

STOMATAL BEHAVIOUR AND WATER STATUS OF COWPEA
AND PEANUT AT LOW SOIL MOISTURE LEVELS

M. C. NWALOZIE* and D. J. M. ANNEROSE

CENTRE DE RECHERCHE REGIONAL POUR L'AMÉLIORATION DE L'ADAPTION A LA SECHERESSE
(CERAAS)/ISRA/CNRA, B. P. 59 BAMBEY, SENEGALNWAL
PHYS
12

(Received: 14 June, 1995; accepted 25 January, 1996)

The drought resistance characteristics of three genotypes each of *Vigna unguiculata* (cowpea) and *Arachis hypogaea* (peanut) were evaluated on a comparative basis to determine the diverse approaches these species utilize in their resistance to soil moisture stress. Stomatal closure during soil moisture stress was significantly more rapid in cowpea than in peanut. When plants were rewatered the stomatal conductance in recovering cowpea was higher than that in peanut. Also, at more negative osmotic concentrations of unsaturated salt solution, the leaf tissue of water-stressed cowpea retained a higher relative water content than that in peanut. Whereas the temporary wilting point (TWP) in cowpea was 78% relative water content (RWC), peanut leaves entered permanent wilting status (PWS) below 55% RWC. However, leaves that had not passed TWP recovered on rehydration. In spite of the low RWC in peanut, the relative fruit yield per unit weight of shoot material was not significantly reduced, as distinct from the situation in cowpea where relative yield was affected by the stress.

Key words: *Arachis hypogaea*, *Vigna unguiculata*, drought resistance strategies

Introduction

Water is one environmental factor that has a great effect on stomatal resistance under field conditions (Turner, 1974). At high soil moisture, the diurnal range of stomatal resistance in maize, sorghum and tobacco resulted from changes in incident radiation. Turner and Begg (1973) observed that as the turgor potential decreased with decreasing leaf water potential tobacco wilted at higher leaf water potential than maize, and maize at a higher leaf water potential than sorghum. Stomatal conductance, therefore, is a major factor controlling plant water loss, and is considered as a veritable tool in assessing drought resistance (Matin et al., 1989).

Loss of water from turgid leaf tissue in response to transpiration results in not only a significant decline in water potential, but also a decline in osmotic potential. Therefore, plants in this condition must be capable of adjusting so as to sustain appropriate stomatal movements, photosynthesis and cell elongation during water stress, and develop enhanced dehydration tolerance, increased capacity for soil moisture uptake, and delayed leaf mortality (Ludlow, 1980; Turner and Jones, 1980; Morgan, 1984; Turner, 1986).

It has been reported (Hall, 1981) that in the middle of the day cowpeas which had not received rain or irrigation for two or three months exhibited leaf water potentials that were only 2 bars more negative than plants irrigated weekly. Also, peanuts have been observed to survive for more than eight weeks in the field

without any form of irrigation (Annerose, 1990). The present study was, therefore, carried out to explain the higher leaf relative water content (RWC) frequently observed in cowpea than in peanut during drought. RWC is one important parameter used in determining plant water status during drought. This study appraises the potential strategies of these species, grown in semi-arid Senegal and other sub-Saharan countries, in resisting a prolonged drought.

Materials and methods

Plant materials

Three genotypes of cowpea (*Vigna unguiculata*) and three of peanut (*Arachis hypogaea*) were studied. The cowpea genotypes were IT84S2246-4 (tagged CV₁ for the purpose of this study), TVU3000 (tagged CV₂) and B89-504 (tagged CV₃), while the peanut genotypes were 55-437 (tagged PV₁), 73-30 (tagged PV₂) and GC835 (tagged PV₃).

Growth conditions, treatments and sampling

The plants were grown in a translucent air-conditioned glasshouse; mean day temperature was $40.6 \pm 2.0^\circ\text{C}$, and mean night temperature was $23.5 \pm 1.4^\circ\text{C}$. Relative humidity was $95\% \pm 3.5\%$ at 11.300 h and $19.8\% \pm 4.1\%$ at 1500 h (universal time). Natural light was not supplemented, and maximal irradiance was $>800 \mu\text{M m}^{-2} \text{s}^{-1}$ at midday. This experiment was carried out in Bambey, Senegal.

