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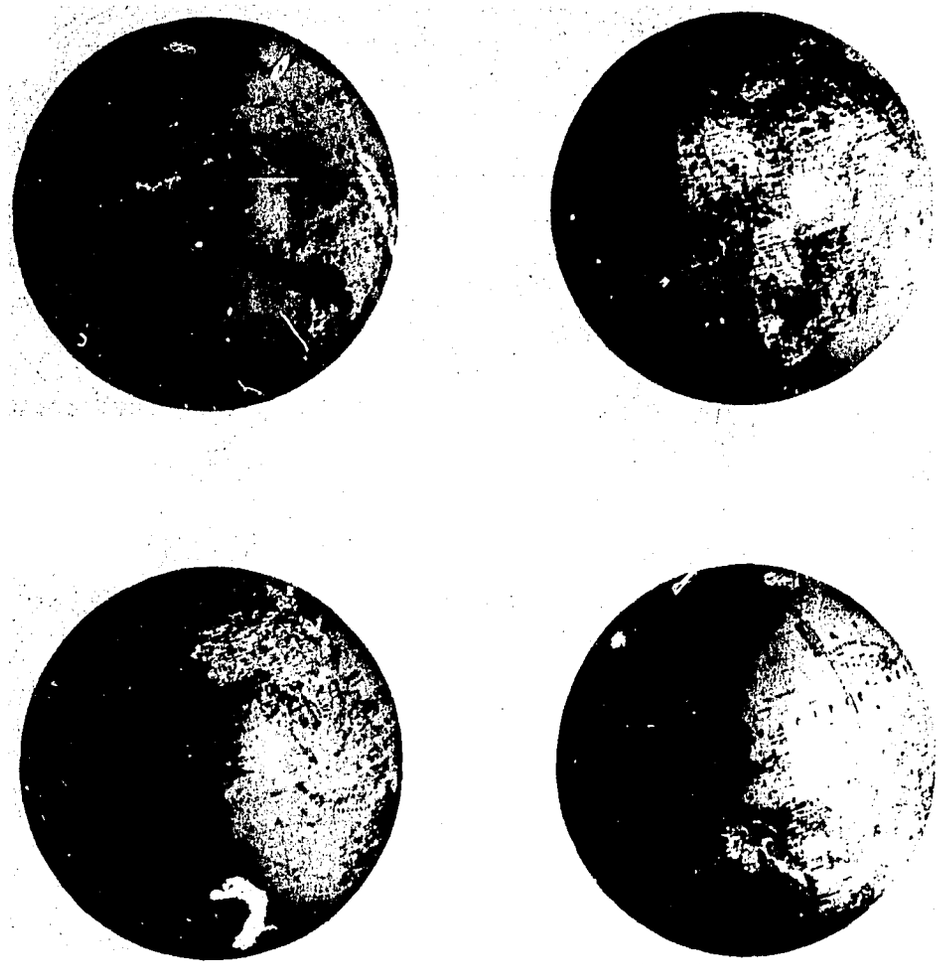

Photosynthetic Response to Drought in Maize

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PHOTOSYNTHETIC RESPONSE TO DROUGHT IN MAIZE[1]

GARY H. HEICHEL and ROBERT B. MUSGRAVE[2]

The photosynthesis of leaves of several corn varieties in the field was measured by infrared gas analysis in a well-ventilated, brightly illuminated chamber. Photosynthesis was correlated with leaf water potentials measured by thermocouple psychrometry on the same leaves. Three distinct patterns of response to drought were found among 12 varieties of maize:

(a) Photosynthesis declined with leaf water potential, but without apparent stomatal control,

(b) Photosynthesis declined with leaf water potential and stomatal conductivity, and

(c) Photosynthesis declined with stomatal conductivity, but responded little to decreasing leaf water potential.

The carbon dioxide compensation concentration was increased by drought, showing that photosynthetic activity was depressed or that respiration increased independent of stomatal closure.

