

Field Measured and Simulated Corn Leaf Water Potential¹

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ABSTRACT

The dynamic nature and magnitude of field-measured leaf water potential for sweet corn (*Zea mays* L.) was compared with that predicted by the model TROIKA. Some plant parameters for corn were estimated from the literature and field observation, whereas the moisture desorption curve and the hydraulic conductivity-water content relationship were determined for the Varina sandy loam. Leaf water potential-relative water content relationships were determined in the greenhouse. Hourly microclimate data were used as input to the model, and the predicted and observed values of leaf water potential were compared for 3 days during the growing season. Generally, the model predicted leaf water potential with reasonable accuracy throughout the day. Water potential gradients in the soil were small as compared with those across the root and across the stomatal opening.

Additional Index Words: simulation, root permeability, soil water potential, microclimate, stem resistance, leaf water potential.

THE DYNAMIC NATURE of plant water stress is of fundamental importance in crop production. Plant-water status is controlled by the relative rates of water loss through transpiration and water uptake by the root system. Generally, the flow of water out of the plant is controlled by the above ground environment and the leaf resistance to water vapor transfer.

Cowan (1965) predicted that leaf water potential will vary diurnally because of the dynamic nature of, and the complex interactions between, the various components of the soil-plant-atmosphere system. If any environmental factor changes, its influence on plant water status would be very difficult to interpret. One approach to studying this complex system has been through the development of

simulation models. Such models are useful in determining the relative importance of parameters and can help in designing experiments to measure the important variables and to give directions in plant breeding. Once the critical variables have been identified, new soil and water management practices can be developed to minimize the plant water stress and increase production. Researchers interested in the physiology and the ecology of plants in contrasting environments are attempting to develop a satisfactory model that relates plant water status to the environmental factors. One such model is TROIKA, developed by Lambert and Penning de Vries (1973). In this paper we compare the dynamic nature of the field-measured leaf water potential for sweet corn (*Zea mays* L.) with that predicted by the model TROIKA.

METHODS AND MATERIALS

The model used in this work was described previously by Penning de Vries (1972) and Lambert and Penning de Vries (1973) and is essentially the same except that we modified the stomatal aperture and photosynthesis sections. We will only discuss the modifications to the original model and to the program listing (Lambert and Reicosky, 1977b).

Details of the methods used in obtaining the leaf water potential and associated microclimate data were reported by Reicosky et al. (1975). The observed leaf water potential data were used on an hourly basis to correspond to the hourly microclimate data by taking the values from a weighted running average. The microclimatological inputs for the model are incoming shortwave radiation, air temperature, relative humidity, and wind speed.

We determined the leaf water potential-stomatal resistance relationship for sweet corn empirically and used it instead of the stomatal aperture section of the original model (Fig. 1). Leaf water potential was determined using the pressure chamber technique as described earlier by Reicosky et al. (1975), with stomatal resistance measured using a commercially available diffusion porometer. The relationship was determined by measuring the leaf water potential on a selected leaf and stomatal resistance on an adjacent leaf. Stomatal resistance was measured on the lower surface of the midportion of the uppermost fully developed leaves. Destructive sampling for the pressure-chamber technique did not permit evaluation of stomatal resistance on the

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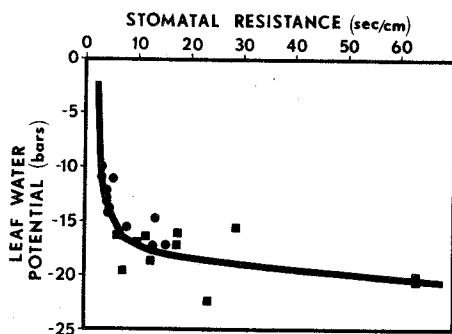


Fig. 1—Stomatal resistance vs. leaf water potential for the sweet corn used in this study. The data were obtained under field conditions.

same sample. The stomatal resistance ranged from 2 to 5 sec/cm as leaf water potential ranged from -1.0 to -15.0 bars. However, as leaf water potential approached -20 bars, stomatal resistance rapidly increased. The stomates were assumed completely closed at a stomatal resistance of 80 sec/cm.

Relative water content was determined by the method of Barrs and Weatherly (1962) and related to leaf water potential in a greenhouse study. The same samples used for leaf water potential were subsequently used for relative water content measurements. The fresh weight of about eight 1-cm square sections of leaf tissue was determined, and then the tissue was floated for 4 hours on distilled water under laboratory light and its turgid weight determined. The tissue was dried at 70°C for 18 hours and the dry weight determined. All plants were irrigated up to 4 days before the data were collected. Then two soil moisture treatments were established with the dry treatment having a final soil water potential of about -2.0 bars, and the wet soil treatment having a soil water potential of -0.1 bars. The results, shown in Fig. 2, indicated a slightly different relative water content-leaf water potential relationship at the lower leaf water potentials. In both soil moisture treatments, the relative water content of the leaf tissue was about 98% near saturation and gradually decreased to about 90% at a leaf water potential of about -12 bars. From a leaf water potential of -15 to -25 bars, the dry and the wet treatments were different. At -15 bars, the plants in the wet and dry treatments had relative water contents of about 88 and 75%, respectively. We assumed without better information, that this relationship was the same for both the leaf and root tissue. The data in Figs. 1 and 2 were used to determine the relative water content-stomatal resistance relationship used in the model.