The seeds were treated with a fungicide (deltamethrin, 12 g htrc^{-1}), and sown in 20-litre PVC pots containing 19 kg of a sandy soil. Prior to sowing, 5 g of a compound fertilizer ($\text{N}_{10}\text{P}_{20}\text{K}_{10}$) were applied and the soil was irrigated to field capacity. After sowing the seeds were allowed to germinate on stored soil moisture, after which 400 cm^3 of water were supplied daily to each pot.

The design was a randomized complete block, with two species, three genotypes and two irrigation schedules (irrigated and stressed), replicated five times. Soil moisture stress was applied by withholding irrigation from day 32 after sowing to day 50, while irrigation was continued for non-stressed plants. Soil moisture stress was terminated when the soil volumic humidity was $1.1 \pm 0.7 \times \text{cm}^3 \text{cm}^{-3}$, i.e. 87.4% less than the control (which was maintained at $8.70 \pm 1.20 \text{ cm}^3 \text{cm}^{-3}$ for most of the period).

On the 20th day after sowing (DAS), and at intervals of seven days thereafter, measurements of stomatal conductance and leaf relative water content (RWC) were taken. All measurements were taken from the third most expanded leaf from the shoot apex. Stomatal conductance was recorded between 1300 h and 1330 h with a Delta-T diffusion porometer (Kancmasu et al., 1969). The adaxial and abaxial stomatal conductances were measured separately on adjacent portions of the leaf, and conductance was calculated assuming that the two leaf surfaces acted as parallel resistors. Intact plant leaf relative water content (RWC) was determined from:

$$\text{intact plant RWC} = [(FW - DW) / (TW - DW)] \times 100.$$

where FW is fresh weight, DW is dry weight and TW is turgid weight after floating for 4 h.

Osmotic adjustment (OA) was determined on the 47th day only. The method used involved collecting leaves of plants pre-dawn in sealed plastic bags containing damp tissue paper. Leaf discs, 6 mm in diameter, were punched, wrapped in parafilm paper and immediately weighed (M_1) on a precision balance. The parafilm paper was subsequently removed and the disc placed on a stainless-steel screen suspended about 5 mm above 26 ml of unsaturated sodium chloride solution of known molality in a sealed test tube at 5°C (the disc is thus in contact only with the vapour of the salt solution). Eleven salt solutions were used whose water potentials (ψ) ranged from 0.09 to -7.5 MPa (Layington and de

long, 1988). After 12 h the discs were reweighed (M) and then oven dried at 65 °C for 24 h to determine their dry weight (M_d). The disc RWC was calculated as:

$$\text{RWC of disc exposed to osmoticum} = (M - M_d) / (M_f - M_d) \times 100,$$

where M is the mass at given μ , M_f is the disc mass at full turgor and M_d is dry weight. This experiment was used to determine the rate of water release from both species when exposed to osmoticum. Leaf water deficit was determined per unit weight of shoot material (Nwaloze et al., 1996).

Data were subjected to analysis of variance, and treatment means were separated using least significant difference (Steel and Torrie, 1980).

Results and discussion

Floral abscission was significantly reduced during drought (Fig. 1). As water stress was withheld, tomato behaved sluggishly and finally closed as time passed. Stomatal closure during soil drying (or soil moisture stress) was more prompt in cowpea than in peanut. The prompt response through stomatal closure in cowpea enabled the plants to check stomatal transpiration as soil moisture deficit persisted, while stomatal closure was delayed in peanut (in PV₁, for example, complete closure was delayed for seven days). Such delays, although beneficial in general for transpiration, involved the risk of continued water loss through radially open stomata. Cowpea has been reported to be one annual crop that exhibits extreme drought avoidance as a result of rapid stomatal response (Hall and Schultze, 1980a, b; Turk and Hall, 1980a, b).

