THE HUMIDITY FACTOR IN STOMATAL CONTROL AND ITS EFFECT ON CROP PRODUCTIVITY

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ABSTRACT

Stomata of various woody and herbaceous plant species respond directly to changes in leaf-to-air vapor pressure difference (VPD). Closure of stomata upon exposure to dry air occurs in many species without changes in bulk leaf water status, suggesting an underlying mechanism different from the well-known closure through reduction in bulk leaf water potential. Recent studies in our laboratory on the response of cassava to water stress demonstrated that plants grown in pots or in the field, with and without soil water stress, were very sensitive to changes in atmospheric humidity. Both CO_2 uptake rate and H_2O loss decreased greatly as VPD increased. This decrease in gas exchange rate was associated with a reduction in leaf conductance in the absence of changes in leaf water potential. The strong stomatal response to changes in VPD may be of particular importance to perennial crops, such as cassava, that may have to endure a long period of drought. Under these conditions, and in the absence of stomatal response to humidity, both photosynthesis and transpiration will continue at relatively high rates until available soil water is depleted and leaf water potential drops to the level required to induce stomatal closure, at which time both photosynthesis and transpiration will approach zero. In such case, most of the transpirational loss will occur during periods of high VPD and low photosynthesis/transpiration ratio, resulting in a low dry matter accumulation per unit water transpired. On the other hand, with a direct stomatal response to changes in air humidity, available soil water will be depleted slowly, as most of the transpirational loss will occur during periods of the day when VPD is low and water use efficiency is highest. With a prolonged period of limited soil water, the greater water use efficiency will lead to a greater total accumulation of photosynthate over the stress period. Thus, the direct stomatal mechanism is beneficial for those crops that experience long period of drought. However, with nonlimiting soil water conditions or only short periods of soil water stress, optimizing water use efficiency would not be as important as maximizing photosynthesis and consequently crop productivity. Under these conditions nonsensitive stomata would be advantageous. An hypothesis is presented which relates stomatal sensitivity to stomatal density and is discussed in the light of selection methods for varieties with optimum productivity under differing conditions of air humidity and soil water availability.

INTRODUCTION

More than a century ago, Leitgeb [cited by G. Haberlandt (9)] noted that stomata of many plant species close upon exposure to dry air without visible symptoms of wilting. In 1937, it was reported by H. A. Razvi [Cited by D. Thoday (24)] that stomata of some succulent plants are sensitive to atmospheric humidity and the response is not correlated with the water content of the leaf as a whole. As suggested by Thoday (24), the epidermal water content and not that of the mesophyll is the factor directly affecting stomatal movement. More recent studies (13, 14, 20)

emphasized the importance of the peristomatal evaporation from the guard cells and their adjacent epidermal cells in the control of stomatal movement. These findings all suggest that stomata can respond to changes in atmospheric humidity irrespective of the bulk mesophyll water status. However, it has generally been supposed that water vapor exchange occurs across all of the exposed internal mesophyll surfaces (21). Kramer (12) cautioned against the proposed role of peristomatal evaporation until more information is available concerning the degree of cutinization of the inner surfaces of guard cells and mesophyll tissue. Nevertheless, many published reports in the last 15 years (1, 8, 10, 11, 16, 17, 18, 23) show that several plant species tend to close their stomata in response to dry air. This closure could be the result of a decrease in bulk leaf water potential as leaf-air vapor pressure difference (VPD) increased. However, El-Sharkawy and Cock (4) and El-Sharkawy et al. (6) have shown that stomatal closure in cassava will occur at high VPD without changes in bulk leaf water potential. The striking sensitivity of cassava to air humidity in absence of changes in leaf water potential, and the concomitant decrease in both CO_2 uptake and H_2O loss as VPD increased, encouraged us to expand our studies over a wide range of species to shed light on the mechanism underlying stomatal response to humidity.

The direct response of stomata to changes in humidity without changes in leaf water potential has important consequences to the ability of crop plants to withstand prolonged edaphic and atmospheric water stress. Therefore, we directed our efforts to a search for plant characteristics that correlate well with the stomatal sensitivity to air humidity and the possibility of genetic variation in those characters. In this report we confine our discussion to data, both published and unpublished, obtained in our laboratory at CIAT, Colombia, South America.

