

# Stomatal Behavior and Water Status of Maize, Sorghum, and Tobacco under Field Conditions

## I. AT HIGH SOIL WATER POTENTIAL

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### ABSTRACT

Diurnal changes in the vertical profiles of irradiance incident upon the adaxial leaf surface ( $I$ ), stomatal resistance ( $r_s$ ), leaf water potential ( $\psi$ ), osmotic potential ( $\pi$ ), and turgor potential ( $P$ ) were followed concurrently in crops of maize (*Zea mays* L. var. Pa 602A), sorghum (*Sorghum bicolor* [L.] Moench var. RS610), and tobacco (*Nicotiana tabacum* L. var. Havanna Seed 211) on several days in 1968 to 1970 when soil water potentials were high. In all three crops the  $r_s$ , measured with a ventilated diffusion porometer, the  $\psi$ , measured with the pressure chamber, the  $\pi$ , measured with a vapor pressure osmometer, and the calculated  $P$ , decreased from sunrise to reach minimum values near midday and then increased again in the afternoon. The diurnal range of all the variables was greater for leaves in the upper canopy than for those in the lower canopy.  $P$  was observed to decrease with decreasing  $\psi$ , but never became zero. Sorghum had a higher  $P$  at a  $\psi$  of, say  $-10$  bars, than did maize, and maize had a higher  $P$  than tobacco at the same  $\psi$ . Moreover, at the same  $\psi$  the upper leaves in all canopies had a higher  $P$  than the lower leaves. When compared at high irradiances,  $r_s$  did not increase as  $\psi$  declined to  $-13$ ,  $-15$ , and  $-10$  bars or as  $P$  declined to 0.3, 3.5, and 1.2 bars in maize, sorghum, and tobacco, respectively. The relation between  $r_s$  and  $I$  in the upper, nonsenescent leaves of all three crops fits a hyperbolic curve, but the response varied with species and leaf senescence. The adaxial and abaxial epidermises had the same response of  $r_s$  to  $I$  in maize and sorghum, whereas in tobacco the adaxial epidermis had a higher  $r_s$  than the abaxial epidermis at all values of  $I$ . At equal values of  $I$ , tobacco had the lowest leaf resistance ( $r_l$ ) and maize had the highest  $r_l$ . Senescent maize leaves had nonfunctional stomata, whereas the lowermost sorghum leaves had higher stomatal resistances on average than the other leaves.

Laboratory studies have indicated that light and water are the two environmental factors that are likely to have the greatest effect on stomatal behavior in the field. Light stimulates the uptake of potassium ions into the guard cells and, in conjunction with a suitable anion, creates turgor changes that result in stomatal opening (7, 14); loss of leaf turgor understandably inhibits opening.

The present study was conducted to compare the stomatal behavior and water balance of three important crop species at high soil water potential, and to study the effect of irradiance and leaf turgor on stomatal resistance; a similar study at low soil water potentials will be the subject of part II. The diurnal changes in the vertical profiles of stomatal resistance were followed concurrently with the vertical profiles of irradiance, leaf water potential, and osmotic potential on clear sunny days. The vertical profiles of turgor potential were calculated from observations of leaf water potential and osmotic potential. The three crop species were representative of plants with either high (maize, sorghum) or low (tobacco) photosynthetic efficiency and water use efficiency (2), and are species considered to differ in their drought tolerance.

### MATERIALS AND METHODS

Adjacent plots of maize (*Zea mays* L. var. Pa 602A), sorghum (*Sorghum bicolor* [L.] Moench var. RS610), and tobacco (*Nicotiana tabacum* L. var. Havanna Seed 211) were established in a well fertilized fine-sandy loam at the Lockwood Farm, Mt. Carmel, Connecticut, in 1968, 1969, and 1970. All plots were sown in north-south rows 0.76 m apart; the 0.5 ha of maize and 0.2 ha of sorghum were sown in mid-May and had final plant populations of 47,000 to 71,000 plants per ha, whereas the 0.2 ha of tobacco was transplanted as seedlings in early June to give final plant populations of 22,000 to 28,000 plants per ha.

Concurrent measurements of stomatal resistance, irradiance, leaf water potential, and osmotic potential were obtained at 5 or 6 heights in the three crops after the canopies were fully developed. Observations were taken over 24 hr from midday to midday. Generally measurements were begun before sunrise ( $\sim 0500$  hr Eastern Standard Time [EST]) and continued until after sunset ( $\sim 1900$  hr EST), with a complete break only between 2200 and 0400 hr EST. Meteorological conditions were obtained from the Mt. Carmel Meteorological Station, 400 m from the experimental site.