The drought adaptive value of a crop would depend on the balance between the regulation of water loss and the maintenance of atmospheric CO₂ assimilation. As in peanut, the results report (Hall and Schultze, 1980b) indicated that the partial stomatal closure in cowpeas during stress resulted in improved water-use efficiency, and that their extreme drought avoidance was a conservative response. However, the responses of annual plants are not conservative; instead, transpiration is maintained at the risk of complete soil water exhaustion, low water potential and damage to the protoplasm (Fischer and Turner, 1978).

The plants that had experienced soil moisture stress had significantly ($P < 0.05$) higher leaf RWC than the non-stressed ones when they in turn were exposed to various concentrations of an osmoticum (Fig. 2). When the osmotic potential of the sodium chloride solutions was more negative the leaf tissue of cowpea retained higher moisture than that of peanut. Cowpea leaf discs thus bound water molecules to the protoplasm with more tenacity than peanut. This could be the result of the higher concentration of total nitrogen per unit leaf tissue (data not included here) which was maintained in stressed cowpea, whereas there were decreases in the quantity of total nitrogen in stressed peanut. Free amino acids contribute to the total nitrogen pool in stressed plants (Sivaramakrishnan et al., 1988; Handa et al., 1983). These nitrogenous compounds could contribute to osmotic adjustment in cowpea. Osmotic adjustment and changes in the cell wall