The soil used in this experiment was Varina sandy loam (Typic Paleudult). The profile description and other soil data are presented by Campbell et al. (1974). Field observations indicated that 85 to 90% of the roots were located in the A1 horizon about 31-cm thick. We assumed that all the roots exploited the soil volume uniformly, and that they were confined to the A1. The moisture desorption curve was presented by Campbell et al. (1974) for the A1 horizon. This curve was typical of a sandy loam

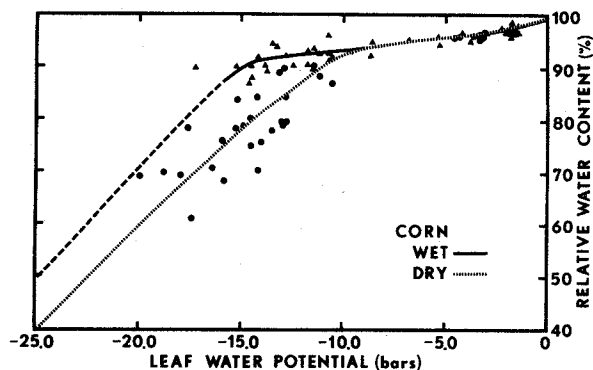


Fig. 2—The relative water content vs. leaf water potential relationship used for sweet corn determined in a greenhouse study in 1972.

soil, showing a relatively rapid decrease in water content from -0.1 to -0.3 bars, then leveling off at lower matric potentials. Soil matric potentials were measured at the 15 and 31 cm depths with mercury tensiometers. The average matric potential and the desorption curve were used to determine the initial volumetric water content (H2OINT). Hydraulic conductivity was calculated using the Millington and Quirk (1960) method. The calculated hydraulic conductivity was matched to the conductivity at saturation (assumed equal to the infiltration rate) determined from field studies. The hydraulic conductivity-water content relationship was then determined by regression analysis to give the following equation:

$$K = 87,946.32 \theta^{8.0025}$$

where K is the hydraulic conductivity (cm/day), and θ is the volumetric water content (cm^3/cm^3).

The plant parameters used as inputs for each of the different days in this experiment are summarized in Table 1. Most of the data were determined on site for sweet corn. However, where certain data were not available, we estimated values from various literature sources.

Net outgoing longwave radiation from the leaf was calculated using the Stefan-Boltzmann equation. Emissivity of the sky was determined using the equation in Fig. 6 of Idso and Jackson (1969). The emissivity for the leaves was assumed 0.97, as suggested by Ritchie (1975). The long-wave radiation was assumed radiated to the atmosphere at air temperature. Leaf temperature was not measured, but calculated in the model, based on an energy balance. The initial leaf temperature (TLI) was assumed equal to the air temperature just before sunrise (Table 1). Field measurements of net radiation over the corn canopy as compared with incoming shortwave radiation indicated that the absorption factor for shortwave radiation was about 0.6.

Leaf area of the field-grown plants was measured on eight plants per treatment in each of four replications at 7- to 10-day intervals. Leaf area was calculated as the product of the leaf

Table 1—List of initial values and constants used as model inputs for corn on the various days.

Julian date	Treatment	Shoot weight g/plant	Shoot root ratio	Leaf area† cm ²	Soil cylinder radius cm	Parameters						
						VOLRT cm ³	ROOTL§ cm × 10 ⁴	H2OINT cm ³ /cm ³	TLI °C	PERRT cm/sec/bar	RESST bar/sec/cm ²	WDTL cm
137	IRR	12.5	2.8‡	950	1.020	45	1.590	0.266	18.3	2.0×10^{-7}	1,000	4.0
	NONIRR	11.0	2.8‡	650	1.278	39	1.378	0.127	18.3	0.8×10^{-7}	1,000	4.0
140	IRR	15.5	3.0‡	1,650	1.020	52	1.838	0.178	17.1	6.0×10^{-7}	1,500	4.0
	NONIRR	14.0	3.0‡	1,050	1.020	47	1.661	0.108	17.1	2.0×10^{-7}	2,000	4.0
167	IRR	87.5	7.8	5,600	0.626	112	3.958	0.112	17.1	2.0×10^{-7}	1,000	6.0
	NONIRR	75.0	7.8	3,450	0.805	96	3.393	0.073	17.1	2.0×10^{-7}	1,000	6.0

† See text for description.

‡ Estimated from data of Foth (1962).

§ Calculation based on root radius = 0.03 cm.

¶ Limited in program to unit leaf area index = 1,548 cm².

length and average leaf width for 32 plants. The average leaf width (WDTL) was calculated as $0.75 \times$ maximum leaf width. Leaf width was used in the model to calculate the thickness of the boundary layer (after Monteith, 1965). Leaf areas between sampling times were estimated by linear interpolation.