The stomatal resistance ( $r_s$ ) of the horizontal portion of a leaf was measured with a ventilated diffusion porometer (21). The adaxial and abaxial stomatal resistances were measured separately on adjacent portions of the leaf, and the leaf resistance ( $r_l$ ) was calculated assuming that the two leaf surfaces acted as parallel resistors.

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Stomata are important regulators of photosynthesis, transpiration, and the uptake of some gaseous pollutants (12, 27). An understanding of their behavior under field conditions is important if we are to predict crop productivity and water use (23), reduce crop evaporation by antitranspirants (25), or estimate the role of vegetation in cleansing the air of pollutants (24).

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Immediately after the completion of the measurements of  $r_s$ , the irradiance incident upon the adaxial epidermis ( $I$ ), in the region that resistance measurements were obtained, was measured with a Model 756 Weston Sunshine Illumination Meter (Weston Instrument Co., Newark, N.J.). The meter was covered by a Wratten 85 C filter and calibrated in energy units with an Eppley pyranometer (Eppley Laboratory, Inc., Newport, R.I.).

The leaf water potentials ( $\psi$ ) were measured with a pressure chamber (22), a modification of that described by Scholander *et al.* (15). The pressure chamber accurately estimates  $\psi$  in the three crops (5, 6).

The osmotic potentials ( $\pi$ ) were measured with a Model 302 B Hewlett Packard (Avondale, Pa.) vapor pressure osmometer. Leaf samples from the opposite half of the leaf to that used for the measurement of  $\psi$  were sealed into a test tube and quickly frozen in Dry Ice. The frozen samples were returned to the laboratory and then allowed to thaw before the cell constituents were expressed from the leaf and quickly transferred to the osmometer.

The  $\psi$  and  $\pi$ , concurrently sampled and measured on the same leaf, were used to determine the turgor potential ( $P$ ) from the equation:

$$\psi = \pi + P + \tau$$

The matric potential ( $\tau$ ) was considered to be zero, a reasonable assumption at  $\psi$  greater than  $-15$  bars (3, 26).

The leaf area was obtained in 20 cm strata from four randomly selected plants in each crop. For maize and sorghum, the formula (10, 17):

$$\text{Leaf area} = \text{length} \times \text{maximum width} \times 0.75$$

was used to determine the area of each leaf. In tobacco the total leaf weight and the ratio of leaf area to dry weight of three to five discs per leaf in each stratum were used to calculate the total leaf area per stratum. The discs were 2.85 cm<sup>2</sup> in area and included midribs and major veins. The LAI,<sup>2</sup> *i.e.*, the total leaf area per unit ground area, could then be calculated. A leaf was classed as senescent when more than 75% of its area was yellow or dead.

Stomatal frequencies were obtained from acrylic resin negatives. The clear acrylic resin was sprayed directly onto the leaf epidermis, allowed to dry and removed with transparent tape. Ten fields from the two or three leaves sampled for resistance measurements at each height in the canopy were counted.

## RESULTS

Concurrent measurements of  $I$ ,  $r_s$ , and  $\psi$  were obtained on 6 days in 1968 and 1969; additionally, concurrent measurements of  $I$ ,  $r_s$ ,  $\psi$ , and  $\pi$  were obtained on 6 other days in 1969 and 1970. Observations were confined to clear days; other meteorological conditions varied within a relatively narrow range from day to day.

**Diurnal Changes in the Vertical Profiles of Irradiance, Leaf Resistance, and Water Potential.** The concurrent measurements of  $I$ ,  $r_s$ , and  $\psi$  are presented in Figure 1. For clarity, only profiles at three or four times of day are shown; each data point is the mean of three observations in maize and sorghum, and two in tobacco. The irradiance within the three canopies rose from zero on all leaves at sunrise to values of 1.0 to 1.25 cal cm<sup>-2</sup> min<sup>-1</sup> at the top of the canopy at midday. At this time the irradiance within the canopy declined to 0.25 cal cm<sup>-2</sup> min<sup>-1</sup> on the lower leaves of corn and sor-

ghum to almost zero on those of tobacco with its greater LAI. The irradiance on all leaves within the canopy decreased as the inclination of the sun decreased.