INTRODUCTION

The water requirements of a maize (*Zea mays* L.) crop growing during the dry season in the Philippines often exceed rainfall, and the moisture stress that results suppresses growth and markedly diminishes yield unless irrigation is used (Uichanco, 1954; Coligado, Aglibut, and Sandoval, 1963). In a temperate climate, soil water potential and leaf water potential were closely coupled during a drought of 15 days, and growth was reduced 18% presumably by a diminution of net photosynthesis (Shinn and Lemon, 1968).

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Increasing soil and atmospheric moisture deficits decrease photosynthesis of maize (Baker and Musgrave, 1964; Moss, Musgrave, and Lemon, 1961), but the relation between leaf water potential and photosynthesis of maize in the field has never been examined. Knowing the relation between leaf water potential and photosynthesis is important because leaves respond primarily to their inherent water status and only indirectly to the water status of the soil and atmosphere (Slatyer, 1967). Field techniques developed to distinguish varieties of crops that differ in their response of photosynthesis to drought are largely unknown. Therefore, our objectives in this study were to (a) examine the relation of photosynthesis to leaf water potential for maize undergoing drought in the field, and (b) to find maize varieties showing differences in their response of photosynthesis to drought in an experimental situation.

MATERIALS AND METHODS

These experiments were conducted between November 1965 and June 1966 at the Central Experiment Station, of the U.P. College of Agriculture, Los Baños, Laguna. The site, material, planting, and culture were described in detail earlier (Heichel and Musgrave, 1969a, b). Briefly, twelve varieties of maize were planted in a completely randomized design in 8- to 10-row plots on beds oriented east-west with rows oriented north-south. All material was grown concurrently. Seeds were planted by hand at 19 -cm intervals in rows 75 cm apart (69,000 plants per hectare). Each seed was planted so that leaves of each plant would be oriented at right angles to the row. This was the dry reason of a tropical monsoon climate, and the atmospheric evaporative demand was great. Since there was insignificant rainfall during the experiments, the authors supplied the crop with its total water supply by irrigation.

The plants were examined over a 9-day-period of increasing drought imposed by withholding irrigation from the crop. Irrigation was terminated 3 days before experiments started. Often leaves of less tolerant varieties wilted by the sixth day. Thus plants examined early experienced little stress, while plants examined later experienced up to 9 days of increasing internal stress.

Net photosynthesis (P) and leaf water potential (φ) were measured on the fifth or sixth leaf from the apex of the plant in the field during the ear-filling stage 2 weeks after pollination. One of these leaves was often

attached to the same node as the ear. All leaves were fully expanded 3 weeks before the experiments were started. Thirty plants of each variety were examined.

Net photosynthesis at 300 ± 3 part per million (ppm) cardon dioxide (CO_2) was measured by infrared analysis of CO_2 in the air surrounding attached leaves in an acrylic plastic, recirculating chamber that was only slightly larger than a leaf. The relative humidity was maintained between 45 and 55% at 32 C by condensing water on cold soils within the heat exchange unit of the chamber. The carbon dioxide compensation concentration, $[CO_2]$ c, was measured on two of the twelve varieties by closing the chamber, lowering the CO_2 concentration to 100 ppm and allowing the leaf to deplete CO_2 to a steady-state between photosynthesis and respiration. Net photosynthesis (mg CO_2 dm^{-2} hr^{-1}) was computed from flow, concentration, and leaf area measurements. All measurements were made at an irradiance of of 1.10 calories cm^{-2} min^{-1} of photosynthetically active (400–700 nanometers) radiation using an artificial light source previously described (Heichel and Musgrave, 1969a). This irradiance, measured with an Epply Model 15 Spectral Radiometer equipped with standard Schott filters, was found to be saturating for photosynthesis by comparison with full sunlight.

Leaf temperature, T, measured with a thermocouple appressed to the abaxial surface of the leaf, often increased above the normal 32±2 C as leaves became dried. Thus under conditions of nearly constant humidity in the leaf chamber, T was an index of stomatal conductivity (Gaastra, 1959; p. 46-51), because heat exchange between leaf and cooling coils became inadequate as the latent transfer through stomata was restricted. This technique gives a logical indication of stomatal function, but lacks the precision of a porometric measurement.