Data on root density and length were determined for the selected days from soil monoliths taken at two times during the growing season. These monoliths resembled those reported by Campbell et al. (1974) and Doty et al. (1975). Monoliths were 15-cm thick by 60-cm wide and 76-cm deep. The soil was carefully washed from the roots, the roots were sectioned in 15-cm increments with depth and the fresh root mass determined. Vegetative samples of the top portion were collected simultaneously and the shoot-root ratio determined. On other days, the root data were not collected but the top weights were determined; the shoot-root ratio was estimated as a function of plant age from the data of Foth (1962). The root fresh weight calculated from the shoot-root ratio and the additional assumption of a density ≈ 1.0 g/cm³ on a fresh weight basis yielded the root volume (VOLRT). The roots were assumed to be 90% water with a radius of 0.03 cm based on the data of Newman (1973). Using these assumptions and cylindrical geometry, the root lengths (ROOTL) were calculated (Table 1). Once we determined the root length, we calculated the number of concentric cylindrical soil compartments, assuming uniform root spacing, to determine the soil volume available for supplying water. The thickness of the first soil layer was assumed to be the same as the root diameter. The thickness of each succeeding cylindrical compartment moving away from the root increased by a factor of 1.2.

The first estimate of root permeability (PERRT) was 6.0×10^{-7} cm/sec/bar, obtained from House and Finlay (1966). Permeability was assumed to be constant and an average for the entire root system. The values shown in Table 1 are within the range of permeabilities for several grass species reported by Newman (1973) and Ginsburg and Ginzburg (1970).

First estimates of stem resistance (RESST) were taken from those used by Lambert and Penning de Vries (1973) and Nobel (1974). In most of the calculations, the initial value of the stem resistance was set equal to 1,000 bar/sec/cm³. This value was based on data for young sunflower and tomato plants and is defined as the resistance from inside the root xylem to the substomatal cavity.

Other details on the model, written in the programming language CSMP, were described by Lambert and Reicosky (1977b). Hourly microclimatological data were input in tabular form and linear interpolation was used between the hourly data points. The method of integration was that of Milne. Output was printed and plotted. Plots of the calculated and observed leaf water potential were provided along with plots of the soil matric potential curves as a function of distance from the root.

RESULTS

The results will be evaluated by comparing the observed and calculated leaf water potentials for the two soil water treatments. We will use 3 days' data to show the sensitivity of the model to the varying microclimatological factors, particularly solar radiation. The leaf water potential and microclimate data are summarized for days 137, 140, and 167 in Fig. 3, 4, and 5, respectively. The calculated and observed leaf water potentials were always very closely related to the change in radiation. Day 137 began as a relatively clear day with solar radiation as high as 1.4 ly/min, and then it became partly cloudy in the afternoon. Both the air temperature and the relative humidity lagged 4 to 5 hours behind solar radiation. The maximum wind speed was 200 cm/sec and varied erratically throughout the day, decreasing to near zero at 2000 hours. The results showed that the leaf water potential is very dynamic,

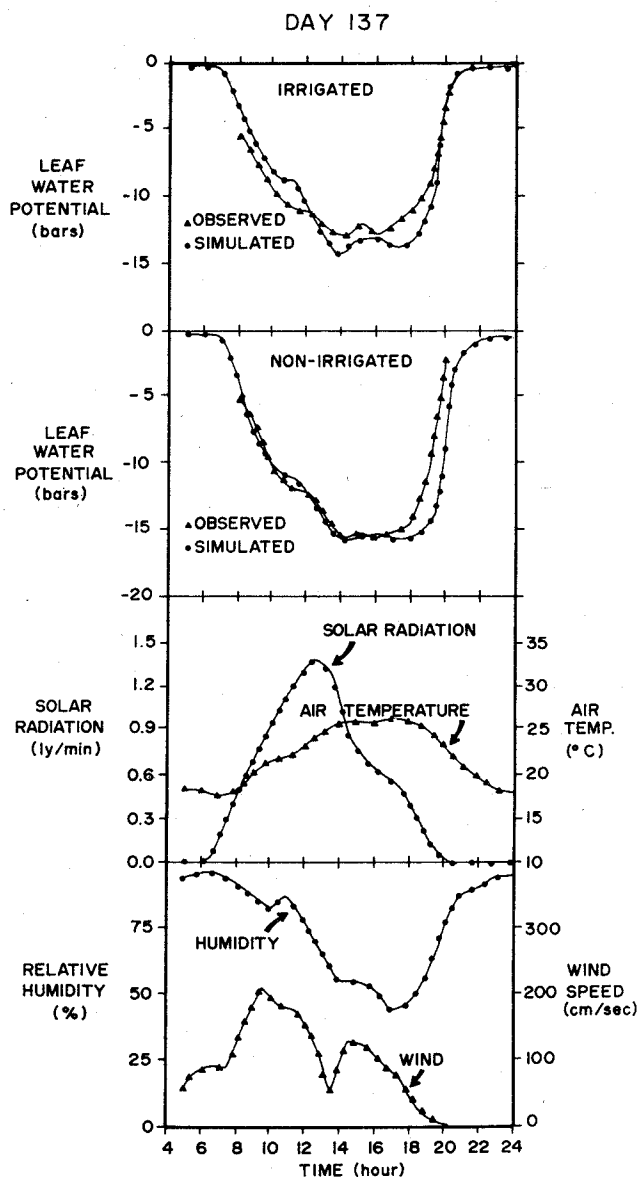


Fig. 3—Leaf water potential for the irrigated and nonirrigated treatments and microclimate data on day 137.