At sunrise, the presence of dew on the leaves precluded any measurement of  $r_s$ , and it was assumed to be high in all leaves. After the dew had evaporated, the  $r_s$  in the upper, sunlit leaves decreased first, reached a minimum  $r_s$  about midday and increased again to the observed high resistances at sunset. The lower leaves in all three crops rarely had low resistances and moved through a small diurnal range compared to the upper leaves.

The  $\psi$  of all leaves was greater than  $-2$  bars in all three crops at dawn; no gradient in potential between leaves at different heights was observed. Assuming that the plant was in equilibrium with the soil at this time, the soil water potential in the root zone was  $-1.0$ ,  $-1.8$ , and  $-0.5$  bars in maize, sorghum, and tobacco, respectively. Soon after sunrise the  $\psi$  began to decrease in all leaves, and particularly in the upper sunlit ones, so that by  $-4.5$  hr (0730 hr EST) the upper maize leaves had a  $\psi$  of  $-10$  bars. There was a steep gradient in  $\psi$  at this time, the lowest leaf having a  $\psi$  of  $-3$  bars. At midday the  $\psi$  was more negative in all maize leaves, but the gradient in  $\psi$  was less than at  $-4.5$  hr as more radiation penetrated through the canopy to the lower leaves; a similar observation was reported previously in tobacco (1). The tobacco in the present study, with a LAI of 8.5 compared with the 2.9 in the earlier study, had the steepest gradient in  $\psi$  at midday; a potential of  $-14$  bars was observed in the uppermost leaves and  $-2$  bars in the lower leaves.

The minimum  $\psi$  usually occurs about 1 hr after midday, and a lag in recovery can be observed (25). A similar lag was observed in the three crop canopies. In the maize, 7 hr after midday the leaves were 2 bars more negative in potential, on average, than the leaves sampled 7 hr before midday; in the sorghum and tobacco the  $\psi$  were also more negative well after sunset than the values obtained at sunrise.

**Diurnal Changes in the Vertical Profiles of Leaf Water Potential, Osmotic Potential, and Turgor Potential.** The concurrent observations of  $\psi$ ,  $\pi$ , and the calculations of  $P$  are presented in Figure 2. Representative profiles at three times of day are shown. Because the data were collected in different years, the profiles of  $\psi$  of the three canopies are not identical with those in Figure 1. However, the soil water potentials, estimated from dawn  $\psi$ , were again all greater than  $-2$  bars, and in all cases the diurnal trends in  $I$ ,  $r_s$ , and  $\psi$  were similar to those in Figure 1.

The  $\pi$  was always more negative than the corresponding  $\psi$  in all leaves and in all three crops. At sunrise  $\pi$  in maize varied between  $-8$  and  $-13$  bars, in sorghum between  $-13$  and  $-15$  bars, and in tobacco between  $-6$  and  $-12$  bars, with the more negative values in the upper canopy. The  $\pi$  of the upper leaves decreased as the day progressed reaching minimum values 2 hr after midday; in all three crops, the steepest gradient in  $\pi$  also occurred at this time.

The corresponding  $P$  showed a decrease from sunrise to minimum values at midday and then an increase in the afternoon. The  $P$  at midday was lowest in maize and highest in sorghum, with intermediate values in tobacco; no consistent trend in the gradient of  $P$  was discernible in the three crops.

**Stomatal Resistance, Leaf Water Potential, and Turgor Potential.**  $\psi$ , the integrator of water absorption, water loss, and transport resistances in the plant, varied diurnally over a range of 12 to 15 bars.  $\pi$  varied over a narrower range and thus, as  $\psi$  decreased,  $P$  decreased. In all three crops  $P$  was greater at equal  $\psi$  for leaves in the upper canopy than for leaves in the lower canopy; data for leaves at intermediate heights in the canopy fell between the data for upper and

<sup>2</sup> Abbreviation: LAI: leaf area index.