Leaf water potential was measured with thermocouple psychrometers having sensitivities of 0.37 to 0.40 microvolts per bar and calibrated with sodium chloride solutions supported on filter paper lining the sample chamber. Our psychrometers closely matched the published theoretical and design requirements (Rawlins, 1966; Dalton and Rawlins, 1968).

The leaves were washed with distilled water to remove osmotic contaminants about 30 minutes before P was measured. Immediately after determining P at 300 ppm CO_2 48-11 mm diameter discs were punched from each leaf directly into a psychrometer sample chamber, which was then sealed with a rubber stopper and taken to a field laboratory. The chamber

was sealed with silicone grease and placed in a water bath at 25 ± 0.001 C within 90 seconds of punching in the field. The time required to attain vapor equilibrium in the psychrometer depended upon ψ, but typically required 4 to 8 hours. Leaf water potential was corrected for tissue respiration (Barrs, 1964; Rawlins, 1966). Relative water content (RWC) of the leaf tissue of six varieties was also measured (Barrs, 1968).

Net photosynthesis was related to ψ and T by the regression $P = a + b\psi + cT$ which was as effective as any non-linear regression tested. The independent variables were entered in the regression only if they accounted for a significant (probability < 0.05) decrease in variation of P. This level of statistical significance applies to each independent variable in the regression equations which follow.

RESULTS

The statistical analysis partitioned the 12 varieties into three distinct groups based on the significance of the variable ψ and T (Table 1). The same range in φ was observed among the varieties within each of the

TABLE 1. *Regression equations relating net photosynthesis, leaf water potential, and an indicator of stomatal conductivity in 12 varieties of maize*

Variety	Regression Equation [a]	r [b]
GROUP I		
W22 x NY821	$P = 95.2 + 2.64\psi$	0.68
Ph13 x Ph17	$P = 76.0 + 2.7\psi$	0.56
Ph9	$P = 72.2 + 1.2\psi$	0.55
Ph10	$P = 57.0 + 1.6\psi$	0.43
GROUP II		
Ph9 x Ph11a	$P = 256.5 + 2.2\psi - 5.2T$	0.73
Ph13	$P = 90.8 + 1.4\psi - 1.4T$	0.61
Ph10 x Ph12	$P = 218.2 + 1.5\psi - 4.5T$	0.47
GROUP III		
Phil. Hy. 1d	$P = 212.6 - 5.0T$	0.69
L317	$P = 195.7 - 4.8T$	0.66
L316	$P = 213.8 - 5.1T$	0.57
Ph17	$P = 195.1 - 4.5T$	0.55
L316 x L317	$P = 217.9 - 5.8T$	0.43

[a] P = rate of net photosynthesis (mg CO_2 dm^{-2} hr^{-1}), U = leaf water potential (bars), and T = leaf temperature (C), an index of stomatal conductivity.
[b] All values of r are significant at the 5% level of probability.

three groupings. Individual varieties did not demonstrate exactly the same range because values of ψ were randomly sampled in this regression situation. The three groupings in the analysis are clearly different, and suggest that three distinct patterns of crop response to drought were observed among the 12 varieties. One example from each of these three patterns of response is reported in more detail.

Net photosynthesis declined with φ but not T in the first four varieties (Group I) in table 1. For example, φ of Ph9 decreased from -6.5 to -26.0 bars during the drying cycle, and P declined about 38% over this range of ψ (Figure 1). Leaf temperature was stable and displayed little variation throughout the experiment. These varieties were unique in that no wilting of leaves occurred during the drought.

Net photosynthesis declined as φ decreased and T increased in the fifth through seventh varieties (Group II) in table 1, exemplified by Ph9 x Ph11a in Figures 2a and 2b. Net photosynthesis declined about 85% at φ decreased from -7.0 to -22.0 bars. Leaf temperature increased as the plants dried, indicating that stomata progressively closed with drought (Figure 2a). Thus P declined with progressively increasing T during the drying cycle (Figure 2b), and leaves wilted and rolled as the drought progressed.

