

## Photosynthesis, Leaf Conductance, and Water Relations of Cowpea Under Saline Conditions \*

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**Summary.** Cowpea (*Vigna unguiculata* L.), grown widely under both irrigated and dryland conditions, is well adapted to drought and high temperature and is moderately salt tolerant. Data on photosynthetic response and regulation of water relations in cowpea under salinity stress is lacking. Therefore, in conjunction with a field plot experiment to establish the leaching requirement of cowpea, measurements were made of carbon dioxide assimilation rates ( $A$ ) by  $^{14}\text{CO}_2$  uptake, leaf conductances to  $\text{H}_2\text{O}$  ( $g_1$ ) by tritium uptake, and to  $\text{CO}_2$  ( $g'$ ), and leaf total water potential ( $\psi_t^1$ ) and osmotic potential ( $\psi_\pi^1$ ).

Cowpeas, grown in field plots containing Pachappa fine sandy loam (mixed, thermic, Mollic Haploxeraff), were irrigated daily with saline water (1,350 mg  $\text{l}^{-1}$  total salt concentration) to achieve leaching fractions of 0.17, 0.13, 0.09, 0.07, and 0.02. Cowpea maintained high leaf water potentials, high rates of  $\text{CO}_2$  assimilation and high leaf conductances under moderately saline conditions (high leaching). Values of  $\psi_t^1$  and  $\psi_\pi^1$  for high leaching were consistently 50 to 200  $\text{J kg}^{-1}$  higher than for low leaching throughout the day. Calculating  $\psi_\pi^1$  at full leaf turgor eliminated diurnal variation in  $\psi_\pi^1$ . As leaching decreased, however,  $A$ ,  $g_1$ , and  $g'$ , decreased significantly. About 45% of the  $^{14}\text{C}$  assimilated by the leaf was incorporated rapidly into ethanol insoluble compounds. The relationship between  $A$  and  $g_1$  for cowpea was similar to that reported for other crops.

Cowpea (*Vigna unguiculata* L.) is an important food crop in many parts of the world, being grown for dry seed and as a green vegetable (leaves and green pods) in East and West Africa and in India. It is reported to be drought resistant through mechanisms for maintaining high plant water potential (Hall and Schulze 1980) and capable of producing seed when other seed crops fail (Turk et al. 1980). Cowpea is also highly productive under irrigation (Turk et al. 1980), moderately

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well adapted to high temperatures (Rachie and Roberts 1974), and moderately salt tolerant (West and Francois 1982). With these attributes, cowpea is a potential irrigated crop for arid climates where salinity is a hazard. While some data exist on the physiological response of cowpea to water deficits (e.g. Hall and Schulze 1980; Shouse et al. 1981; Turk and Hall 1980), little information has been published on the regulation of water loss and photosynthesis under salt stress.

Photosynthesis, estimated by the assimilation of  $^{14}\text{CO}_2$ , and leaf conductance to water vapor, estimated by the uptake of tritiated water vapor, can be measured simultaneously with the dual isotope pulse apparatus (DIPA) (Johnson et al. 1979). Carbon-14 techniques used in the DIPA to measure  $\text{CO}_2$  assimilation are well established (e.g. Shimshi 1969), although there is still doubt as to whether  $^{14}\text{CO}_2$  uptake methods measure gross or net photosynthesis (Ramos et al. 1982) or some intermediate value. The use of tritium influx to determine leaf conductance to water vapor ( $g_1$ ) is a more novel technique than the use of  $^{14}\text{CO}_2$  for photosynthesis and has not been widely tested. However, Johnson et al. (1979) reported close agreement between the tritium method and a gravimetric method of estimating  $g_1$  and Ramos et al. (1982) presented data showing good agreement of DIPA values of  $g_1$  with those obtained by a gas exchange method for corn and wheat.

Our objective was to evaluate the influence of salt stress on carbon dioxide assimilation, leaf conductance, and water relations in plants grown with saline irrigation water as part of a study to determine the influence of different leaching treatments on yield.