decreasing from -1 to -12 bars on the irrigated treatment, and changes in response to climatic conditions. In both the irrigated and nonirrigated treatments, the calculated and observed leaf water potential compared favorably and were generally within a few bars of each other. The confidence interval of the observed values was about ± 2.0 bars for the pressure chamber measurements under field conditions where different plants were used in destructive sampling. This included errors in reading the pressure chamber besides the plant-to-plant variation.

Both the calculated and the observed leaf water potential in the irrigated treatment agreed most of the day, with excellent recovery after the sunset at about 1900 hours. Between 1600 and 1800 hours, the calculated and the observed leaf water potential differed slightly, indicating that the model did not respond rapidly enough to the decrease in radiation. For the nonirrigated treatment, calculated and observed leaf water potential agreed most of

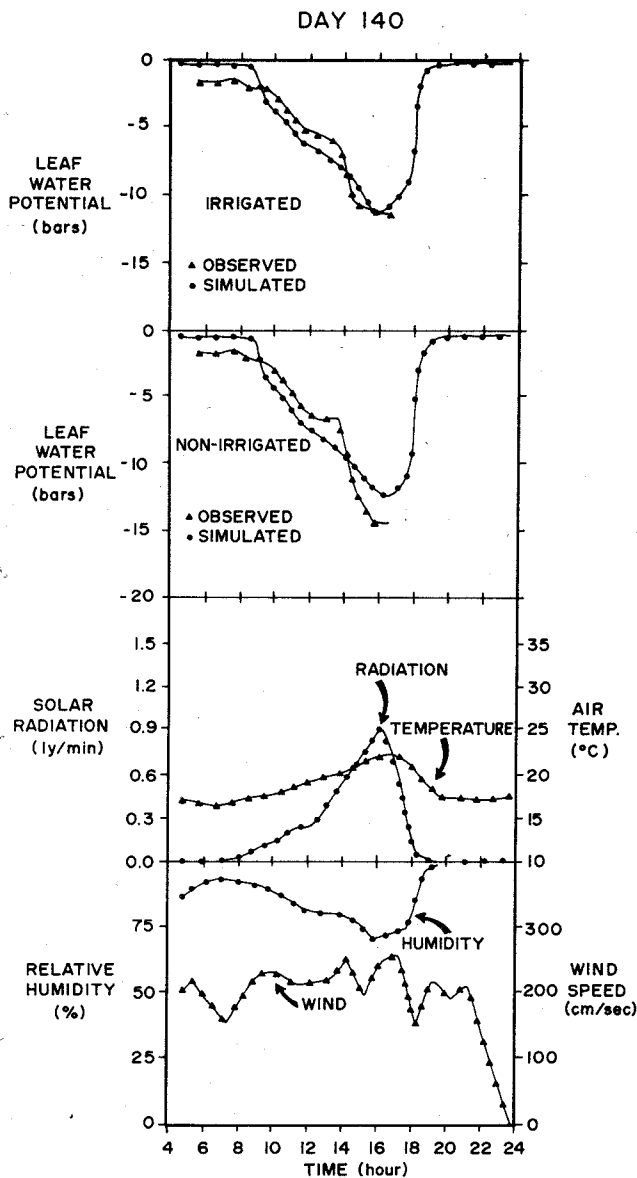


Fig. 4—Leaf water potential for the irrigated and nonirrigated treatments and microclimate data on day 140.

the day and then the calculated value seemed to also lag behind the observed value by about 1 hour as the radiation decreased. This lag may have resulted from the need to incorporate a parameter into the model to simulate water storage in the stem tissue ("capacitance" factor), which enables leaf tissue to rehydrate with the decrease in radiation. The observed lag may also be related to a hysteresis phenomenon in the observed data that was not included in the tissue water content-potential relationship in the model.

The effect of low radiation was demonstrated on day 140, which was heavily overcast (Fig. 4). Solar radiation increased slowly to about 0.3 ly/min, indicating considerable cloud cover until about 1300 hours, and then it changed to partly cloudy conditions with the maximum radiation of 0.9 ly/min at 1600 hours. The relative humidity ranged from 70 to 100% during most of the day, and the maximum air temperature was 22°C, which was essentially