Leaf gas exchange characteristics, both CO_2 uptake and H_2O loss, as related to air humidity, were monitored using a standard differential infra-red gas analyzer and an electronic dew-point hygrometer connected to leaf chambers under controlled laboratory conditions (4). Gas exchange measurements were conducted in normal air (330 $\pm$ 15 μ LL^{-1} CO_2), near optimum temperatures and saturation light for CO_2 uptake. Later (3), the technique was modified to allow for field measurements of leaf CO_2 uptake using a syringe injection method and a ventilated hand-held leaf chamber.

RESPONSE OF CASSAVA TO HUMIDITY AND SOIL WATER STRESS UNDER CONTROLLED CONDITIONS

When lobes of attached leaves of well-watered and water-stressed cassava plants (Manihot esculenta Crantz) were exposed to a gradual decrease in VPD, rates of CO_2 uptake (P_A) decreased by 83% at the lowest tested range of VPD (Table 1). The transpiration rates of these leaves initially increased to a maximum at 2 kPa VPD and then declined by 75-80% at 3.5 - 4.5 kPa VPD. These trends in gas exchange rates corresponded to decreases in leaf conductance as VPD increased (Fig. 1). Moreover, the decline in leaf conductance was not associated with reduction in bulk leaf water potential (Y_L) during the measurement period of 5-6 hours. The Y_L of a lobe adjacent to that enclosed in the gas exchange leaf chamber was measured immediately before the start of each experiment. Final Y_L of the enclosed lobe was determined at the end of the gas exchange measurements. The Y_L was consistently lower in the stressed plants as compared with the controls. These results (Table 1 and Fig. 1) clearly demonstrate that the changes in gas exchange rates of cassava leaves in response to VPD were mainly due to changes in leaf conductance irrespective of plant water

status. The regressions of P_A, leaf conductance and the intercellular CO_2 concentration (C_i) over VPD all were negative with significant correlation coefficients (Table 2). On the other hand, the mesophyll conductance to CO_2 diffusion, showed either a weak or significantly positive association with VPD. All cassava cultivars tested behaved similarly. Figure 2 illustrates the observed decrease in C_i with increased VPD. These data imply that the decrease in leaf conductance, and consequently in P_A, was not confounded by internal changes in the mesophyll as a whole or in the photosynthetic apparatus as might have been the case had Ψ_L changed during the measurements.

Table 1.   Cassava apparent photosynthesis (P_A), transpiration (T), and bulk leaf water potential (Ψ_L) as affected by water stress and VPD. Values are means $\pm$ standard deviations.

Water Treatment	P_A		T		Ψ_L	
	1-1.5 kPa VPD	3.5-4.5 kPa VPD	2 kPa VPD	3.5-4.5 kPa VPD	Initial	Final
	μ mol CO_2 m^{-2}s^{-1}		m mol H_2O m^{-2}s^{-1}		MPa	
Well-watered	22.7 $\pm$ 2	3.8 $\pm$ 1	4.8 $\pm$ 0.3	1.2 $\pm$ 0.4	-0.69 $\pm$ 0.02	-0.65 $\pm$ 0.08
Stressed	14.5 $\pm$ 1.6	2.5 $\pm$ 1.5	2.8 $\pm$ 0.4	0.6 $\pm$ 0.4	- 1.0 $\pm$ 0.12	- 0.92 $\pm$ 0.17

Table 2.   Correlation between VPD and cassava apparent photosynthesis (P_A), leaf conductance, mesophyll conductance and intercellular CO_2 (C_i).

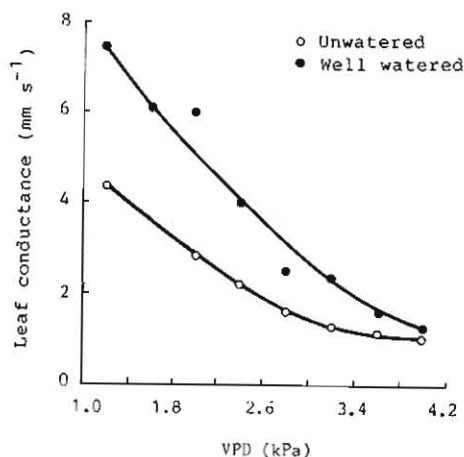| Cultivar/Water treatment	Correlation Coefficients (r)			
	P_A	Leaf Conductance	Mesophyll Conductance	C_i
M Col 88 Well-watered	- 0.55	- 0.67	0.37	- 0.36
M Col 88 Stressed	- 0.52	- 0.75	- 0.02 (NS)	- 0.40
Average of nine cultivars well-watered	- 0.76	- 0.79	0.22 (NS)	- 0.30