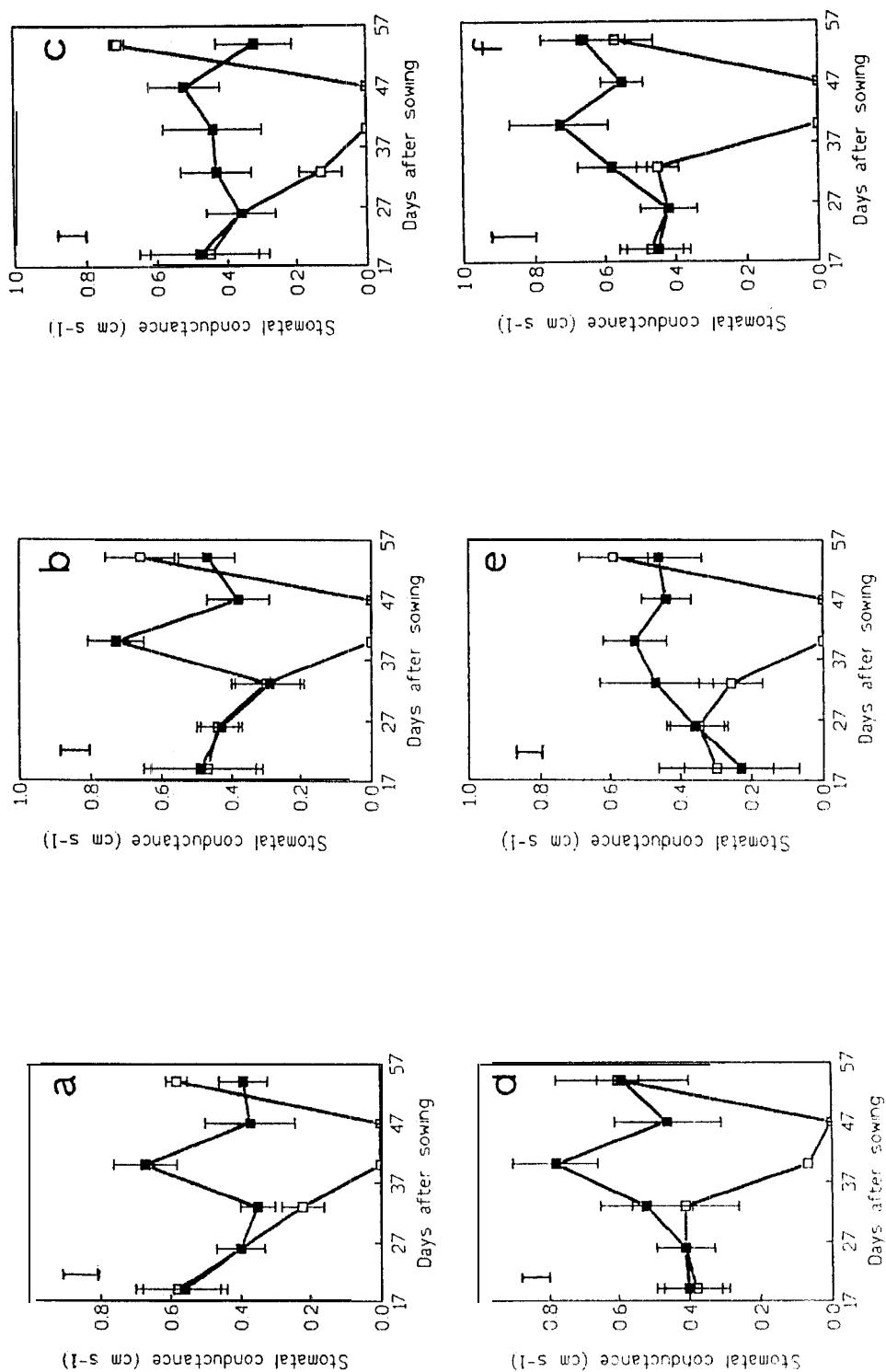


Fig. 1. Stomatal conductance (cm s⁻¹) in cowpea, CV₁ to CV₃ (a to c), and peanut, PV₁ to PV₃ (d to f), is represented for stressed (shaded squares) and irrigated (unshaded squares) plants. Each point is a mean of five replicates \pm SD. Isolated vertical bars represent LSD_(0.05).