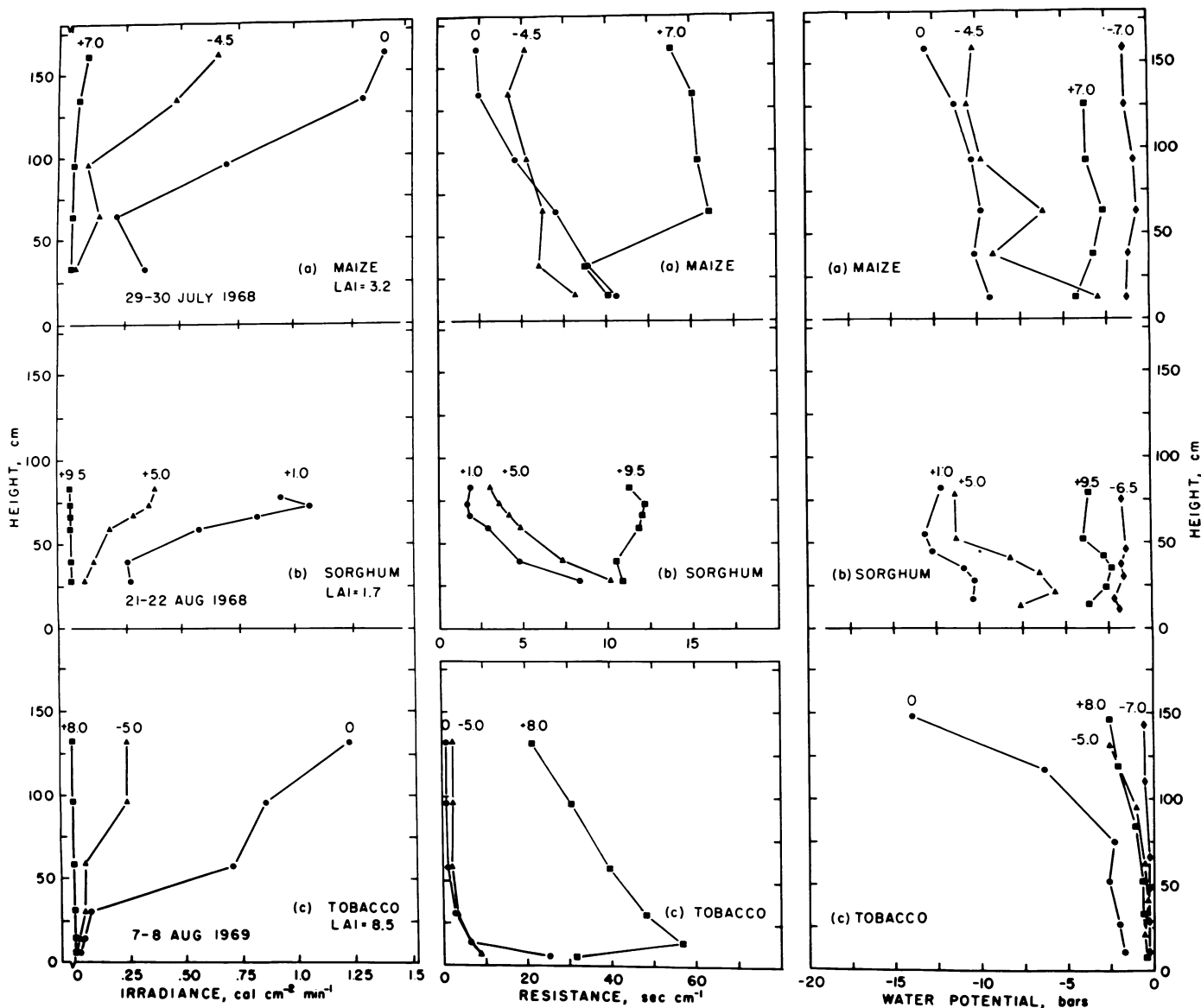


FIG. 1. Vertical profiles of adaxial irradiance ( $I$ ), leaf resistance ( $r_l$ ), and leaf water potential ( $\psi$ ) within crops of (a) maize, (b) sorghum, and (c) tobacco at three or four times of day. Times are calculated from noon, EST, e.g., +7.0 is 1900 hr EST. Note that the leaf resistance scale in (a) and (b) differs from that in (c).

lower canopy leaves. Additionally, species differences were apparent: at a  $\psi$  of, say,  $-10$  bars, the upper leaves of sorghum had a higher  $P$  than either tobacco or maize and the upper leaves of maize had a higher  $P$  than tobacco. This suggests that the upper leaves of sorghum may wilt at a more negative  $\psi$  than maize, and maize may wilt at a more negative  $\psi$  than tobacco; in the lower leaves, the tobacco may wilt at a much less negative  $\psi$  than either maize or sorghum. At no time were zero turgor potentials observed in this study. Similarly, wilting was not observed on any of these days.