Net photosynthesis declined only with increasing T in the last five varieties (Group III) in table 1. For example, the hybrid Ph 1d showed a decrease in P of about 85% as T increased during the drying cycle (Figure 3a). Although about the same range in ψ (-8.5 to -24.5 bars) was observed in Ph 1d as in the previous two examples, P was not significantly correlated with φ (figure 3b). Note the more severe decrease of P with increasing drought when stomata are close (Figures 2 and 3) than when stomata are largely unaffected (Figure 1).

The $[CO_2]_c$ is attained by an illuminated leaf in a closed chamber when a steady state is reached between photosynthesis and respiration, and does not vary with stomatal diffusive resistance. The varieties of Group I (Table 1) did not display significant stomatal closure during the drought, suggesting that one of the effects of drought on P was non-stomatal in origin. This hypothesis was substantiated by comparing measurements of $[CO_2]_c$ on two varieties, one each from Groups I and III,

taken at the inception of drought (low stress) and again at the end of the drought (high stress) (table 2). The $[CO_2]_c$ was increased 36% in W22 x NY821 and 75% in L316 x L317 by drought. Both increases were significant at the 5% level of probability.

The regression of φ on RWC (figure 4) was calculated from observations of 180 leaves from 30 plants of each six varieties. There were no varietal differences in either the shape or slope of this regression A change of 1% RWC corresponds to a change in φ of 2.5 bars for the range of stress we observed, and the correlation coefficient r = 0.35 is significant at the 1% level of probability. The regression predicts that zero φ corresponds to about 97% RWC. Similar maximum values of RWC are commonly observed (Ehlig, 1966).

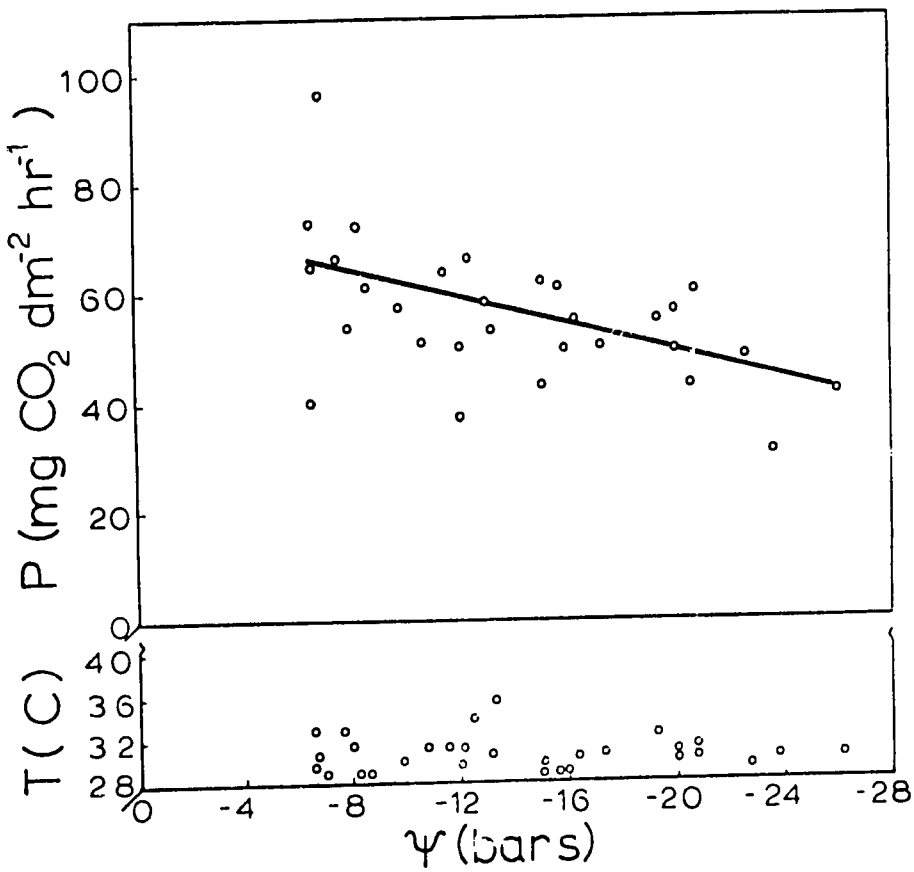

Figure 1. Relation of net photosynthesis and leaf temperature to leaf water potential for 30 leaves of inbred Ph 9.

