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Relationships Among Water Potential Components, Relative Water Content, and Stomatal Resistance of Field-Grown Peanut Leaves[1]

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ABSTRACT

Limited data exist describing the physiological responses of peanut (*Arachis hypogaea* L.) plants to tissue water deficits. Detailed field experiments which accurately define the water status of both the plant and soil are required to better understand the effects of water stress on a peanut crop. The objectives of the present study were 1) to describe the changes in leaf water potential components during a drying cycle, and 2) to define the relationships among soil water content, leaf water potential, leaf turgor potential, relative water content, leaf-air temperature differential, and leaf diffusive resistance as water stress was imposed on a peanut crop.

During a 28-day drying period where both rainfall and irrigation were withheld from peanut plants, midday measurements of the physiological parameters and volumetric soil water contents were taken concurrently. As soil drying progressed, water extraction from the upper soil depths was limited as soil moisture approached 0.04 m^3m^{-3}. Leaf water potentials and leaf turgor potentials of nonirrigated plants decreased to approximately -2.0 and 0 MPa, respectively, by the end of the experimental period. Leaf water potentials declined only gradually as the average volumetric soil water content in the upper 90 cm of soil decreased from 0.12 to 0.04 m^3m^{-3}. Further reductions in soil water content caused large reductions in leaf water potential.

As volumetric soil moisture content decreased slightly below 0.04 m^3m^{-3} in the upper 90 cm, leaf relative water content dropped to 86%, leaf water potential approached -1.6 MPa and leaf turgor potential decreased to 0 MPa. Concurrently, stomatal closure resulted and leaf temperature increased above air temperature. Osmotic potentials measured at 100% relative water content were similar for irrigated and nonirrigated plants, suggesting little or no osmotic regulation.

Key Words: *Arachis hypogaea*, Drought, Leaf water potential, Osmotic potentials, Stomatal resistance, Turgor potential, Water stress.

Several studies of peanut crops have been conducted to determine water use rates, to identify growth stages which are particularly sensitive to water deficits, and to develop efficient techniques for scheduling water applications (9,10,12,15). However, many studies have been primarily concerned with the effects of water stress on yield and quality only, with little emphasis given to understanding the physiology of the peanut plant during the onset of tissue water deficits. Experiments have often been limited by the lack of information with which to quantify either the soil or plant water status, thus precluding valid comparisons among separate experiments (10).

Several physiological studies of peanut have focused on photosynthesis, translocation, stomatal resistance, transpiration, and respiration (3,4,6,8,11,14). A few studies have evaluated physiological responses of the peanut plant during water stress while concurrently defining the soil or plant water status (1,12,14). Phloem sap exudation during attempts to measure xylem water potential with the pressure chamber has undoubtedly hampered progress in the area of water relations (1,12). However, by utilizing thermocouple hygrometers, several researchers have reported leaf water potentials as low as -3.0 to -4.0 MPa in water stressed peanut leaves (1,5,12). Recently, Bennett *et al.* (2) used thermocouple psychrometers to effectively measure both osmotic and total water potentials of peanut leaves.

Pallas *et al.* (12) reported an increase in stomatal resistance as leaf water potential of peanut declined during water deficits which were imposed at several growth stages. Bhagsari *et al.* (5) observed large reductions in photosynthesis and stomatal conductance as relative water content of peanut leaves decreased from 80 to 75%. Slatyer (14) reported that dry matter accumulation and transpiration rate of peanut was first reduced when relative water content of the leaves dropped below 90%.

Although some information exists concerning the physiological responses of peanut to water stresses, detailed field experiments are required to describe the responses and relationships of many processes. The relationships among the components of leaf water potential, stomatal activity, and soil moisture content have not been fully described for a peanut crop. Therefore, the objectives of the present study were: 1) to describe the

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changes in peanut leaf water potential components during a natural drying cycle, and 2) to define the relationships among soil water content, leaf water potential, leaf turgor potential, relative water content, leaf-air temperature differential, and leaf diffusive resistance as water stress was imposed on a peanut crop.

Materials and Methods

The present study was conducted using peanuts (*Arachis hypogaea* L., cv. Florunner) grown as part of a larger experimental area which included several irrigation management treatments. Procedural details reported in this section apply only to one irrigation treatment which was selected for this particular study.