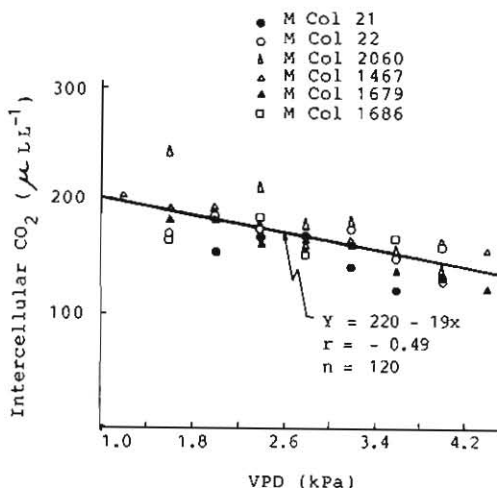NS: Not significant at 5%

Fig. 1. Leaf conductance as a function of VPD

Fig. 2. Intercellular CO_2 as a function of VPD. Points are means of cultivars.

Stomata of cassava leaves appear to be strikingly sensitive to humidity, as illustrated by their pronounced closure in dry air over a wide range of photosynthetic photon flux density (PPFD) (Fig. 3). Irrespective of plant water status, P_A dramatically decreased in dry air at all tested irradiance levels. At the lower range of VPD (> 1.5 kPa) the light-saturated P_A of the water-stressed plants were equivalent to the light-saturated P_A of the well-watered plants at the higher range of VPD (> 2.5 kPa). These rates were 50% greater than light-saturated P_A of the stressed plants at VPD > 2.5 kPa and 50% lower than light-saturated P_A of the well-watered ones at VPD > 1.5 kPa. Since stomatal conductance of the stressed plants were always lower than the well-watered plants at any given VPD (See Fig. 1), it appears that the corresponding differences in P_A between the water treatments are controlled by both stomatal and nonstomatal factors. This conclusion is further supported by the consistently higher C_i in the stressed plants over a range of leaf conductance that was induced by changes in VPD (Fig. 4). Regardless of the relative magnitudes attributable to stomatal and nonstomatal factors, however, it is apparent that stomatal control of P_A is predominant in cassava leaves.

RESPONSE OF FIELD GROWN CASSAVA TO AIR HUMIDITY

In a field experiment, CO_2 uptake rate of cassava leaves was determined over a range of relative humidity within the canopy induced by artificial misting. The cultivar M Col 1684 was planted at normal density (1 m x 1 m) on ridges of two adjacent plots (17 m x 50 m each). The plot to be misted was protected by rows of Pennisetum purpureum. High pressure misters were installed in one plot to provide intermittent misting from 1000h to 1500h daily. Furrow irrigation was applied weekly to both plots. The apparent CO_2 exchange rate of the upper mature canopy leaves which received PPFD greater than 1200 μ mol $m^{-2} s^{-1}$ was determined on several days using the syringe technique with the small hand-held ventilated leaf
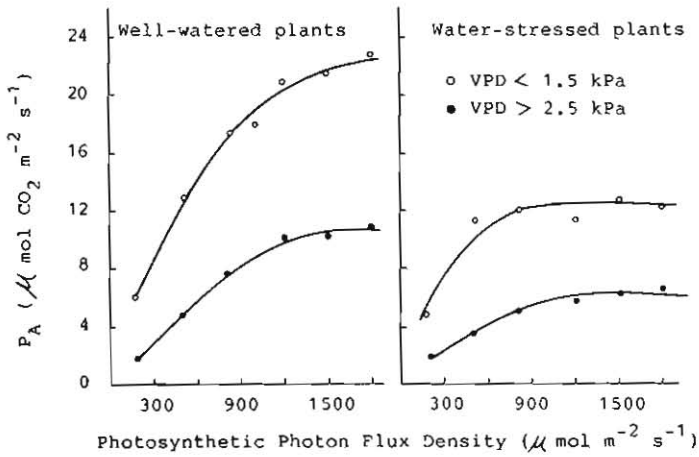
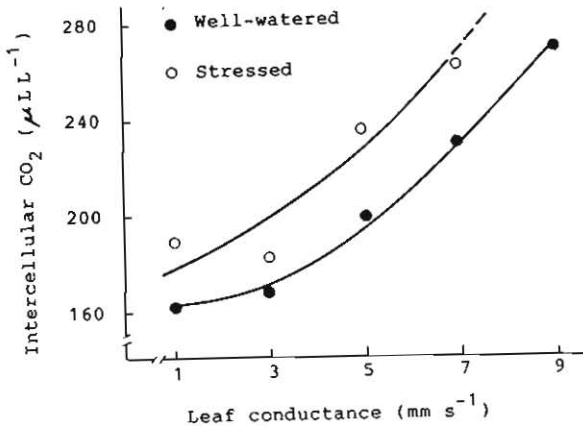Fig. 3. Leaf P_A as affected by light intensity, VPD and plant water status.