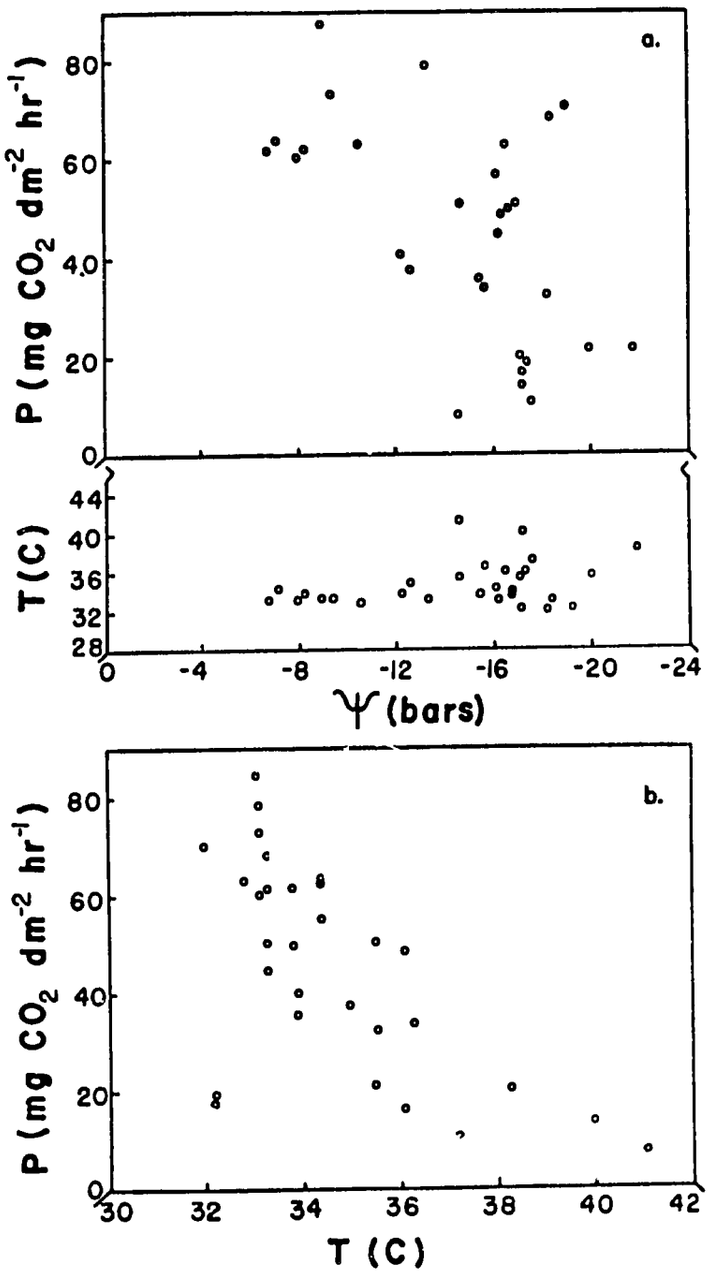

Figure 2a. Relation of net photosynthesis and leaf temperature to leaf water potential for 30 leaves of the hybrid Ph 9 x Ph 11a

2b. Relation of net photosynthesis to leaf temperature for the hybrid Ph 9 x Ph 11a.