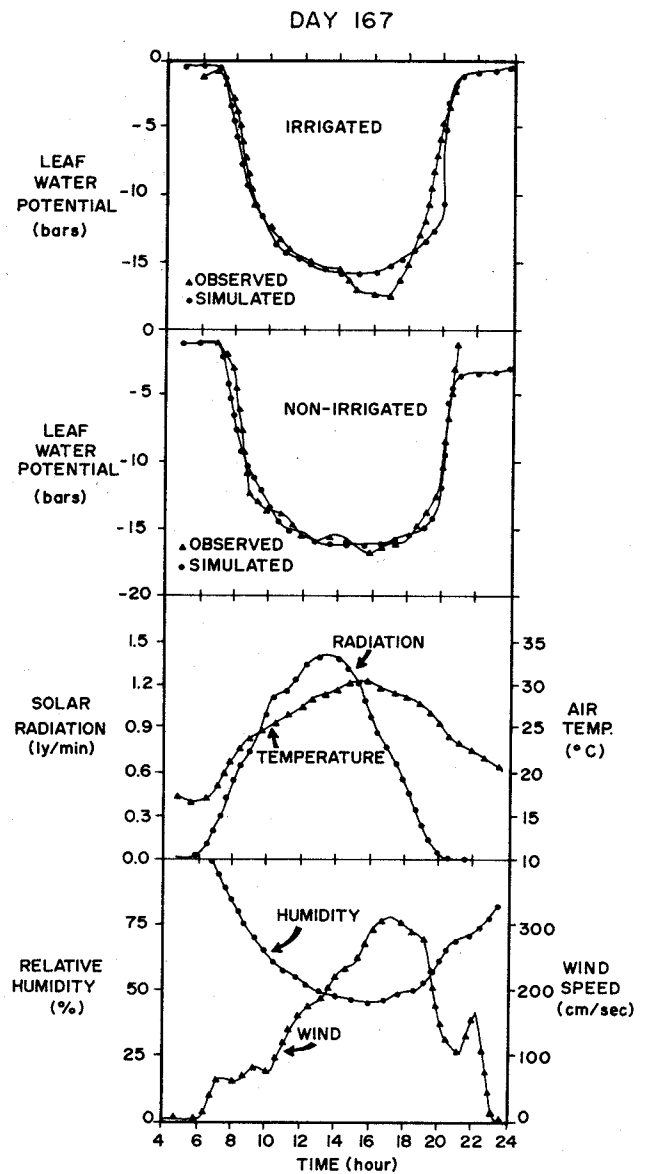


Fig. 5—Leaf water potential for the irrigated and nonirrigated treatments and microclimate data on day 167.

in phase with the radiation. In both the irrigated and nonirrigated treatments, the observed and calculated leaf water potentials generally agreed.

Both the irrigated and the nonirrigated leaf water potentials separated between 1400 and 1600 hours. During this time, the minimum observed leaf water potential value for the nonirrigated treatment was about -15.0 bars. The observed leaf water potential was not measured after 1700 hours; however, the data showed that the calculated leaf water potential did respond to the microclimate.

Figure 5 shows the relationship between the calculated and observed leaf water potential on day 167, a relatively clear day, much later in the season when the leaf area index was about 4.2. The solar radiation data indicated only a very few clouds early in the morning with a maximum of 1.4 ly/min at 1300 hours. The air temperature ranged from about 16.5°C before sunrise to about 31°C at 1500 hours. The relative humidity varied diurnally from 100% before