The experimental plot was hand planted on a Kendrick fine sand (a member of the loamy siliceous, hyperthermic family of Arenic Paleudults) with Florunner peanut on April 1, 1981. Seeds were planted in 76 cm rows and established plants were thinned to approximately 10 plants m^{-1} of row on April 21, 1981, resulting in a final plant population of approximately 132,000 plants ha^{-1}. Fertilizer (0-10-25) was applied at the rate of 785 kg/ha^{-1} and incorporated before planting. Weed control was achieved with preplant and cracking stage herbicides. Periodically, the experimental area was sprayed to control both insects and foliage diseases.

Data reported were taken from an area comprising an optimally irrigated treatment within the larger experimental area. Within the selected treatment, one half of the plants remained optimally irrigated while the remaining area consisted of two locations, each covered by a portable rain shelter (4.3 m x 4.9 m) to exclude both irrigation and rainfall. The rain shelters were placed over the crop only at night and when rainfall was imminent. Previous experiments indicated that the rain shelters were quite satisfactory on the sandy soils where this experiment was conducted. There was little evidence of lateral water flow into the soil which was covered by the rain shelters.

Irrigation water was applied to the optimally irrigated treatments whenever the soil water potential at 15 cm declined to -15 to -20 KPa. On June 12, 1981 (73 days after planting), rain shelters were placed on the designated locations. The treatment period began at the R5 growth stage as defined by Boote (7). On June 18, 1981 a thunderstorm damaged the portable rain shelters and allowed a small amount of rainfall (estimated at less than 0.6 cm) to fall on the drying treatments. The rain shelters were repaired the following day and the treatments remained free of rainfall until the completion of the measurements.

During the treatment period, which lasted 28 days, midday measurements of leaf water potential (Ψl), leaf osmotic potential ($\Psi\pi$), percent relative water content (RWC), air temperature, leaf temperature, leaf diffusive resistance, and volumetric soil moisture content were periodically collected. For the plant measurements, two locations were selected in both the irrigated and sheltered portions of the plot. Three uppermost, fully expanded main stem leaves within each location were selected and tagged, giving a total of six measured plants from each treatment. All leaf measurements were conducted during full sunlight between 1200-1400 hours EDT.

Stomatal resistance, leaf and air temperatures.

A steady-state diffusion resistance porometer (Li-Cor Model LI-1600) was used for measuring ambient temperature, leaf temperature and leaf diffusive resistance on one leaflet of the pre-selected leaves. Measurements on the abaxial and adaxial leaf surface were made and total leaf resistance was calculated assuming the resistances act in parallel.

Leaf water potential components.

Immediately following measurements with the porometer, two of the four leaflets of each leaf were sampled for measurements of leaf water potential components. One of the two remaining leaflets was also harvested and placed in a humidified vial for determination of RWC.

Four 1-cm diameter leaf discs (two discs from each of two leaflets) were removed, quickly placed in a sample chamber, and attached to a thermocouple psychromter (J. R. D. Merrill Speciality Equipment Co. Model 84-13). The thermocouple psychromter assembly was then transported to the laboratory and placed in a thermostatically controlled water bath at 30 C. After 4 h of vapor and temperature equilibration, the psychrometric output was recorded using a strip chart recorder and a dewpoint microvoltmeter (Wescor Model HR 33T) operating in the psychrometric mode. Leaf water potential was determined by comparing the outputs to calibration curves which were constructed individually for each thermocouple psychromter using NaCl solutions. The thermocouple psychrometer units were then removed from the water bath, frozen at -15 C for 12 hours before $\Psi\pi$ was determined on the thawed tissue in a similar manner to that described above. Leaf turgor potential (Ψp) was calculated as $\Psi p = \Psi l - \Psi\pi$. Although slight underestimations of $\Psi\pi$ may occur because of dilution of the cell sap by apoplastic water after freezing and thawing, this error was previously found to be small until severe desiccation occurred (2).

Relative Water Content.

For RWC, the harvested leaflet was weighed, floated on deionized water for 4 to 6 h, reweighed, and oven-dried at 80 C for 12 h. Previous studies had shown that very little water uptake occurred after 4 h. Weight of the oven-dry leaflet was then determined. Relative water content was calculated as:

$$\%RWC = \frac{\text{Fresh weight - Dry weight}}{\text{Turgid weight - Dry weight}} \times 100$$

Osmotic potential at full turgor.