Fig. 4. Intercellular CO_2 as a function of leaf conductance and plantwater status.

chamber (3).

The P_A rate as a function of air humidity within the canopy is shown in Fig. 5. The photosynthetic rate increased linearly as air humidity increased suggesting that stomata of field grown cassava are sensitive to changes in humidity. The maximum obtainable P_A rate of 25 μ mol $CO_2 m^{-2} s^{-1}$ in the field at the higher range of humidity is equivalent to P_A rates obtained under controlled laboratory conditions at low VPD, as measured with a standard open system infra-red gas analysis. These results again confirm the pronounced effect of air humidity on leaf gas exchange through controlling stomatal movement. The misting trial was continued for two months throughout July-August, 1982. Sequential harvests were carried out every 3 weeks and dry matter yields were determined. There were substantial increases in dry root and total dry matter due to misting. Fig. 6 demonstrates the effect of misting on root dry weight. After 40 and 60 days of misting, there was 91% and 76% increase, respectively, in root yield over the control. At another experimental site, two plots were planted with the same cultivar in June and September, respectively, of the
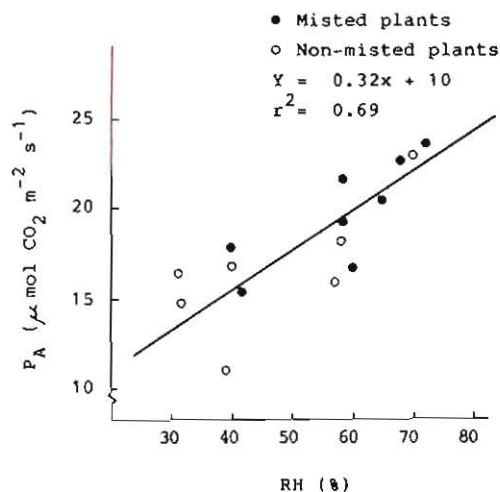
Fig. 5. Leaf P_A as a function
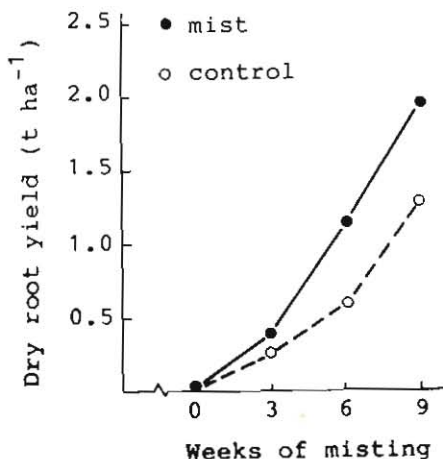by of relative humidity
at within canopy.

Fig. 6. Dry root yield as affected
artificial misting. Age harvest
is 65, 85 and 105 days for 0, 3,
6 and 9 weeks of misting, respec-
tively.

same year. Both plots were regularly irrigated to supplement natural rain-
fall over the first 6 months of growth. The September-planted plot
outyielded the June-planted one by 85% and 130% in total dry matter and dry
root, respectively (3). Since the two plots were well watered, the
difference in yield was partly attributed to the consistently lower
relative humidity during the June-September period than in the period of
September-December. The increase in dry matter under low VPD and in
absence of soil water stress was probably due to the greater stomatal
opening and higher P_A rates.

COMPARATIVE RESPONSE TO HUMIDITY OF CASSAVA AND
SOME HELIOPHYTE CROP SPECIES

Cassava's response to VPD under controlled conditions was compared
with several other crop species. All plants were grown outdoors in large
pots and were kept well-watered and adequately fertilized. Cassava showed
a greater sensitivity to VPD than other species tested (Table 3). The
dramatic decrease in P_A and leaf conductance with high VPD was associated
with a greater reduction in C_i for cassava. While cassava leaves showed no
changes in Ψ_L, other species with lesser degrees of sensitivity showed a
reduction in Ψ_L (e.g. maize Ψ_L decreased from -0.3 to -0.9 MPa before and
after exposure to dry air). It appears that the greater closure of stomata
in cassava reduced the total leaf transpiration and maintained a constant
Ψ_L (Fig. 7). On the other hand, maize leaves, with less sensitive
stomata, maintained higher and increasing transpiration with increased VPD,
and thus Ψ_L decreased. These contrasting responses indicate that under
high atmospheric evaporative demand, cassava is better able to reduce its
transpirational water loss through greater stomatal closure without
lowering plant Ψ_L.