The change in  $\psi$  or  $P$  over the ranges encountered in this study had no observable effect *per se* on the  $r_l$  of any crop. To demonstrate this, concurrent measurements of  $r_l$ ,  $\psi$ , and  $P$  in all three crops were selected for those occasions when  $I$  was 1.0 to 1.25 cal  $\text{cm}^{-2} \text{min}^{-1}$ . Within the range of the observations,  $r_l$  did not change as  $\psi$  decreased from  $-8$  to  $-13$  bars in maize and  $-8$  to  $-15$  bars in sorghum or as  $P$  decreased from 6 to 0.3 bars in maize and 11 to 4 bars in sorghum (Fig. 3). This was also true for tobacco: at 0.5 to 0.6

cal  $\text{cm}^{-2} \text{min}^{-1}$  the  $r_l$  was 4.4 sec  $\text{cm}^{-1}$  at a  $P$  of 8 bars ( $\psi$  was  $-5$  bars), and 4.6 sec  $\text{cm}^{-1}$  at a  $P$  of 1.5 bars ( $\psi$  was  $-12$  bars). In all three crops both the adaxial and abaxial stomata were equally unaffected by the changes in  $P$  or  $\psi$ .

**Stomatal Resistance and Irradiance.** Since the diurnal changes in  $\psi$  and  $P$  were not measurably affecting  $r_l$ , we used the extensive data available on  $r_l$  and  $I$  to compare the stomatal response to irradiance in the three crop species. The individual observations used in Figure 1, plus those from profiles at other times of day, are presented in Figure 4. Since no differences in response between adaxial and abaxial stomata could be distinguished in maize and sorghum, the response of  $r_l$  to adaxial irradiance is presented (Fig. 4, a and b); the adaxial and abaxial epidermises of tobacco clearly responded differently (Fig. 4, c and d).

The older senescent leaves of maize responded differently from the younger green leaves. Figure 4a shows that the stomata in senescent maize leaves are nonfunctional. In sorghum the lowermost leaves tended to have a higher  $r_l$  than