Determinations of osmotic potential at 100% RWC ($\Psi\pi^{\circ}$) were also made on three dates during the experimental period. Leaves from each treatment were harvested at 0730 hours EDT and floated on deionized water for 4 h. Leaf discs were blotted dry and then placed in thermocouple psychrometer units and frozen before $\Psi\pi^{\circ}$ was determined on the thawed tissue as described above.

Soil moisture measurements.

Gravimetric measurements of soil water content were taken at each sampling location each day after measuring the plant water stress parameters. Soil water content was determined for three depth intervals, 0-15 cm, 15-45 cm, and 45-90 cm. Gravimetric soil water content data were then converted to volumetric soil water content by multiplying by the bulk density of the soil at the corresponding depth. A few water content measurements were collected at depths greater than 90 cm, but due to a clay layer which fluctuated in depth, data were quite variable. For purposes of this study, only the soil moisture contents in the 0-90 cm depths are considered. Previous experience has suggested that peanut growth is most affected by soil water in this sandy layer of soil.

Results and Discussion

Volumetric soil water contents measured during the drying period at three depths down to 90 cm indicated that soil moisture remained relatively high in the irrigated treatment, but declined quite rapidly at the shallow depths in the nonirrigated treatments (Figure 1). The systematic fluctuations in the soil water contents for the upper soil profile of the irrigated treatments reflect rainfall and irrigation events. A thunderstorm damaged the rain shelters on day 7 of the drying period but soil moisture measured on day 11 does not suggest an increase in water content, indicating that only a small amount of rain fell on the nonirrigated treatments. After day 11 of the drying period, water extraction by the nonirrigated peanut crop was primarily from the deeper soil profile as indicated by continued reductions in soil water content between 45 and 90 cm. As the volumetric soil water content dropped to about 0.04 m^3m^{-3} in the upper soil profile, water extraction from those depths by the nonirrigated plants was reduced.

Both irrigated and nonirrigated plants showed appreciable water uptake deep in the soil profile. In fact, a limited number of soil water content determinations below 100 cm indicated that the plants in both treatments were extracting water from deeper subsoil horizons (data not shown). Similarly, water extraction and roots of peanut plants at depths of 120 cm and deeper have been reported by others (1,13,15). Deep penetration of peanut roots and water extraction from deeper, heavier textured subsoils which are capable of providing larger amounts of available soil water may offer drought-avoidant capabilities to the peanut crop. However, data to follow