Table 3. Response of local cultivars of some sun crop species to VPD as compared with cassava.

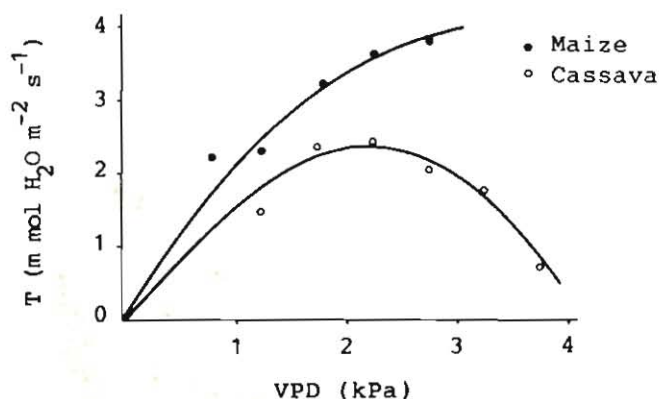| Species | 1 - 1.5 kPa VPD | | | Reduction at 3.5 - 4.5 kPa VPD | | |
	P_A	Leaf Conductance	Inter-cellular CO_2	P_A	Leaf Conductance	Inter-cellular CO_2
	μ mol CO_2 m^{-2} s^{-1}	mms^{-1}	μ LL^{-1}		%	
Maize	46	6	140	29	32	15
Field bean	25	6	210	26	29	16
Upland cotton	21	4	180	37	41	18
Tomato	27	7	215	33	32	23
Cassava	26	7	200	64	70	38

Fig. 7. Transpiration rate of cassava and maize leaves as a function of VPD.

COMPARATIVE RESPONSE TO HUMIDITY OF THE PARASITIC
MISTLETOE, Phthirusa pyrifolia AND ITS HOST,
THE MANDARIN ORANGE

During a study of the response of mandarin orange leaves to humidity a few seedlings were naturally infected with the parasitic mistletoe. The infected seedlings were grown in large pots outdoors and were adequately fertilized and irrigated. The gas exchange rates of both the parasite and the host were determined as a function of VPD. Both leaf conductance and apparent photosynthetic rate of the host declined rapidly with increased VPD (Table 4). The reduction in P_A was associated with reduction in intercellular CO_2.
Ψ_L varied from -0.6 to -0.75 MPa before and after exposure to dry air. On the other hand, P_A and leaf conductance of the parasite did not significantly change with VPD. The intercellular CO_2 of the parasite also did not show appreciable changes. It appears that the stomata of the host were much more sensitive to VPD than those of the parasite. The host and parasite leaves have a common pathway for liquid water flow through soil, host roots and stem, to the point of attachment and penetration of

the parasite haustoria into the host vascular tissue. Therefore, any differences in hydraulic conductivity between the host and parasite should lie somewhere beyond the host-parasite attachment point.

TABLE 4. Response of the parasitic mistletoe, Phthirusa pyrifolia, to VPD as compared with the host, mandarin orange.

Species	P_A	1 – 1.5 kPa VPD			P_A	Reduction at 3.5 – 4.5 kPa VPD		
		Leaf Conduc- tance	Inter- cellular CO_2			Leaf Conduc- tance	Inter- cellular CO_2
	μ mol CO_2 $m^{-2}s^{-1}$	mms^{-1}	μLL^{-1}			%	
Host	13	4	245	65	69	34
Parasite	8	6	295	9	15	-7

DISCUSSION

Stomatal movement is a complex phenomenon controlled by multiple plant and environmental factors (12, 15, 21). However, the direct role of VPD in controlling stomatal movement remained unappreciated until recently (8, 13, 14, 20). It has been generally assumed that the effects exerted by changes in VPD on stomata is expressed via changes in leaf mesophyll water status. Thus, it was widely accepted that stomata would close when leaf water potential decreased to a level sufficient to induce a loss of turgor in the guard cells (15, 12, 21). The rapid and remarkable response of stomata to VPD observed in cassava, as well as in several other species, without appreciable changes in bulk leaf water potential, has been clearly demonstrated [Tables 1, 3, 4, and (4, 6)]. Rates of CO_2 uptake and H_2O loss both decreased markedly at large VPD. A corresponding reduction occurred in leaf conductance and in the intercellular CO_2 concentration. This implies that stomatal closure in dry air, particularly in this highly sensitive species, was not primarily mediated via internal changes in the mesophyll.

