solved problems. Some of these will be outlined.

The stomatal resistance measurements show that instruments can be designed to measure environmental responses of stomata. Further refinement of instrumentation and sampling techniques is necessary in order to obtain measurements on a large number of leaves. The same holds true in measurement of water status in the plant. This refinement in instrumentation is necessary in order to define more accurately the critical water potential for stomatal closure and to evaluate environmental factors that might influence this critical value.

The nature of water stress effects, particularly the after-effects of drought, and the changes of sensitivity of the stomata after stress is a large unknown. The mechanism appears to be linked to changes in internal CO_2. More complete models of stomatal response should include these factors.

The light intensity-stomatal resistance relationship, based on mean, instantaneous values, shows that only small changes in stomatal aperture occur for a wide range in light intensity. However, the influence of wind on leaf flutter and resulting intermittent light flashes may have considerable influence on the stomatal aperture.

The testing of stomatal changes in the model and the comparison with energy balance show that the model can be used as a tool for predicting responses. The water stress effects as they are exhibited through the stomatal aperture were linked to the other plant community factors.

The surface soil moisture characteristics have considerable influence on the radiation regime and, depending on the radiation load at the surface, the total flux from the canopy. The need for more accurate estimation of the surface soil moisture tension has been emphasized by the testing of the model. The values used were largely "guessed" values because of the lack of understanding as to exact values.

The need for accurate measurement or evaluation of the radiation regime in the canopy has been emphasized.

Finally, the testing of the various models is only as good as the measured, experimental values. Accurate description of the environment as well as the appropriate physiological responses of the plant go hand in hand with the model.

Hopefully, this report will stimulate further work and offer some guidelines as to the direction it should take for the most beneficial return.

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13. ABSTRACT

The study described is an attempt to separate the effects of light intensity and water stress on stomatal behavior under field conditions. A simple model has been developed as a means of systematically approaching the problem. The model is based on measurements of leaf resistance and relative water content through the day for a range of different stress conditions. The results of the model indicate that after-effects of stress must be considered and that a more complete model must include the effects of internal CO_2 concentration. Testing of the changes in stomatal resistance in response to changes in leaf water relations shows how the effects of water stress can be included as a sub-model in the larger plant community model. The agreement between the energy balance measurements and the model calculations using the measured resistances strengthens the confidence in the approach. Comparison of the total flux values for the crop appears to be a good test of the model and illustrates how small differences in profiles can influence the overall exchange processes. The modeling approach has been discussed as an example of how the plant parameters and meteorological parameters can be combined in a systematic way to evaluate the plant response to a change of a large number of factors. The model can be manipulated to arrive at "answers," but this is a dangerous procedure. The value of the exercise lies in the fact that it forces us to systematize our approach and helps to identify areas where more precise information is needed.

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