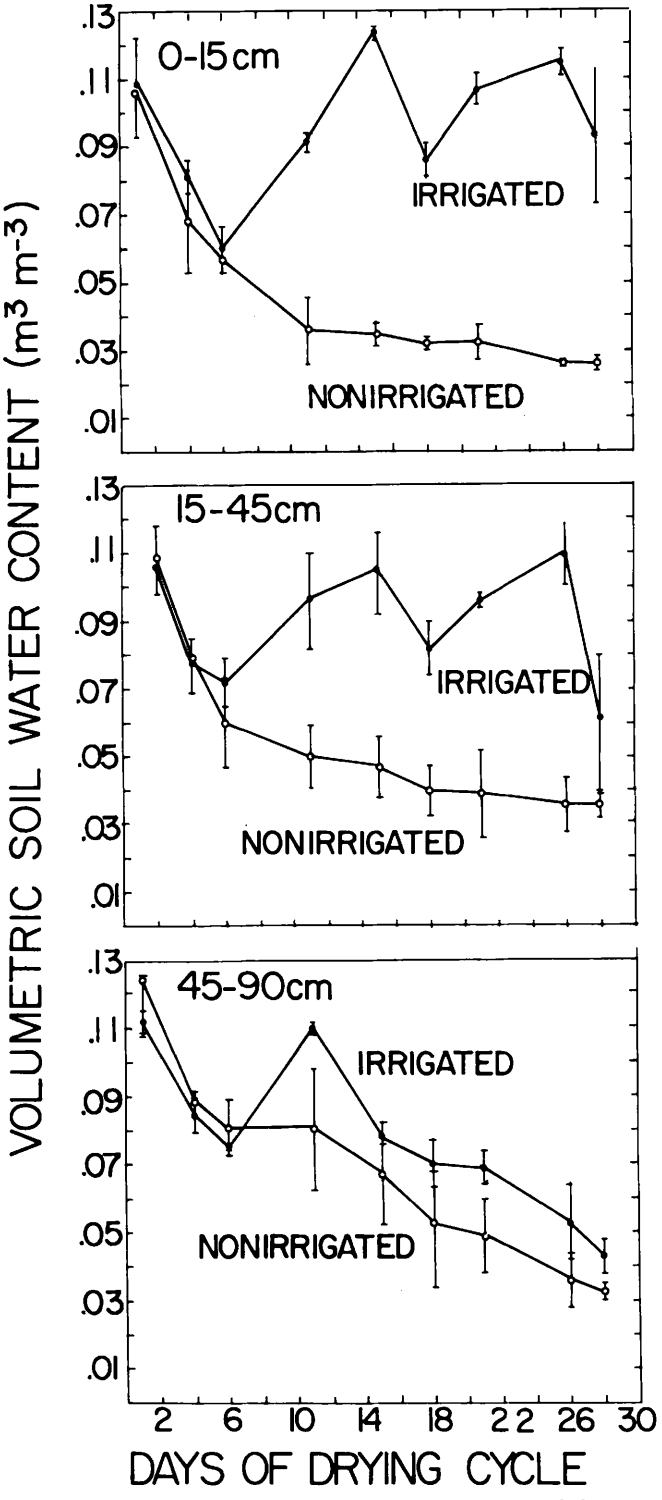

Fig. 1. Volumetric soil water contents at three depth intervals for irrigated and nonirrigated peanut plants during a 28-day drying cycle imposed at Gainesville, Florida, in 1981. Vertical bars represent the standard error of the mean.

suggests that the upper layers of the profile must be moist to avoid plant water deficits.

Leaf water potentials (Ψl) and leaf turgor potentials (Ψp) of irrigated plants remained between -0.6 to -1.1 MPa and 0.3 to 0.6 MPa, respectively, throughout the experimental period (Figure 2). Some of the day-to-day variation in the irrigated treatment was probably due to irrigation, rainfall, or slightly differing environmental

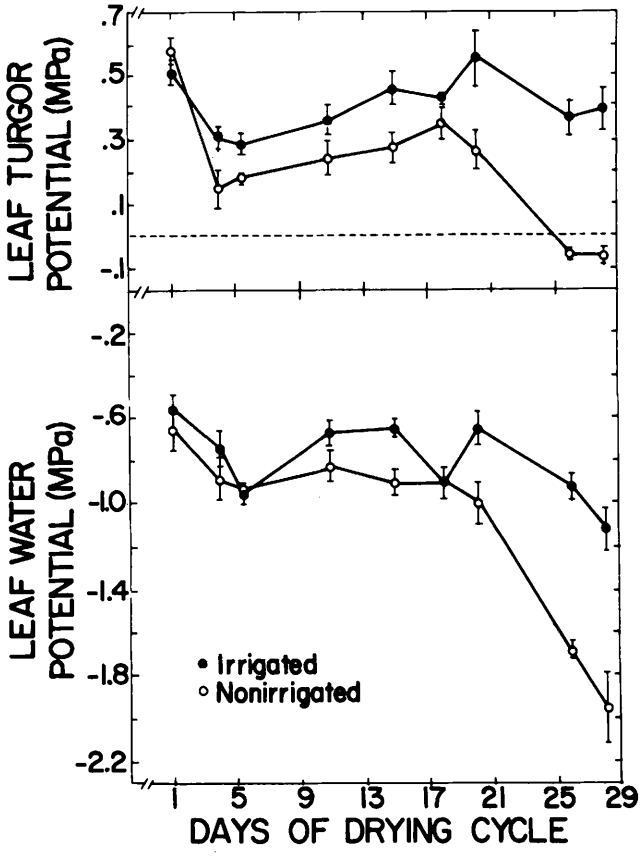

Fig. 2. Leaf turgor potentials (upper) and leaf water potentials (lower) of irrigated and nonirrigated peanut plants during a 28-day drying cycle imposed at Gainesville, Florida, in 1981. Vertical bars represent the standard error of the mean.