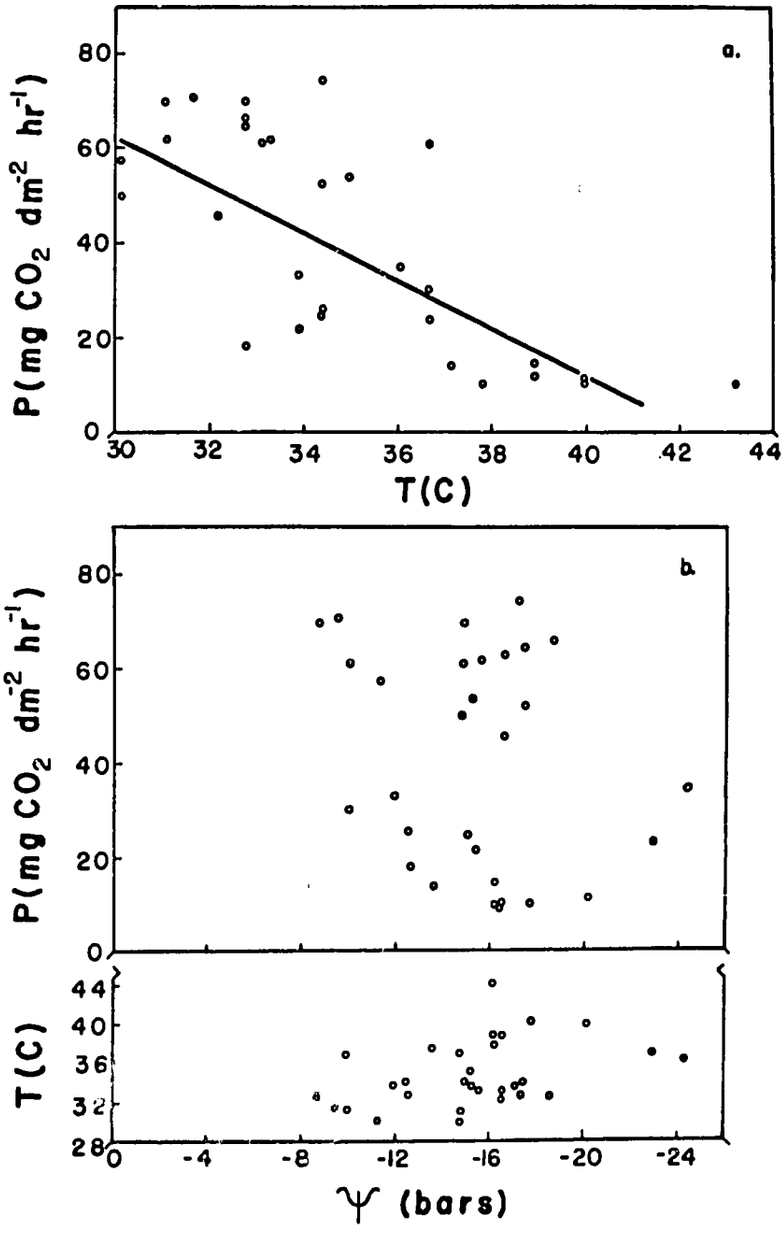

Figure 3a. Relation of net photosynthesis to leaf temperature for the hybrid Ph 1d.

3b. Relation of net photosynthesis and leaf temperature to leaf water potential for 30 leaves of the hybrid Ph 1d.

TABLE 2. *Increase of the carbon dioxide compensation concentration at 32 ± 2C with drought in two varieties of maize. Data are mean ± standard error of ten leaves*

Variety	$[CO_2]_C$ (ppm) Start of drought	End of drought
W22 x NY821	11 ± 1	15 ± 1
L316 x L317	16 ± 1	28 ± 1