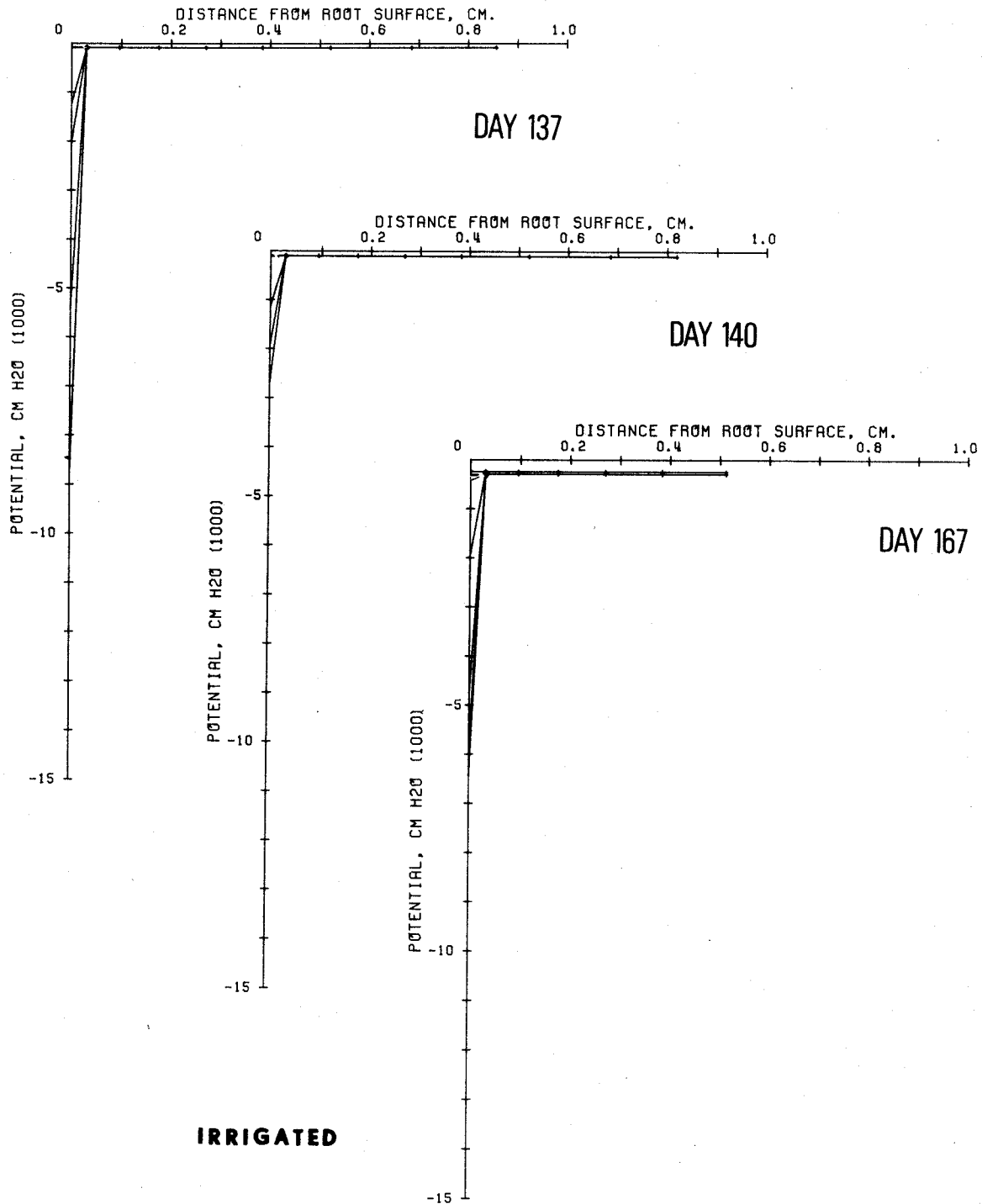


Fig. 6a—Soil matric potential as a function of distance from the root at 3-hour intervals for irrigated treatments.

sunrise to nearly 48% at 1600 hours. Wind velocity gradually increased throughout the day and reached a maximum of 320 cm/sec about 1700 hours. Both the magnitude of the minimum leaf water potential and the dynamic nature of both the calculated and the observed values were similar.

In the nonirrigated treatment, both the calculated and the observed leaf water potential values were very closely related. However, the irrigated treatment had small dif-

ferences between the calculated and observed leaf water potential shortly after solar noon. The calculated leaf water potential decreased much more rapidly with increasing radiation and recovered more slowly with decreasing radiation than did the observed value. Part of the difference probably reflected the selected values of root permeability and stem resistance used on this treatment. However, the inclusion of a tissue storage factor in the model should bring these two values closer together. Evidence for this