conditions. Pallas (12) also reported midday peanut Ψl in the range of -0.5 to -1.0 MPa. Both Ψl and Ψp declined in the nonirrigated plants as the duration of the drying period increased. Although slight differences in Ψp appear to be present as early as the fourth day of the experiment, distinct Ψl and Ψp differences between irrigated and nonirrigated plants were observed only after 11 days of withholding water. Slight increases in Ψp of nonirrigated plants between day 7 and 18 are probably related to varying environmental conditions or may be a result of the small amount of rain which fell on the plots on day 7. Drastic reductions in Ψl and Ψp of the nonirrigated plants occurred between day 20 and 26 of the drying period. Calculated negative Ψp on days 26 and 28 probably resulted from a slight underestimation of $\Psi\pi$ caused by dilutions of the cell sap by apoplastic water during the freezing and thawing of the leaf tissues. Assuming that the tissue actually approached zero Ψp, it is evident that the errors involved in the procedure for estimating $\Psi\pi$ were slight.

Leaf water potentials in this experiment only decreased to -2.0 MPa and were not as low as some reported by other investigators (1,12). Although the plants appeared stressed at midday by the end of the study, the plants were turgid at midmorning. It is likely that somewhat lower Ψl would have been measured if the stress cycle had been prolonged. However, as will be shown later, stomatal closure occurred rapidly at zero Ψp and further tissue water loss would be expected to be slowed considerably after stomatal closure occurred. Data pre-

sented in Figure 2 clearly show a rather gradual imposition of tissue water deficits until day 20 at which time stress development became more rapid.

Data from both the irrigated and nonirrigated treatments for all measurement dates were pooled to define the relationships among the measured parameters. Figure 3 demonstrates the effect of volumetric soil water content (averaged over the 0 to 90 cm depth) on midday peanut Ψl. Between soil water contents of 0.12 and 0.04 m^3m^{-3}, Ψl declined slowly from approximately -0.6 to -1.0 MPa. Further reductions in soil water content below 0.04 m^3m^{-3} caused sharp reductions in Ψl. Data presented in Figure 1 suggested that water extraction was reduced at a similar volumetric soil water content. Although the reduced water uptake seemed to occur in soil which was dried to 0.04 m^3m^{-3}, the total depth of soil which can be depleted to those moisture contents before growth completely ceases was not determined in this study and deserves further evaluation.

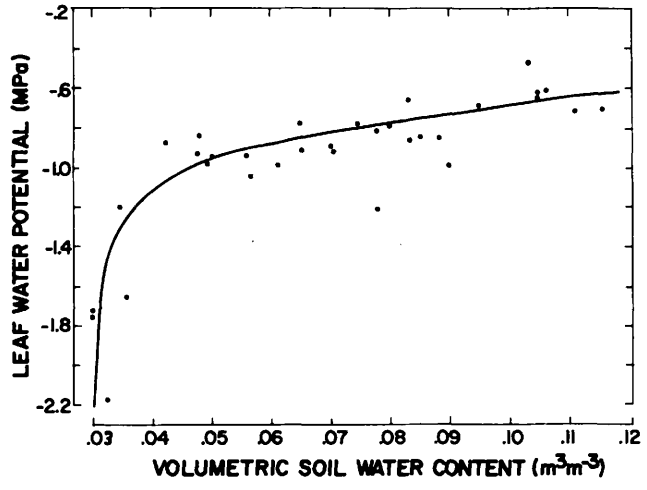

Fig. 3. The relationship of volumetric soil water content (averaged over a 0-90 cm depth) and peanut leaf water potential.

Leaf turgor potential declined as Ψl decreased from -0.4 to -1.6 MPa (Figure 4). Maximum midday Ψp measured in this study was approximately 0.7 MPa. Zero Ψp was approached as Ψl fell below -1.6 MPa. Similar relationships were previously found for peanut leaves which were artificially dried in the laboratory (2).

At high values of Ψp, relative water contents (RWC) were approximately 95 to 97% (Figure 5). As RWC decreased from 97% to 87%, Ψp dropped from 0.7 MPa to zero. Minimum RWC measured in the present study was somewhat higher than that at which photosynthesis was reduced and stomata closed in the experiment conducted by Bhagsari *et al.* (5), but similar to RWC reported by Allen *et al.* (1) for water stressed peanut leaves.