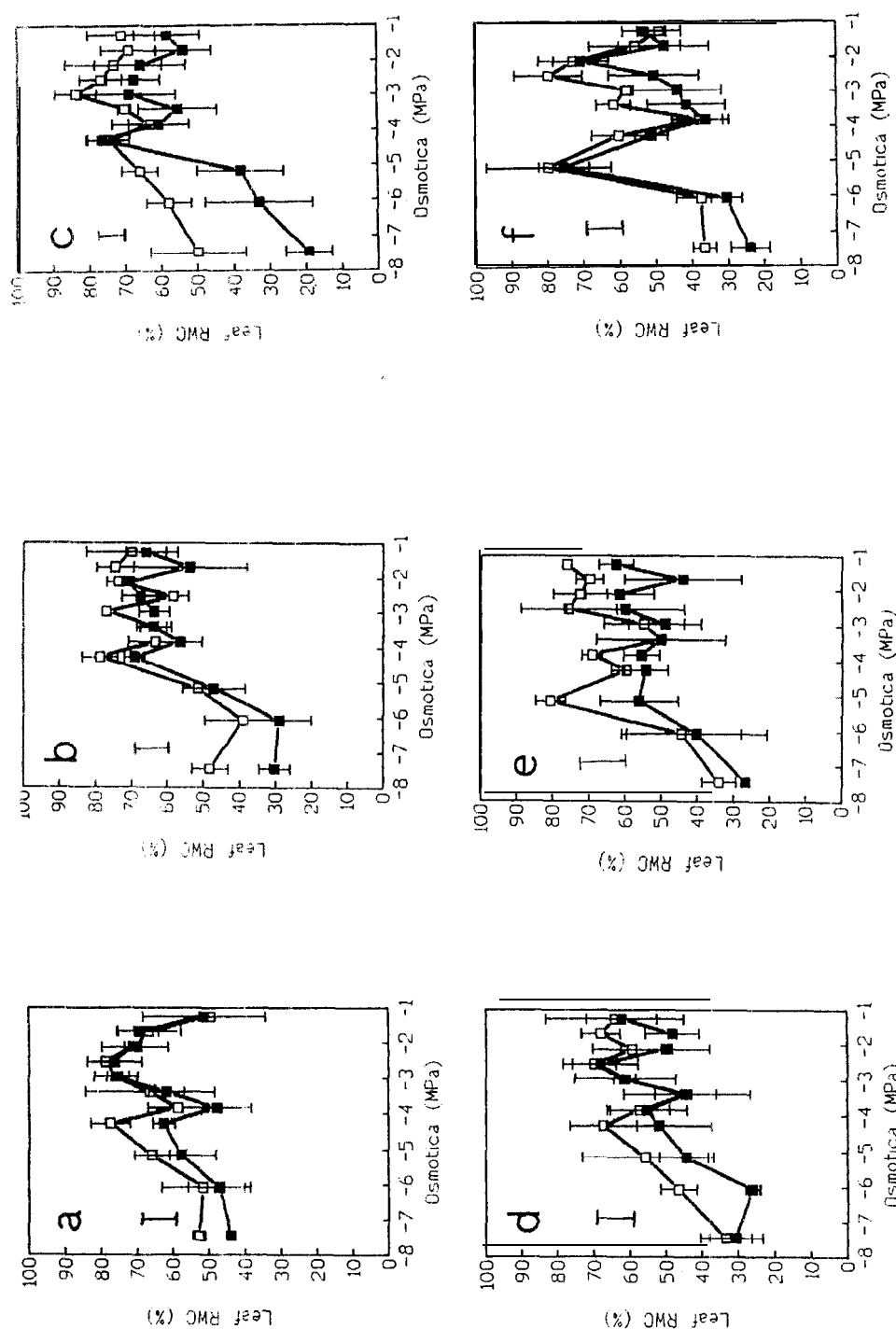


Fig. 2. Osmotic adjustments measured as RWC of discs from cowpea, CV₁ to CV₃ (a to c), and peanut, PV₁ to PV₃ (d to f). Discs were suspended over unsaturated salt solutions with a water potential ranging from -0.09 to -7.5 MPa and were maintained at 5 °C. See Figure 1 for legends