The mechanism by which stomata react directly to changes in atmospheric humidity remains a debatable subject (13, 19, 25). In order to effect a stomatal closure in response to changes of VPD and in absence of a major reduction in bulk leaf water potential, a localized water stress in the stomatal apparatus and the adjacent epidermal cells must develop through evaporation from the exposed internal and external walls of the stomatal complex (13, 14, 20, 25). Water stress at the guard cells and the surrounding exposed epidermal cells is expected to be greatest in leaves with a large number of stomata per unit surface area and with greater hydraulic resistance between the bulk of the mesophyll and the epidermis (7). The greater the stomatal density the larger would be the area of exposed wall surfaces of guard cells. The reduced proportion of epidermal cells to buffer changes in Ψ of the guard cells may also be important. An illustrative example is the apparent and contrasting difference in stomatal density and mesophyll anatomy of the highly sensitive cassava leaf as compared with stomata and mesophyll anatomy of the much less sensitive mistletoe leaf (compare Figs. 8 and 9). Cassava leaves possess greater

stomatal density mostly or entirely on the lower surface (~ 500 stoma mm^{-2}). The figures also show a greater exposed area of epidermal cells around the stomatal apparatus of cassava. On the other hand, the mistletoe leaf has much lower stomatal density (98 and 130 stoma mm^{-2} on the upper and lower surface, respectively). The mesophyll of the mistletoe leaf is compact with few and small intercellular air spaces and shallow substomatal cavities. This anatomical system results in a reduced area of exposed walls in the vicinity of the stomata. Moreover, the better connection between the epidermis and the mesophyll should increase the hydraulic conductance toward the stomata of the mistletoe.
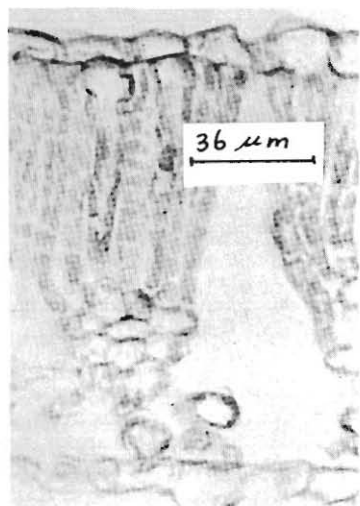

Fig. 8. Cross section of
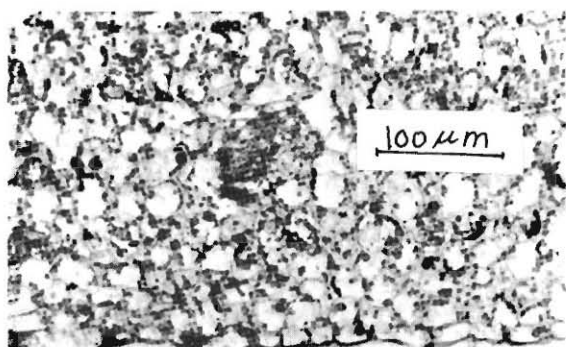   cassava leaf

Fig. 9. Cross section of mistletoe
          leaf.

The strong stomatal response to changes in VPD is particularly important in perennial or long season crops, such as cassava, that have to endure the long dry season commonly encountered during their production cycle. Under these stressful conditions, with stomata less sensitive to VPD, both CO_2 uptake and H_2O loss will occur at a relatively high rates until available soil water is rapidly depleted. The leaf water potential will then decrease to the level required to induce stomatal closure, at which time both photosynthesis and transpiration will approach zero. A greater proportion of daily transpirational loss will take place at periods of peak VPD. In such a case water use efficiency (WUE) either of a single leaf or of a crop canopy will be low. On the other hand, with a larger and more direct stomatal response to VPD, the limited amount of available water during the dry season will be consumed slowly, as transpirational loss will occur mainly in periods of lower VPD and higher WUE. This will lead to a greater total carbon gain over the stress period.