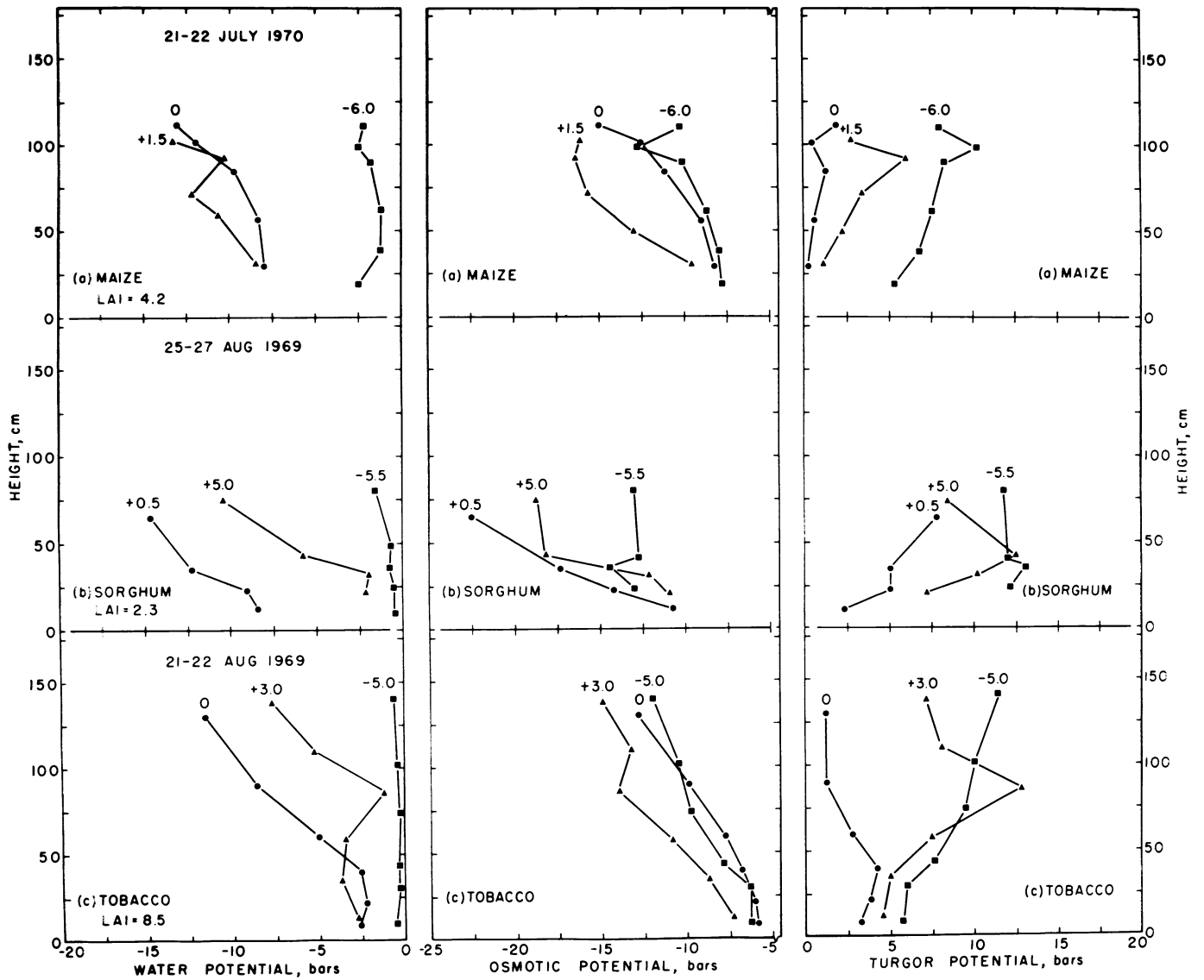


Fig. 2. Vertical profiles of leaf water potential ( $\psi$ ), leaf osmotic potential ( $\pi$ ), and leaf turgor potential ( $P$ ) in crops of (a) maize, (b) sorghum and (c) tobacco at three times of day. Times are calculated from noon, EST.

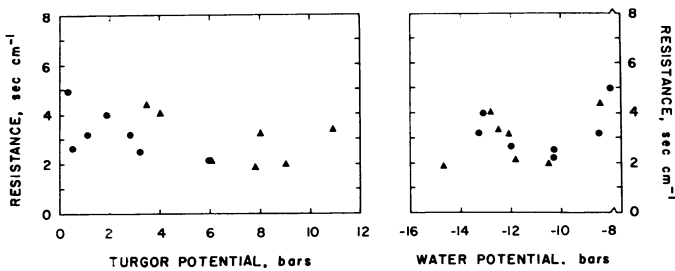


Fig. 3. Relation between leaf resistance ( $r_l$ ) and turgor potential ( $P$ ) and between leaf resistance ( $r_l$ ) and leaf water potential ( $\psi$ ) in maize (●) and sorghum (▲).

the upper leaves, but the stomata still responded to irradiance. Senescent tobacco leaves were always poorly irradiated, and thus it was not possible to determine whether their ability to respond to irradiance was impaired; the data for sorghum and tobacco were omitted from Figure 4 for clarity.

After exclusion of the data from the senescent maize leaves, the relation between resistance ( $r_l$  or  $r_s$ ) and irradiance

( $I$ ) is clearly hyperbolic. The lines in Figure 4 were fitted by the following linear transformation:

$$Ir_l = Ir_{\min} + I_m r_{\min} \quad (2a)$$

or

$$Ir_s = Ir_{\min} + I_m r_{\min} \quad (2b)$$

where  $r_{\min}$  is the minimum resistance and  $I_m$  is the irradiance at  $2r_{\min}$ . The correlation coefficients were between 0.79 and 0.86 in maize, sorghum, and the abaxial epidermis of tobacco, but the coefficient was only 0.35 in the adaxial epidermis of tobacco. The summarized data (Table I) show that the  $r_{\min}$  in sorghum was smaller than that for maize and the  $r_l$  of sorghum was smaller than that for maize at all irradiances; this probably reflects the greater frequency of stomata in sorghum (Table II). In tobacco the adaxial epidermis had a much greater resistance to diffusion at all irradiances than the abaxial epidermis. The latter had a smaller resistance than either leaf surface of maize or sorghum. This smaller resistance of the abaxial epidermis of tobacco compared to maize or sorghum did not, however, arise from a greater stomatal