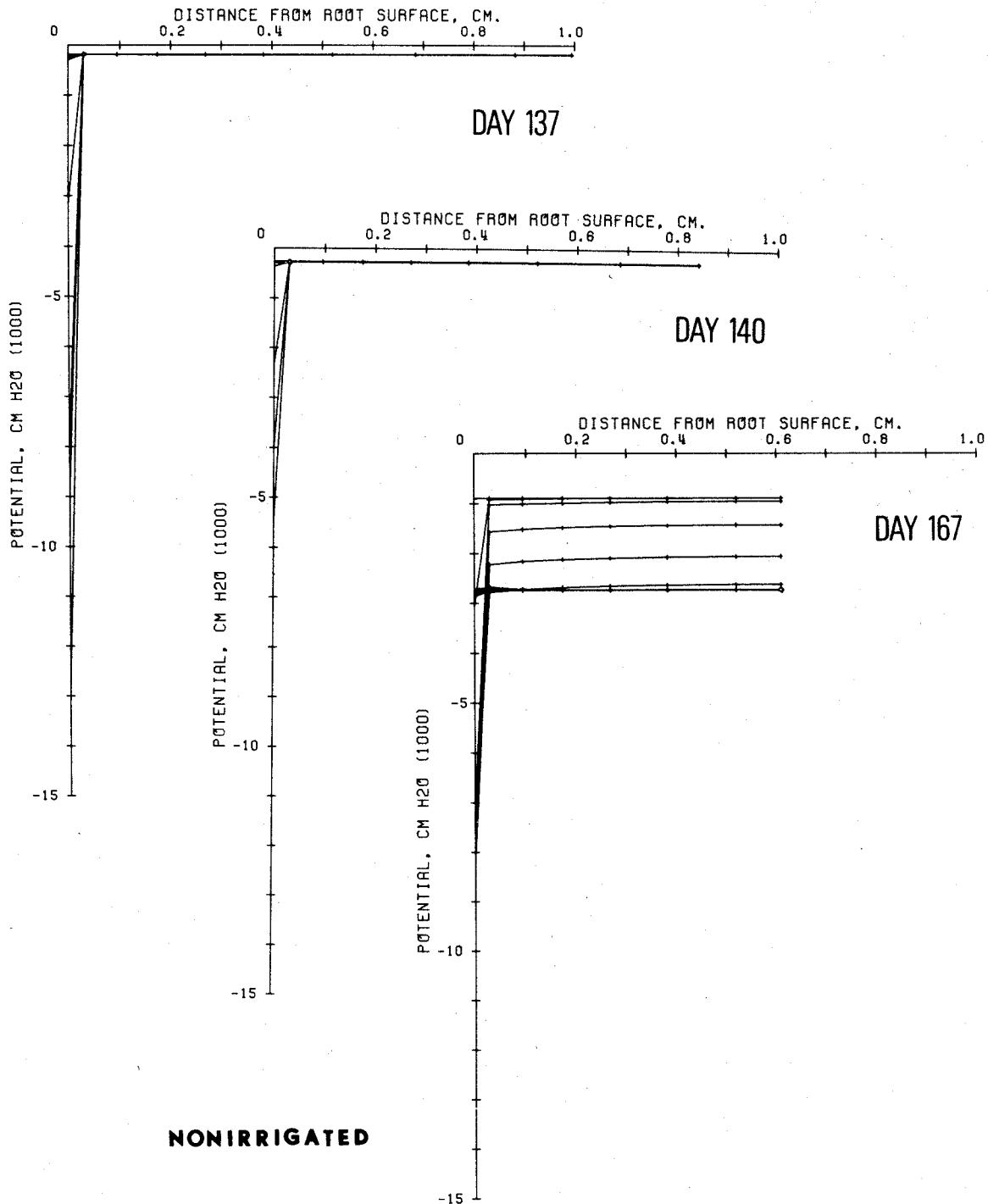


Fig. 6b—Soil matric potential as a function of distance from the root at 3-hour intervals for nonirrigated treatments.

concept is the shrinking and swelling of stem diameters when plants encounter soil water stress. The "capacitance" within the stem tissue would buffer out any dramatic changes in the calculated leaf water potential and the calculated leaf water potential values would recover more rapidly, which would yield values closer to those observed.

In Figures 6a and b, the soil matric potential is plotted as a function of distance from the root for both the irrigated and the non-irrigated treatments at 3-hour intervals. In

general, these figures show the effects of initial soil matric potential. The larger spread in the matric potential profiles and a lower potential at the root on the nonirrigated treatment than on the irrigated treatment was noted. The value plotted on the ordinate represents the water potential in the root tissue and shows a potential decrease as large as 12 bars from the soil into the root xylem for the non-irrigated treatment on day 137. Our results in general agreed with the calculations of Hillel et al. (1975), Molz (1975), and Williams (1974). Hillel et al. (1975) found that

Table 2—Summary of calculated water potentials in the soil-plant-atmosphere system at selected times during the day.

Time hour	Location	Day 137		Day 140		Day 167	
		Irrigated	Nonirrigated	Irrigated	Nonirrigated	Irrigated	Nonirrigated
		bars					
0.500	air	-66.907	-66.907	-149.880	-149.880	-0.0	-0.0
	leaf	-0.084	-0.181	-0.101	-0.269	-0.244	-0.900
	root	-0.084	-0.181	-0.101	-0.269	-0.244	-0.900
	soil-1†	-0.083	-0.181	-0.100	-0.269	-0.244	-0.900
	soil-4†	-0.083	-0.181	-0.100	-0.269	-0.244	-0.900
0800	air	-90.100	-90.100	-78.052	-78.052	-151.900	-151.900
	leaf	-3.448	-3.999	-0.156	-0.334	-5.388	-6.309
	root	-2.042	-3.136	-0.113	-0.296	-1.954	-3.053
	soil-1	-0.083	-0.181	-0.100	-0.269	-0.240	-0.925
	soil-4	-0.083	-0.181	-0.100	-0.269	-0.245	-0.905
1100	air	-139.935	-139.935	-150.500	-150.500	-604.260	-604.260
	leaf	-8.514	-10.854	-4.381	-5.160	-14.217	-14.701
	root	-5.356	-9.009	-1.123	-2.355	-5.847	-7.019
	soil-1	-0.084	-0.183	-0.101	-0.271	-0.257	-1.030
	soil-4	-0.084	-0.182	-0.101	-0.270	-0.254	-0.983
1400	air	-663.307	-663.307	-229.140	-229.140	-822.630	-822.630
	leaf	-13.950	-15.585	-7.571	-8.783	-15.621	-16.051
	root	-8.764	-12.778	-1.906	-4.029	-6.431	-7.914
	soil-1	-0.084	-0.184	-0.101	-0.276	-0.270	-1.567
	soil-4	-0.084	-0.184	-0.101	-0.274	-0.267	-1.465

† Refers to concentric soil cylinder numbered from root.

the decrease of matric potential from the far reaches of the soil toward the root is much steeper than the osmotic potential. In our work, we considered the osmotic potential as negligible when we compared it with the matric potential components. Molz (1976) calculated water potential distributions in the root cortex, as well as in the surrounding soil, and noted small water potential gradients in the soil relative to those in the root in the upper 90% of the water availability range. In this work, water potential gradient was largest across the root tissue with even smaller potential gradients in the soil than those calculated by Williams (1976).