The water use efficiency of cassava as a C_3 crop is indeed much greater than that of field beans (C_3) which are less sensitive to VPD (Table 5). Moreover, WUE of cassava compares favorably with that of grain sorghum, a C_4 crop. Due to the greater harvest index of cassava, the amount of economic yield produced per unit water transpired in many cases exceeds that of grain sorghum. However, with nonlimiting water supply or with brief soil water shortage, maximizing total harvestable yield would be

of greater value than optimizing WUE. Under these conditions, varieties less responsive to changes in humidity would be more useful.

TABLE 5. Comparative water use efficiency of cassava, grain sorghum and field bean.

Species/ Carbon pathway	Water Use Efficiency		
	Single leaf gas exchange	Total biomass of field grown crops	Economic yield
	μ mol CO_2 $\overline{\text{m mol}^{-1} H_2O}$	g dry weight $\overline{\text{kg}^{-1}}$ water	g dry weight $\overline{\text{kg}^{-1}}$ water
Cassava C_3	5.3	2.9	1.7 (HI 60%)*
Sorghum C_4	6.2	3.1	1.2 (HI 40%)
Bean C_3	3.5	1.7	0.7 (HI 40%)
		%	
Cassava/sorghum	85	94	140
Cassava/bean	150	170	240

* HI: Harvest Index = $\dfrac{\text{Dry grain or Dry root} \times 100}{\text{Total dry weight}}$

The great sensitivity of the majority of the cassava cultivars tested led us to look for plant characteristics that might be an indicator of stomatal sensitivity to VPD. In a wide range of warm climate C_3 species, El-Sharkawy et al. (7) found that maximum photosynthesis is directly related to leaf conductance. Also, stomatal sensitivity to VPD was found to be positively correlated with both maximum conductance and stomatal density (Fig. 10). This indicates that selection for high P_A could be associated with greater sensitivity to VPD. In order to minimize stomatal sensitivity and at the same time select for high conductance and high P for wet conditions, it was hypothesized that selection of amphistomatous leaves with a lower stomatal density in either side would be useful (7). On the
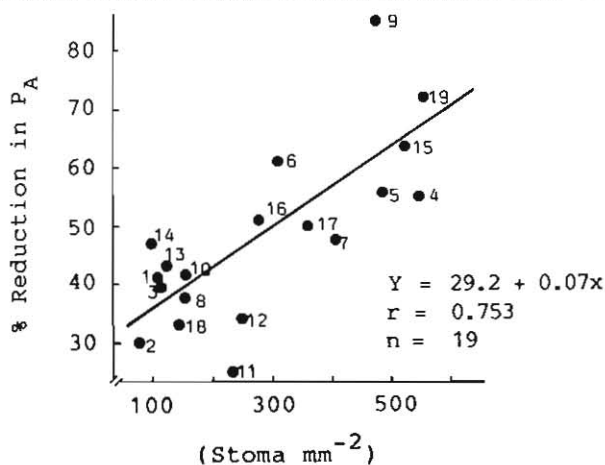

Fig. 10. Reduction in P_A as a function of stomatal density. Numbers indicate: sorghum (1), maize (2), andropogon (3), eucalyptus (4), mandarin (5), swinglea (6), papaya (7), cotton (8), cassava (9), cowpea (10), bean (11), mungbean (12), seed peanut (13), forage arachis (14), siratro (15), water-melon (16), squash (17), tomato (18), rice (19).

$Y = 29.2 + 0.07x$
$r = 0.753$
$n = 19$

other hand, crop cultivars expected to be grown under limited water supply coupled with high evaporative demand should be equipped with high stomatal density on one or both sides of the leaf, thus making them potentially efficient in terms of P_A and also sensitive to high VPD. Genetic variability in stomatal density and in the pattern of their distribution on the upper surface of the leaf are known to exist within species, including cassava (5). A few cultivars with significant stomatal density on the upper surface were recently isolated from the predominantly hipostomatous germplasm of cassava. It is important to study the reaction of some of these cultivars to VPD and to test the validity of the aforementioned hypothesis. Furthermore, research efforts should be directed toward other plant characteristics that might correlate with stomatal sensitivity to VPD, such as root length density in relation to leaf area (2, 22).