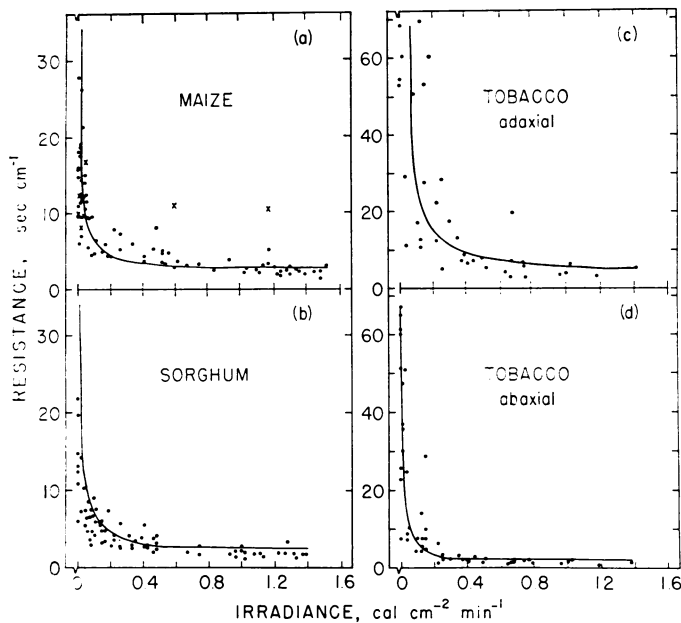


FIG. 4. Relation between leaf resistance ( $r_l$ ) and adaxial irradiance ( $I$ ) in (a) maize and (b) sorghum, and between stomatal resistance ( $r_s$ ) and adaxial irradiance ( $I$ ) in (c) the adaxial and (d) the abaxial epidermises of tobacco. Resistances greater than  $70 \text{ sec cm}^{-1}$  were omitted. ●: Green leaves; ×: senescent leaves. Parameters of the fitted lines are given in Table I.

Table I. Minimum Resistance ( $r_{min}$ ), the Irradiance at  $2r_{min}$  ( $I_m$ ) and the Correlation Coefficient ( $r$ ) for the Relation between Leaf or Stomatal Resistance and Irradiance (Equation 2) in Three Field Crops

The calculated resistances in the dark ( $0.02 \text{ cal cm}^{-2} \text{ min}^{-1}$ ), in intermediate light ( $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$ ), and in full sunlight ( $1.2 \text{ cal cm}^{-2} \text{ min}^{-1}$ ) are given.

Crop	$r_{min}$	$I_m$	$r$	Resistances in		
				Dark	Intermediate light	Full sunlight
	sec/cm	cal/cm <sup>2</sup> ·min		sec/cm		
Maize	2.42	0.19	0.83 <sup>1</sup>	25.4	3.3	2.8
Sorghum	2.18	0.13	0.86 <sup>1</sup>	16.7	2.8	2.4
Tobacco				16.0	1.7	1.3
Adaxial	3.64	0.65	0.35 <sup>1</sup>	122.6	8.4	5.6
Abaxial	1.49	0.23	0.79 <sup>1</sup>	18.4	2.2	1.8

<sup>1</sup> Correlation significant at 0.01% level.

Table II. Adaxial and Abaxial Stomatal Frequencies of Maize, Sorghum, and Tobacco

Standard errors are also given.

Maize				Sorghum				Tobacco			
Leaf <sup>1</sup>	Height	Adaxial stomata	Abaxial stomata	Leaf <sup>1</sup>	Height	Adaxial stomata	Abaxial stomata	Leaf <sup>1</sup>	Height	Adaxial stomata	Abaxial stomata
No.	cm	No./mm <sup>2</sup>		No.	cm	No./mm <sup>2</sup>		No.	cm	No./mm <sup>2</sup>	
3	160	66 ± 1	88 ± 3	1	90	71 ± 4	141 ± 5	4	104	24 ± 1	75 ± 2
5	134	64 ± 2	79 ± 2	3	74	99 ± 5	157 ± 3	7	86	31 ± 1	76 ± 1
7	97	67 ± 2	80 ± 2	5	69	116 ± 5	164 ± 4	10	51	28 ± 1	68 ± 1
9	64	62 ± 1	78 ± 2	7	60	102 ± 3	154 ± 5	15	16	34 ± 1	76 ± 1
11	32	54 ± 1	73 ± 1	9	49	92 ± 3	112 ± 2	19	6	38 ± 1	61 ± 1

<sup>1</sup> Numbered from the uppermost leaf.

frequency (Table II) suggesting that the abaxial stomata are larger or open wider in tobacco than in sorghum or maize.