## Materials and Methods

All measurements were made on cowpea grown in small salinized field plots at the U.S. Salinity Laboratory during the summers of 1980 and 1981. Twelve plots, each 18.2 m<sup>2</sup> in area, were irrigated daily with water containing a total salt concentration of 1,350 mg l<sup>-1</sup> (an osmotic potential of -88 J kg<sup>-1</sup>) to achieve six different leaching fractions (0.17, 0.13, 0.09, 0.07, 0.04, and 0.02) with two replications of each. Leaching fraction (L) is the proportion of the applied water that percolates below the rootzone. Composition of the irrigation water (mol m<sup>-3</sup>) was Ca, 4.6; Mg, 1.9; Na, 10.8; K 0.1;  $\text{CO}_3 + \text{HCO}_3$ , 3.1; Cl, 7.8;  $\text{SO}_4$ , 4.9; and  $\text{NO}_3$ , 2.6. Nitrogen fertilizer was added continuously as calcium nitrate and the nitrogen application ranged from 70 to 120 kg ha<sup>-1</sup> as the leaching fraction increased from 0.02 to 0.17. A traveling drip irrigation system applied a 0.2 mm depth of water for each traverse over a plot. The plots, containing Pachappa fine sandy loam (coarse-loamy, mixed, thermic Mollic Haploxeralf), had been maintained at steady salinity levels for eight years prior to the cowpea crop. Cowpea (cv. California Blackeye No. 5) was sown in rows 47 cm apart with a spacing of 15 cm between plants on 13 June 1980 and 29 May 1981. After establishment the plants were thinned to a spacing of 30 cm. Further experimental details are given by Hoffman and Jobes (1983).

During 1980, measurements were made of  $^{14}\text{CO}_2$  assimilation (A) and leaf conductance to water vapor ( $g_1$ ) on 18, 21, and 28 August. On 18 August twenty measurements were made between 13.30 and 14.50 h PST. On the other two days approximately 20 measurements were taken three times during the day (09.30 to 10.30; 11.15 to 12.00; and 13.30 to 14.30 PST). Four fully expanded leaves at the top of the canopy were sampled from different plants in each of five leaching fraction treatments for each measuring period. No measurements were made on the 0.04 leaching treatment. All plants selected for measurement were at least 1 m from the nearest plot border and only leaves with a healthy appearance and full sun exposure in the top layer of the canopy were measured. Assimilation and  $g_1$  were measured using a carbon-14

and tritium dual isotope pulse apparatus (DIPA) (Johnson et al. 1979). Assimilation of both leaf surfaces was determined simultaneously by measuring the uptake and incorporation of <sup>14</sup>CO<sub>2</sub> into a small area (127 mm<sup>2</sup>) of an attached leaf enclosed in a lucite chamber. The enclosed leaf tissue was exposed to an air stream containing 323 μl CO<sub>2</sub> l<sup>-1</sup> air enriched with <sup>14</sup>CO<sub>2</sub> (1.06 Ci mol<sup>-1</sup>) for 15 s. The air stream also contained tritium, obtained by bubbling the air through tritium-enriched water (tritium activity, 18 mCi mol<sup>-1</sup>) prior to reaching the enclosed leaf area. Uptake of tritium-enriched water vapor occurred simultaneously with the uptake of <sup>14</sup>CO<sub>2</sub> and permitted determination of g<sub>1</sub>.

A small disc (35.6 mm<sup>2</sup>) was punched from the center of the leaf area exposed to the radioactive isotopes and was placed immediately into 2 ml of 95% ethanol in a scintillation vial. After extraction at room temperature for 24 h, the chlorophyll in the solution was bleached by exposure to sunlight for 1 h. The bleached leaf disc was then transferred to 1 ml 0.1 M HCl and extracted further at 90 °C for 1 h. Both isotopes were then measured by scintillation counting after adding scintillation 'cocktail'. The double extraction procedure permitted the determination of the amount of <sup>14</sup>CO<sub>2</sub> fixed into ethanol soluble and ethanol insoluble fractions. Johnson et al. (1979) extracted leaves in 80% methanol at dry ice temperature and found that approximately 25% of the assimilated <sup>14</sup>CO<sub>2</sub> was not extracted. Combustion or the extraction procedure described here and developed by Shimshi (D. Shimshi, personal communication) recovers almost all of the <sup>14</sup>CO<sub>2</sub>. The reader is referred to Ramos et al. (1982) for details on the calculation of A and g<sub>1</sub> from the scintillation counts.