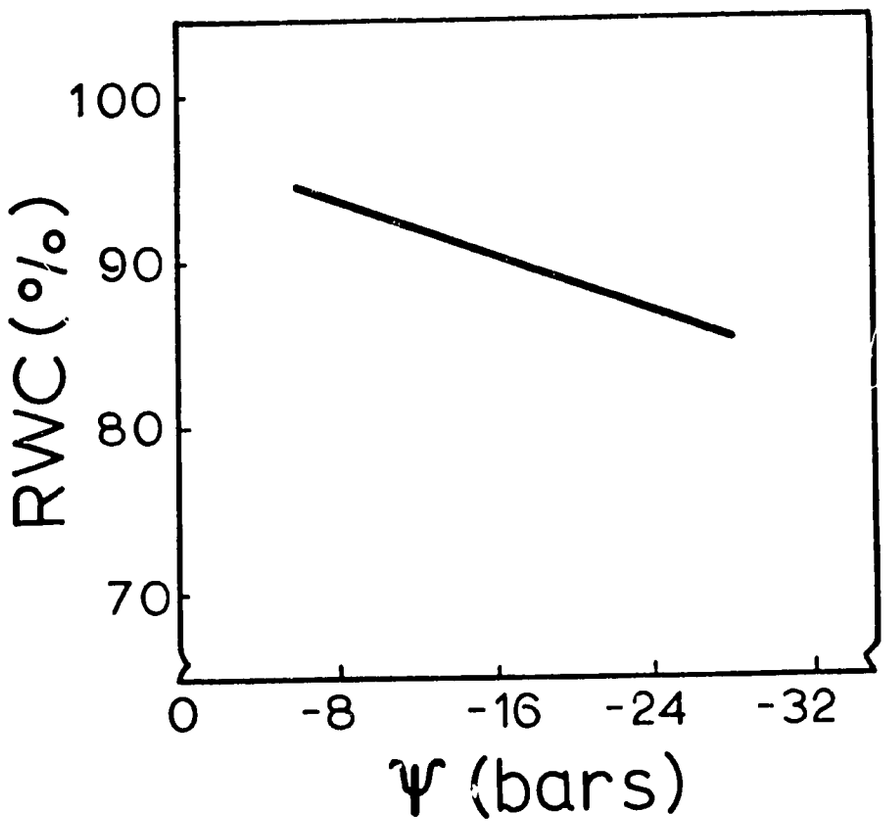

Figure 4. Relation of relative water content to leaf water potential for 180 leaves of maize. The regression shown is RWC = 96.9 + 0.4ψ, with Sy.x = 4% RWC and r = 0.35 ($P < 0.01$).

DISCUSSIONS

Moisture stress limits carbon dioxide exchange by two mechanisms. Stomatal conductivity decreases with increasing stress, limiting the carbon dioxide available for P. Moisture stress also directly affects non-stomatal components of CO_2 exchange. These latter components are often expressed as changes in mesophyll resistance (Slatyer, 1967).

The variability of the data in figures 1–3 deserves comment. Variation in P is small and uniform throughout the range of φ observed in figures 1, where stomata were not significantly altered by drought. Indeed, the variation in P at low moisture stress in the studies reported here was not greater than the plant-to-plant variation in P commonly observed among well-watered maize plants in the field (Heichel and Musgrave, 1969a). Once the stomata are modified by drought, the variability in P increases markedly, especially at low water potentials of −12 to −24 bars (figures 2 and 3). This behavior can be explained by an after-effect of φ on stomatal opening, characterized by a slow recovery of stomata after closure by drought (Glover, 1955; Fisher, Hsiao, and Hagan, 1970). The stomata likely recover from closure by drought more slowly than the general water balance of the tissue, resulting in a poor correspondence between stomatal aperture and φ. The diffusive resistance of partly closed stomata exerts a powerful control on P, so that the correlation between T and P is more clearly defined than the response of P to φ (figures 2 and 3).

Ph 9 (figure 1) was typical of varieties in which φ, but not T, caused a decrease in P. The lack of visible wilting and the uniformity of T implies that the stomata were stable, and that the depression of P was by non-stomatal action. This interpretation is supported by the significant increase in $[CO_2]$ c, which is normally low under field conditions (Heichel and Musgrave, 1969b), at constant leaf temperature during drought (table 2). Thus drought also depressed P by increasing respiration (e.g., Vaadia, Raney, and Hagan, 1961), decreasing photosynthetic capacity, or by a combination of the two factors.

Decreasing stomatal conductivity with drought, which was implied by wilting of leaves and demonstrated by increasing T, combined with the non-stomatal factors discussed above to decrease P in the second and third groups of varieties, exemplified by Ph 9 x Ph11a (figure 2) and Ph ld

(figure 3). Respiration may have risen with warming, which would also depress P, but temperature depression of P is unlikely in this range (Hofstra and Hesketch, 1969).

We tried to use the relation between φ and RWC (figure 4) to predict φ from RWC measured in the field. However, large standard errors were associated with predicted φ (e.g., RWC = 90% corresponds to $\varphi = -16.3 \pm 3.8$ bars), so we conclude that the relation had limited usefulness.