## DISCUSSION

Diurnal changes in both the stomatal resistance and water balance of the leaves have been demonstrated in all three crops. The vertical profile of stomatal resistance observed at a particular time of day is a function of the radiation incident upon the leaf, the species, and the degree of senescence of the leaf. However, at the given soil water potentials, estimated to be greater than  $-2$  bars, and under the evaporative conditions encountered in these studies, the diurnal changes in  $\psi$  to minimum values of  $-13$ ,  $-15$ , and  $-10$  bars in the maize, sorghum, and tobacco, respectively, were insufficient to affect the stomatal resistance.

The radiation incident upon the adaxial leaf surface was measured in these studies, and clearly it is a function of the solar radiation above the crop, the angle of the sun and the canopy architecture. The stomatal response to the irradiance at the leaf was shown to vary with the species under study, but in all cases the resistances were high in low light and rapidly decreased as the irradiance increased (Fig. 4). The relation between  $I$  and  $r_s$  was approximated by a hyperbolic function. The characteristics of these functions for the three crops (Table I) indicate that all three crops had a high  $r_s$  of 16 to 25  $\text{sec cm}^{-1}$  in the dark, but in intermediate and high light maize had a resistance twice as great as did the tobacco with sorghum intermediate. Clearly, the high rates of photosynthesis observed in the two tropical grasses (28) cannot be attributed to more widely open stomata; this was verified under field conditions in a report published separately (20). Moreover, the high rates of photosynthesis in maize and sorghum, coupled with the high stomatal resistance to transpiration, make these two species comparatively more efficient in their water use than tobacco.

The measured irradiance,  $I$ , was that incident upon the adaxial leaf surface; the abaxial irradiance was probably only one-fifth of  $I$ . Nevertheless, in maize and sorghum the adaxial  $r_s$  was the same as the abaxial  $r_s$ , and in tobacco the abaxial  $r_s$  was lower than the adaxial  $r_s$ , at equal adaxial irradiances. Since the size and frequency (Table II) of the abaxial stomata are not 5-fold greater than those of the adaxial stomata, the abaxial stomata must open in lower light than the adaxial stomata in all three species, and particularly in tobacco, an observation that was conclusively demonstrated in the laboratory (19).

The nonfunctional nature of the stomata in senescent maize leaves (Fig. 4) confirms the previous observation that resistances were greater at high irradiances in yellowing leaves than in green leaves (18). In sorghum, while yellowing

leaves were absent, the lower leaves did have a higher resistance on average than the upper leaves, but still responded to irradiance. The failure of the stomata to open in the senescent maize leaves may result from the translocation of potassium from the leaf during senescence. Changes in stomatal aperture are known to arise from turgor changes created by the movement of potassium ions into or out of the guard cells (7, 14). The movement of these ions from the leaf during senescence may, therefore, lead to the observed nonfunctional nature of the maize stomata.

The lack of any observable change in leaf resistance as  $\psi$  declined to  $-13$  bars in maize and  $-15$  bars in sorghum makes the hyperbolic functions between  $r$ , and  $I$  (Table I) applicable over a wide range of  $\psi$ . The results, however, do contrast with those obtained by Boyer (4) and Sanchez-Diaz and Kramer (13), who observed increased resistance to diffusion at  $-8$  to  $-10$  bars in maize and  $-12$  bars in sorghum. However, their experiments were done in constant environment chambers with potted plants, and other evidence suggests that stomata in plants grown in constant environment chambers and with a restricted root zone do not behave in the same manner to a decline in  $\psi$  as do stomata of plants in the field (9, 11), probably because of differences in  $\pi$ . One field study indicated that maize stomata close at a  $\psi$  of  $-6$  bars (16). In this case the  $\psi$  were estimated from measurements of relative water content; the estimation of  $\psi$  from relative water content is subject to large experimental errors in maize (8). The direct measurement of  $\psi$  obtained in this study should be more precise.

The fact that a simple hyperbolic relationship between irradiance and  $r$ , can be applied over a wide range of  $\psi$  in all three crops widens the applicability of previous observations of the relationship between stomatal resistance and irradiance (18–20, 25). The observed differences in the relationship, depending on the species, can now be used in simulators of crop growth, water use, and pollutant uptake. The effect of low  $\psi$  on the relationship between irradiance and  $r$ , is the subject of a subsequent paper.

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