Leaf CO<sub>2</sub> conductance (g') was calculated as described by Jarvis (1971) and Nobel (1974) from data of A and external (C<sup>o</sup>) and internal (C<sup>i</sup>) concentrations of CO<sub>2</sub> according to  $g' = A / (C^o - C^i)$ . The value of C<sup>o</sup> for cowpea was assumed to be constant at a value of 50 μl CO<sub>2</sub> l<sup>-1</sup> air (Lush and Rawson 1979), while C<sup>i</sup> changes with leaf water stress (Lawlor 1976). Values of leaf xylem water potential (ψ<sub>x</sub>) measured in these plants ranged diurnally between -500 and -1,200 J kg<sup>-1</sup> with no differences among leaching treatments. Thus the plants maintained high values of ψ<sub>x</sub> in a manner similar to that reported for cowpea under drought stress (Hall and Schulz 1980; Turk and Hall 1980). External (boundary layer) and leaf conductances to CO<sub>2</sub> (g<sub>a</sub>' and g', respectively) were calculated from the conductance to water vapor using conversion factors of 1.37 for g<sub>a</sub> and 1.61 for g' (Jarvis 1971).

Values for g<sub>1</sub>, g' and A (both total and ethanol-soluble fractions) were calculated for individual leaves and these values were treated as observations within a nested design. All data were analysed using a split-split-split plot design with factors of leaching fraction, date, time of day and individual plants (Wilson 1979). While this analysis would normally provide no separate error term for the first three factors the main effects at each level were separated into a linear and a quadratic component. The remaining degrees of freedom were used to estimate the error component.

On four occasions in 1981, 14 and 17 July and 4 and 5 August, leaf total water potential (ψ<sub>l</sub>) and its components were measured about every 2 h between 06.00 and 20.00 h. Water potentials were measured on single discs of leaf tissue, 9 mm in diameter, using thermocouple psychrometers in chambers 9 mm in diameter and 2.5 mm deep (Brown and Collins 1980). Measurements were made on samples taken from a young, but fully expanded, leaf of five plants for each treatment at each time of measurement. After a 4 h equilibration period at 25 °C total potential was measured using a cooling current of 4 ma for 10 s and reading the output after a delay of 10 s. Leaf osmotic potential (ψ<sub>π</sub>) was determined after the ψ<sub>l</sub> measurements by placing the psychrometers in crushed dry ice for 30 min and allowing them to equilibrate for 2 h at 25 °C before measurement. Pressure potential (ψ<sub>p</sub>) was calculated by difference between ψ<sub>l</sub> and ψ<sub>π</sub>. Leaf relative water content (RWC) was determined on a leaf segment taken simultaneously with the disc for potential measurements. Leaf weight at full turgor was measured after floating the segment on water for 4 h while illuminated at light compensation (Barrs and Weatherly 1962). Osmotic potential of turgid tissue was calculated based on the RWC, assuming the cells behaved as perfect osmometers and that bound water was negligible.

The diurnal course of g<sub>1</sub> was measured on two cloudless days in 1981, 8 and 28 July, with a steady-state diffusion porometer (LII-1600, Licor Inc. Lincoln, Nebraska). Photosynthetic photon flux density was measured with a quantum-flux meter on the porometer. In the calculation of g<sub>1</sub>, allowance was made for boundary conductance. The dimensions used to

express conductance values are predicated on the fact that gases diffuse along gradients of partial pressure (or of mole fraction), which are dimensionless. The dimensions of conductance and transpiration ( $\text{mole m}^{-2} \text{s}^{-1}$ ) are therefore the same. For comparison  $g_1$  of  $1 \text{ mol m}^{-2} \text{ s}^{-1}$  at  $30^\circ = 25 \text{ mm s}^{-1}$ .