Figure 6 shows that little change in stomatal resistance occurred as Ψl and Ψp remained above -1.4 and 0.1 MPa, respectively. Rapid increases in stomatal resistance occurred as Ψl and Ψp dropped below those values. Pallas *et al.* (12) reported a 5-fold increase in diffusive resistance as Ψl of peanut leaves reached -3.0 MPa. As stomata closed and diffusive resistance increased, leaf temperature also increased above air temperature as a result of decreased transpirational cooling of the leaf

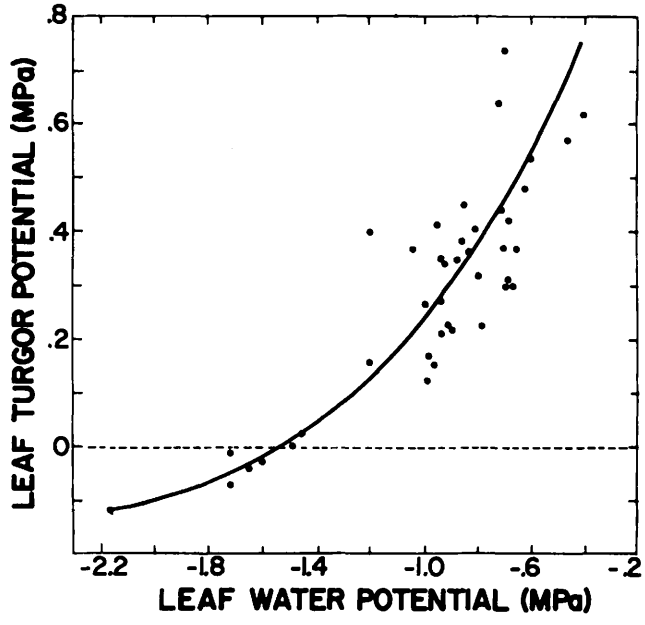

Fig. 4. The relationship of leaf water potential and leaf turgor potential of peanut leaves. Each point represents the mean of three leaves.

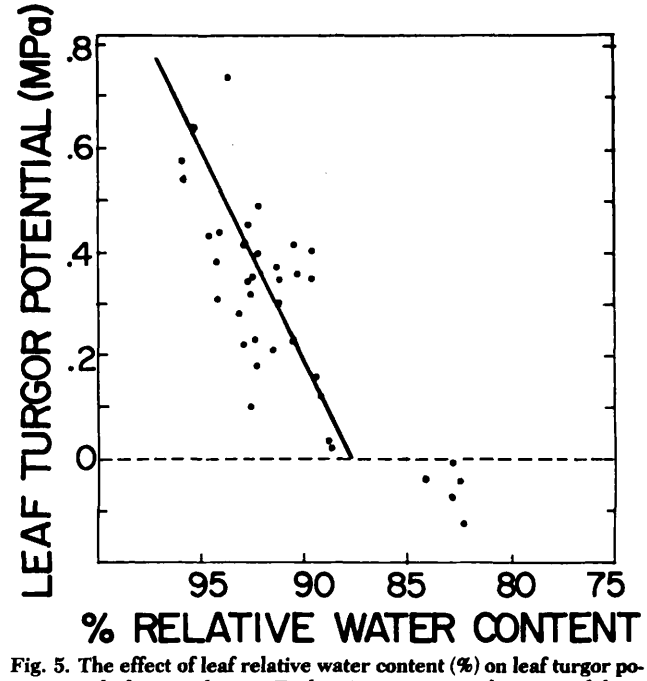

Fig. 5. The effect of leaf relative water content (%) on leaf turgor potential of peanut leaves. Each point represents the mean of three leaves.

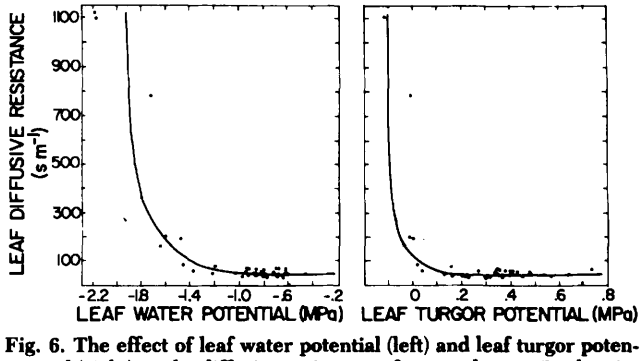

Fig. 6. The effect of leaf water potential (left) and leaf turgor potential (right) on the diffusive resistance of peanut leaves. Each point represents the mean of three leaves.