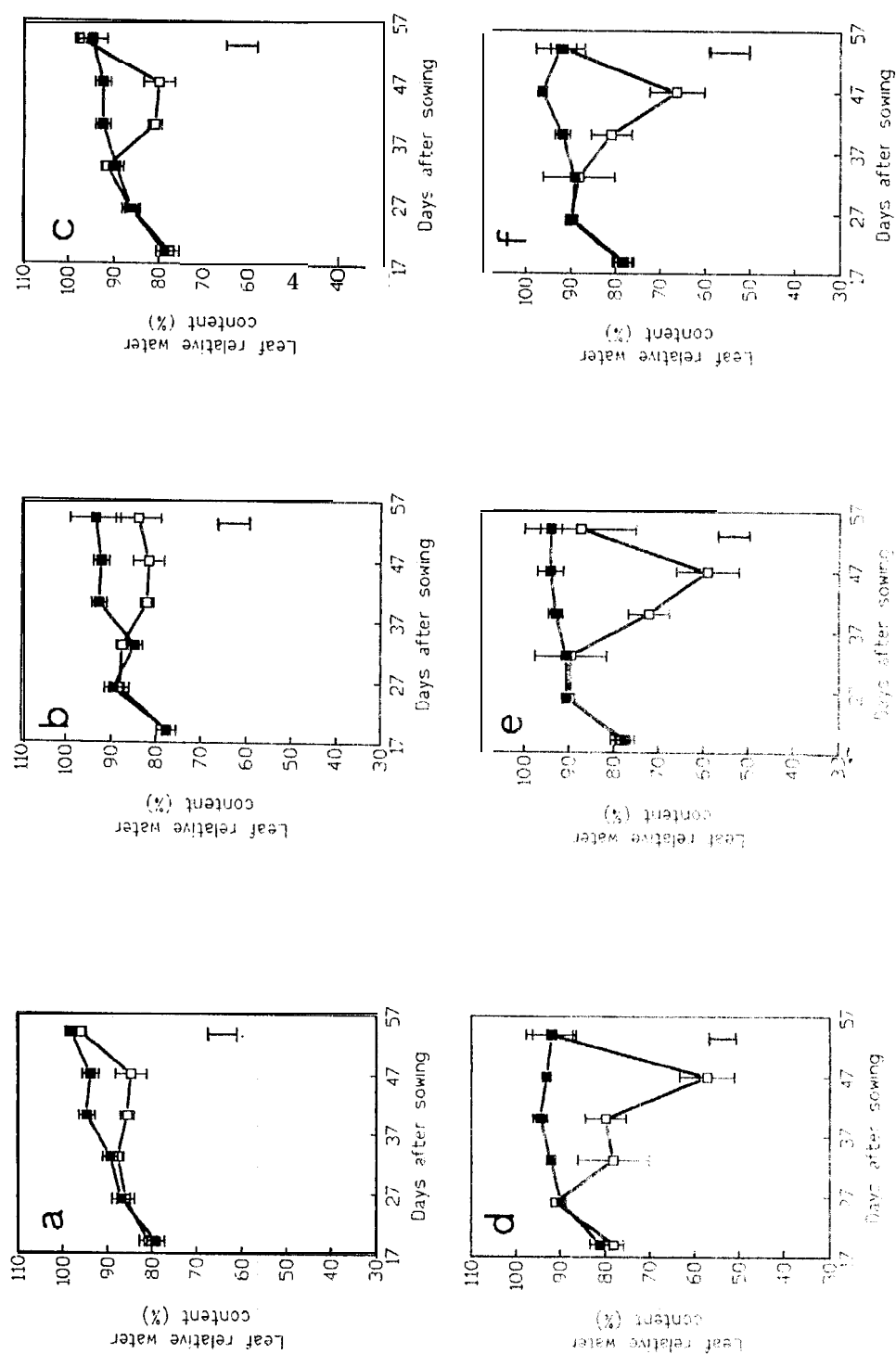


Fig. 3 Leaf relative water content of intact plants of cowpea, CV₁ to (V₁ to c), and peanut, PV₁ to PV₄ (d to f). See Figure 1 for legends

elastic modulus may be one of several mechanisms that enable cowpea to maintain physiological activity and prolong leaf survival as plant water deficits persist.

Generally, drought caused significant ($P < 0.05$) reductions in the leaf RWC of intact plants (Fig. 5). However, whereas the RWC in cowpea did not drop below 80.8% during drought, the RWC in peanut dropped as low as 57.3% (see peanut PV₁). A high temporary wilting point (TWP) was observed in cowpea (78% RWC), below which the leaves entered an irreversible permanent wilting status (PWS). Peanut leaves entered PWS below 55% RWC. Leaves that had not passed TWP recovered after rehydration on the 51st DAS.

Although cowpea had higher RWC and promptly closed its stomata, the relative pod yield (g g^{-1} shoot weight) in stressed cowpea was not higher than in peanut (Table 1). Rapid stomatal closure may have interfered with CO_2 assimilation, especially during reproductive growth in cowpea. However, a prompt stomatal response and the ability to bind water molecules to the protoplasm with high tenacity appear to be significant factors, responsible, among others, for the higher leaf RWC in cowpea than in peanut. On the resumption of irrigation peanut, which appeared to have largely suspended its growth, recovered its lush growth more rapidly than cowpea. In conclusion, therefore, cowpea and peanut appear to exhibit two different but efficient strategies in response to drought, since relative yield was not affected. Cowpea utilizes a conservative strategy, whereas peanut has an evasive mechanism (a strategy not fully understood), in which growth appears to be largely suspended while awaiting a resumption of irrigation.

Table 1
Relative fruit yield (g g^{-1} shoot weight) in cowpea
and peanut genotypes grown under two soil moisture regimes

	Irrigated	Stressed
Cowpea		
CV ₁	1.29 ^b	0.90 ^a
CV ₂	1.32 ^b	1.03 ^a
CV ₃	1.63 ^b	1.20 ^a
Peanut		
PV ₁	1.42 ^a	1.24 ^a
PV ₂	1.07 ^a	0.83 ^a
PV ₃	1.74 ^a	1.45 ^a

Means within a horizontal row with different letters
are significantly ($P < 0.05$) different.

Acknowledgements

This study was conducted at Centre d'Etude Régional pour l'Amélioration à la Sécheresse (CERAAS), Bambey, Senegal and was supported with funds from EEC grant number ST2A-01GMCD).