The effect of the evaporative demand on the plant was also reflected in the matric potential profiles. On day 167, which had a fairly high evaporative demand, the calculated minimum root water potential for the irrigated treatment was about 4 bars more negative than on day 140, which had a low evaporative demand. The spread in the matric potential profiles for the nonirrigated treatment on day 167 reflected the interaction of the evaporative demand and low conductivity resulting from soil dryness as the primary factors contributing to these matric potential distributions. Although there are other factors that are probably contributing to the differences observed on days 140 and 167; the primary differences are the incoming radiation and the air temperature.

The soil matric potential drawdown curves are impossible to measure with the current techniques. However, by using the model and dividing the soil into several layers around the roots, we can make certain predictions. Especially interesting is the magnitude of the water potential decrease across the root tissue from the soil into the xylem, which reflects the importance of the root permeability. This agreed with the earlier work of Newman (1969a, 1969b, 1973) and Hansen (1974a and 1974b).

In the soil and plant, mass flow of water is the result of the movement of the water along hydraulic gradients, and the flow in both the soil and plant system obey the same

laws governing the unsaturated flow. Calculated water potentials at various points in the pathway from the soil through the plant are summarized in Table 2 at selected times during the day. The water potentials at the various locations in the soil and plant system are assumed to be in equilibrium before sunrise, except the water potential in the air on days when the relative humidity was < 100%. Our results indicated that on day 167 the water potential decreased as much as 8 bars across the root tissue. The largest water potential decrease, however, was from the interior of the leaf to the atmosphere outside of the leaf.

DISCUSSION

The model combines a knowledge of the physics of both transport processes with plant physiology so as to adequately describe the dynamic response of plant water potential to the microclimatological conditions. The results of the simulation illustrated both quantitatively and qualitatively the dynamic relationships in the soil-plant-atmosphere system. The basic relationships were assembled in the model development, independent of the data collection used to verify the model. Furthermore, all the basic parameters were either determined experimentally or obtained from the literature. The only parameters adjusted in any of the computer runs were root permeability and stem resistance. The small variation in the values of the root permeability, shown in Table 1, suggested this parameter was relatively constant. Few data are available on these two parameters, hence, a sensitivity analysis will be reported elsewhere (Lambert and Reicosky, 1977a).

The data showed the dependence of the leaf water potential on the diurnal energy flux. Because the resistances to water movement in the plant and the soil are finite, the plants did not absorb water fast enough to replace that lost by transpiration, even though the water potential gradient in the plant increased and the soil matric potential was relatively high. In this work, the largest water potential

gradient was that from the leaf through the stomates to the atmosphere during high evaporative demand. The next largest water potential gradient was that from the soil across the root into the xylem vessels. Under the dynamic conditions of rapid flow through the system, larger gradients across the root are expected and could be as large as 8 to 10 bars, depending on the evaporative demand and the soil water status (Table 2). Under conditions of low radiation, we calculated a water potential difference of about 3 bars at 1100 hours on day 140, whereas under maximum radiation with a relatively dry soil, we found a 8-bar difference at 1400 hours on day 167.

The calculated soil matric potential drawdown curves generally agreed with those reported by other workers. Our results indicated that the assumed values for root density were not unrealistic for field grown plants and generally agreed with the conclusions of Newman (1969b), Williams (1974), and Molz (1975) that the water potential gradients in the soil are relatively small as compared with those across the root. These conclusions for corn resembled results for Italian rye grass (Hansen, 1974b) and for wheat (Hansen, 1974a). Using a correction for the soil-root-interface resistance as a function of soil water content, Hansen (1974b) concluded the soil resistance at root densities as high as 18 cm/cm³ was not limiting within -0.1- to -15-bar range of soil water potential. He further showed the resistance of the plants decreased as transpiration rate increased, but did not find any unique relationship between the plant resistance and the leaf water potential. In this work, only in the nonirrigated treatment on day 167 was there a significant decrease in the soil matric potential, and even in this case, the matric potential gradient in the soil still was small. Molz (1976), using a Pachappa sandy loam, found that, until the water potential at the root surface reached -5.5 bars, there was little water potential gradient in the soil relative to that in the root. He concluded that the soil water potential and the soil resistance were not limiting until the soil had lost over 90% of its available water. On the nonirrigated treatment on day 167, the soil matric potential was as low as -1.5 bars, which is considerably higher than that reported by Molz (1976).

An important implication of our work is that models designed to predict the pattern in which roots extract water from the soil must include the rate-limiting aspect of the root tissue, specifically the root permeability. The root permeability is a key factor in determining the magnitude and the dynamic nature of the leaf water potential. Further information is needed on how the tissue water potential and aeration status in the root affect the root permeability.

As the competition for water resources becomes greater, the agricultural scientist must learn how to beneficially use the limited water supply as it affects plant water status. He must properly understand the dynamics of the plant water status and how it affects the high levels of productivity. The accuracy of the model in this study in predicting the dynamic nature and the magnitude of the leaf water potential observed under field conditions suggests progress is being made. However, parameters that need further work are root permeability, root-length characteristics, stem resistance, tissue-storage factor, hysteresis in the tissue water content-potential relationship, and how these pa-

rameters are affected by the age of the plant and a dynamic microclimate.

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