For a crop like cassava with its high sensitivity to air humidity, it would be beneficial to grow the crop in any convenient system of intercropping. The intercropping under nonlimiting soil water should improve the microenvironment within the canopy (e.g. elevated humidity) and thus enhance the photosynthetic rate and the yield of cassava. Under limiting soil water coupled with dry atmosphere, the use of windbreaks might be beneficial, particularly under rainfed conditions. In those cases where cassava is to be grown intensively under irrigation (presumably in semi-arid areas with large daily VPD) it would be wise to choose nonsensitive cultivars, if available, or adopt a combination of irrigation systems that might increase the humidity within the crop canopy.

REFERENCES

1. Aston MJ. Variation of stomatal diffusive resistance with ambient humidity in sunflower (Helianthus annuus). Aust. J. Plant Physiol. 3:489-501, 1976.
2. Bunce JA. Identifying soybean lines differing in gas exchange sensitivity to humidity. Ann. Appl. Biol. 105:313-318, 1984.
3. Cock JH, MCM Porto & MA El-Sharkawy. Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange of field grown cassava. Crop Sci. 25:265-272, 1985.
4. El-Sharkawy MA & JH Cock. Water use efficiency of cassava. I. Effects of air humidity and water stress on stomatal conductance and gas exchange. Crop Sci. 24:497-502, 1984.
5. El-Sharkawy MA, JH Cock & J de Cadena. Stomatal characteristics among cassava cultivars and their relation to gas exchange. Exp. Agric. 20:67-76, 1984.
6. El-Sharkawy MA, JH Cock & AA Held. Water use efficiency of cassava. II. Differing sensitivity of stomata to air humidity in cassava and other warm climate species. Crop Sci. 24:503-507, 1984.
7. El-Sharkawy MA, JH Cock & AP Hernandez. Stomatal response to air humidity and its relation to stomatal density in a wide range of warm climate species. Photosynth. Res. (in press), 1985.
8. Farquhar GD, E.-D. Schulze & M Kuppers. Responses to humidity by stomata of Nicotiana glauca L. and Corylus avellana L. are consistent with the optimization of carbon dioxide uptake with respect to water loss. Aust. J. Plant Physiol. 7:315-327, 1980.
9. Haberlandt G. "Physiological Plant Anatomy". McMillan and Co. London, 1914.
10. Jarvis PG. Stomatal response to water stress in conifers. pp. 105-122. In: Turner NC & Kramer PJ (ed.). Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York, 1980.

11. Kaufman MR. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. Plant Physiol. 69:1018-1022, 1982.

12. Kramer PJ. "Water Relations of Plants". Academic Press, New York, 1983.

13. Maier-Maercker U. The role of peristomatal transpiration in the mechanism of stomatal movement. Plant Cell Environ. 6:369-380, 1983.

14. Meidner H. Water vapour loss from a physical model of a substomatal cavity. J. Exp. Bot. 27:691-694, 1976.

15. Raschke K. Stomatal Action. Annu. Rev. Plant Physiol. 26:309-340, 1975.

16. Rawson HM, JE Begg & RG Woodward. The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. Planta 134:5-10, 1977.

17. Schulze E.-D. & AE Hall. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. pp. 181-230. In: Lange O.L. et al (ed.). Encyclopedia of Plant Physiology. Vol 12B. Springer-Verlag, Berlin, 1982.

18. Schulze E.-D., OL Lange, U Buschbom, L Kappen & M Evenari. Stomatal response to changes in humidity in plants growing in the desert. Planta 108:259-270. 1972.

19. Sheriff DW. The hydraulic pathway in Nicotiana glauca (Grah.) and Tradescantia virginiana (L.) leaves, and water potential in leaf epidermes. Ann. Bot. 50:535-548, 1984.

20. Sheriff DW. The stomatal aperture and the sensing of the environment by guard cells. Plant Cell Environ. 2:15-22, 1979.

21. Slatyer RO. "Plant Water Relationships". Academic Press, New York, 1967.

22. Taylor HM. Modifying root systems of cotton and soybean to increase water absorption. pp. 75-84. In: Turner N.C. & Kramer P.J. (ed.). Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York, 1980.

23. Tazaki TK, Ishihara & T. Ushijima. Influence of water stress on the photosynthesis and productivity of plants in humid areas. pp. 309-321. In: Turner N.C. & Kramer P. J. (ed.). Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York, 1980.

24. Thoday D. Stomatal movement and epidermal water-content. Nature 141:164, 1938.

25. Tyree MT & P Yianolis. The site of water evaporation from sub-stomatal cavities, liquid path resistances and hydroactive stomatal closure. Ann. Bot. 46:175-193, 1980.