References

- Annerose, D. J. M. (1990): Recherches sur les mecanismes physiologiques d'adaptation á la sécheresse. Application au cas de l'arachide (*Arachis hypogaea*) cultivée au Sénégal. *Thèse de doctorat en sciences naturel*, Université Paris VII. 281 pages.
- Fischer, R. A., Turner, N. C. (197X): Plant productivity in arid and semi-arid zones *Ann Rev. Plant Physiol.*, 29, 277-317.
- Hall, A. E. (1981): Adaptation of annual plants to drought in relation to improvements in cultivars. *Hort. Science*, 16, 15-16.
- Hall, A. E., Schultze, E. D. (1980a): Drought effects on transpiration and leaf water status of cowpea in controlled environments. *Aust. J. Plant Physiol.*, 7, 141-14X.
- Hall, A. E., Schultze, E. D. (1980b): Stomatal response to environment and a possible interrelation between stomatal effects on transpiration and CO₂ assimilation *Plant Cell and Environment*, 73, 834-843.
- Handa, S., Bressan, R. A., Handa, A. K., Carpita, N. C., Hasegawa, P. M. (1983): Solutes contributing to osmotic adjustment in cultured plant cells adapted to water stress *Plant Physiol* 73, X34-843.
- Kanemasu, E. T., Thurtell, G. W., Tanner, C. B. (1969): Design, calibration and field use of a stomatal diffusion porometer. *Plant Physiol.*, 44, XX 1-885.
- Livingston, N. J., de Jong, E. (1988): Use of unsaturated salt solutions to generate leaf tissue water-release curves. *Agron. J.*, 80, 815-81X.
- Ludlow, M. M. (1980): Adaptive significance of stomatal responses to water and high temperature stress. In: N. C. Turner and P. J. Kramer (eds). *Adaptation of Plants to Water and High Temperature Stress*. John Wiley and Sons. New York. pp 123-138.
- Matin, M. A., Brown, J. H., Ferguson, H. (1989): Leaf water potential, relative water content, and diffusive resistance as screening techniques for drought resistance in barley. *Agron. J.*, 81, 100-105.
- Morgan, J. M. (1984): Osmoregulation and water stress in higher plants *Ann Rev Plant Physiol.*, 35, 299-319.
- Nwalozie, M. C., Ogbonnaya, C. I., Ononiwu, F. Y. (1992): Preliminary observations on the effect of hydration-dehydration on the growth of cowpea (*Vigna unguiculata*) seedlings under two soil moisture regimes. *Delta Agric.*, 1, 60-65.
- Sivaramakrishnan, S., Patell, V. Z., Flower, D. J., Peacock, J. M. (1988): Proline accumulation and nitrate reductase activity in contrasting sorghum lines during mid-season drought stress. *Physiol. Plant.*, 74, 418-426.
- Steel, R. G. D., Torrie, J. H. (1980): *Principles and Procedures of Statistics: a Biometric Approach*. McGraw-Hill Book Company. New York. p. 633.
- Turk, K. J., Hall, A. E. (1980a): Drought adaptation of cowpea II. Influence of drought on plant water status and relations with seed yield. *Agron. J.*, 72, 421-427.
- Turk, K. J., Hall, A. E. (1980b): Drought adaptation of cowpea. IV Influence of drought on plant water use, and relations with growth and seed yield. *Agron. J.*, 72, 434-439.
- Turner, N. C., Begg, J. E. (1973): Stomatal behavior and water status of maize, sorghum and tobacco under field conditions. I. At high soil water potential. *Plant Physiol.*, 51, 31-36.
- Turner, N. C. (1974): Stomatal behavior and water status of maize, sorghum and tobacco under field conditions. II. At low soil water potential. *Plant Physiol.*, 53, 360-365.
- Turner, N. C., Jones, M. M. (1980): Turgor maintenance by osmotic adjustment: a review and evaluation. In: N. C. Turner and P. J. Kramer (eds). *Adaptation of Plants to Water and High Temperature Stress*. John Wiley and Sons. New York. pp. X6-103.
- Turner, N. C. (1986): Adaptation to water deficits: a changing perspective *Aust. J. Plant Physiol.*, 13, 175-190.