Our results support previous reports of non-stomatal effects of drought on photosynthesis of maize (Baker and Murgrave, 1964), but contrast with recent findings on cotton (Troughton, 1969). The manner in which drought depresses photosynthesis and the severity of this depression varies among varieties of maize. The partitioning of the varieties into three distinct groups in table 1 suggests that stomata of some maize varieties may be less susceptible than other varieties to closure by drought. Examining this hypothesis is a logical extension of the work reported here, and could be more easily tested with a ventilated diffusion porometer (e.g. Turner and Parlange, 1970) than with leaf chambers in the field. Indeed, finding varieties whose stomata and photosynthesis are more tolerant than others to drought may be one way of increasing productivity in arid climates.

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LITERATURE CITED

BAKER, D. N., and R. B. MUSGRAVE. 1964. The effects of low level moisture stresses on the rate of apparent photosynthesis in corn. Crop. Sci. 4:249-53.

BARRS, H. D. 1964. Heat of respiration as a possible cause of error in the estimation by psychrometric methods of water potential in plant tissue. Nature 203:1136-37.

——— 1968. Determination of water deficits in plant tissues. p. 235-368, *In* T. T. Kozlowski (ed.) Water deficits and plant growth. Vol. I. Acad. Press, New York.

COLIGADO, M. C., A. P. AGLIBUT, and A. R. SANDOVAL. 1963. Agricultural drought and its effect on corn. Phil. Agri. 46:602-17.

DALTON, F. N., and S. L. RAWLINS. 1968. Design criteria for Peltier-effect thermocouple psychrometers. Soil Sci. 105:12-17.

EHLIG, C. F. 1966. Water retention characteristics: plant leaves. p. 463. *In* P. L. Altman and D. S. Dittmer (ed.) Environmental Biology. Federation Amer. Soc. Exp. Biol., Bethesda, Md.

FISHER, R. A., T. C. HSIAO, and R. M. HAGAN. 1970. After-effect of water stress on stomatal opening potential. J. Exp. Bot. 21:371-85.

GAASTRA, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. Mededel. Landbouwhogesch., Wageningen. 59:1-68.

GLOVER, J. 1959. The apparent behavior of maize and sorghum stomata during and after drought. J. Agric. Res. 53:412-16.

HEICHEL, G. H., and R. B. MUSGRAVE. 1969a. Varietal differences in net photosynthesis of *Zea mays* L. Crop Sci. 9:483-86.

——— 1969b. Relation of CO_2 compensation concentration to apparent photosynthesis in maize. Plant Physiol. 44:1724-28.

HOFSTRA, G., and J. D. HESKETH. 1969. Effects of temperature on the gas exchange of leaves in the light and dark. Planta 85:228-37.

MOSS, D. N., R. B. MUSGRAVE, and E. R. LEMON. 1961. Photosynthesis Under field conditions. III. Some effects of light, carbon dioxide and soil moisture on photosynthesis, respiration, and transpiration of corn. Crop Sci. 1:83-87.

RAWLINS, S. L. 1966. Theory for thermocouple psychrometers used to measure water potential in soil and plant samples. Agr. Meteorol. 3:293-310.

SHINN, J. H., and E. R. LEMON. 1968. Photosynthesis under field conditions. XI. Soil-plant-water relations during drought stress in corn. Agron. J. 60:337-43.

SLATYER, R. O. 1967. Plant-water relationships. Acad. Press. New York. 366 p.

TROUGHTON, J. H. 1969. Plant water status and carbon dioxide exchange of cotton leaves. Aust. J. Biol. Sci. 22:289-302.

TURNER, N. C., and J-Y. PARLANGE. 1970. Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol. 46:175-77.

UICHANCO, E. I. 1954. The influence of sprinkler irrigation on the yield of corn grown from March to June. Phil. Agri. 37:578-86.

VAADIA, Y., F. C. RANEY, and R. M. HAGAN. 1961. Plant water deficits and physiological processes. Ann. Rev. Piant Physiol. 12:265-92.