(Figure 7). At low diffusive resistance values, the leaf-air temperature differential fluctuated considerably but was generally at or below zero, indicating that the leaf was cooler than the air.

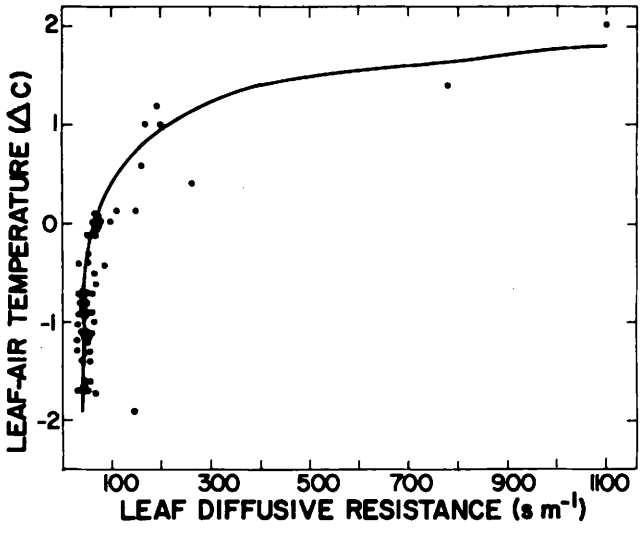

Fig. 7. The relationship of leaf diffusive resistance to leaf minus air temperature. Each point represents the mean of three leaves.

Measurements of the osmotic potential at 100% RWC ($\Psi\pi^\circ$) gives an indication of osmotic adjustment which occurs in some plants during water stress. Midday Ψl differences between irrigated and nonirrigated plants became larger as the drying period progressed from day 18 to day 26 (Table 1). Measurements of $\Psi\pi^\circ$ on dates where midday Ψl differences were apparent (days 20 and 26) indicate very little differences in $\Psi\pi^\circ$. These results suggest that if osmotic regulation occurred at all during the drying cycle, it was indeed very small or did not persist overnight as the tissue rehydrated. Since the tissue for determination was harvested in early morning, these data may not reveal diurnal osmotic adjustments as tissue water deficits developed from morning to midday. Furthermore, since midday osmotic potential of nonirrigated plants decreased from approximately -1.1 MPa to -2.0 MPa by the end of the stress period, while RWC fell from 95% to only 82%, it is suggested that some daily osmotic regulation occurred in response to midday tissue water deficits. However, this adjustment did not persist overnight (Table 1).

Table 1. Midday leaf water potentials (Ψl) and osmotic potentials at full turgor ($\Psi\pi^\circ$) of irrigated and nonirrigated Florunner peanut leaves.

Day of Drying Cycle	Nonirrigated		Irrigated	
	Ψ_l	$\Psi_\pi{}^\circ$	Ψ_l	$\Psi_\pi{}^\circ$
	MPa			
18	-0.90 ± 0.07	-1.26 ± 0.05	-0.88 ± 0.05	-1.17 ± 0.05
20	-1.00 ± 0.10	-1.33 ± 0.04	-0.66 ± 0.08	-1.14 ± 0.07
26	-1.68 ± 0.40	-1.16 ± 0.05	-0.92 ± 0.06	-1.29 ± 0.06

Conclusions

Evidence presented in this study suggests that the drought resistance often attributed to a peanut crop is related to factors other than unique relationships between stomatal resistance, leaf water potential components, and leaf water content. Since peanut stomata close as Ψl decreases below -1.6 MPa, it is unlikely that the peanut plant is capable of maintaining significant carbon exchange at Ψl lower than those attained by many other agronomic crops. Although the exact drought resistance mechanisms of peanut deserve further study, factors such as the ability to maintain relatively high tissue water status during periods of low soil water and an ability to maintain developmental plasticity are probably partially responsible for peanut's drought resistance.

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