## Results and Discussion

Measurements were made on selected days with similar climatic conditions. Sky conditions on all days were hazy sunshine with a mean photosynthetic photon flux density of  $1.84 \pm 0.10 \text{ mmol m}^{-2} \text{ s}^{-1}$  ( $\pm$  standard deviation) during measurement periods. This exceeds the level of  $1.6 \text{ mmol m}^{-2} \text{ s}^{-1}$  required for light saturation of photosynthesis in cowpea (Lush and Rawson 1979). The mean values for other climatic factors ( $\pm$  standard deviation) were: ambient temperature, maximum  $33 \pm 3^\circ \text{C}$ , minimum  $15 (\pm 1)^\circ \text{C}$ ; relative humidity, maximum  $82 \pm 2\%$ , minimum  $30 \pm 8\%$ .

The leaching treatment caused large differences in soil osmotic potential which reduced plant growth and yield significantly (Hoffman and Jobses 1983). Soil matric potential rarely dropped below  $-30$  to  $-40 \text{ J kg}^{-1}$  in any leaching treatment. Values of soil osmotic potential ( $\psi_\pi^s$ ) were calculated from measurements of the electrical conductivity of the soil solution ( $\sigma_{sw}$ ) through the relationship  $\psi_\pi^s (\text{J kg}^{-1}) = -36 \sigma_{sw} (\text{dS/m})$  (Maas and Hoffman 1977). The three leaching treatments sampled, 0.17, 0.07, and 0.02, showed mean values of  $\sigma_{sw}$  in the top 30 cm of the soil profile of 4.8, 8.6, and  $11.7 \text{ dS m}^{-1}$ , respectively. This depth was chosen because at least 60% of the roots of cowpea plants were found in this depth interval in an experiment adjacent to this study (West and Francois 1982). Converting these salinity values to  $\psi_\pi^s$  gives values of  $-170$ ,  $-310$ , and  $-420 \text{ J kg}^{-1}$  for the 0.17, 0.07, and 0.02 leaching fractions, respectively. The relationship between A and mean values of  $\psi_\pi^s$  was  $A = -0.25 \psi_\pi^s + 27.3$ ,  $r^2 = 1.00^{**}$ .

### *CO<sub>2</sub> Assimilation Rates*

Assimilation rates for  $^{14}\text{CO}_2$  as a function of L (leaf status was either normal or senescing, see below) and time of day are presented in Table 1 for both the ethanol extract (ethanol) and the ethanol extract followed by acid extraction (total). A consistent and significant decline in A with decreasing leaching fraction in both extraction fractions can be described by the relationships:

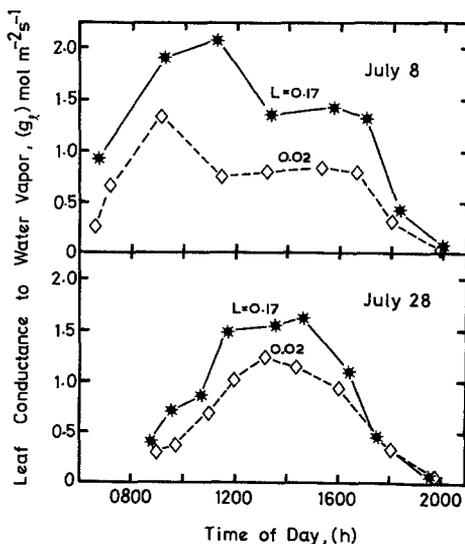
$$\begin{array}{lll} \text{A (total)} & = 0.39 \text{ L} + 15.7 & r^2 = 0.78^* \\ \text{and A (ethanol)} & = 0.25 \text{ L} + 8.6 & r^2 = 0.85^* \end{array}$$

The highest mean rates of A (total) were obtained with normal leaves at the 0.17 leaching fraction treatment and these values are very similar to those reported for well irrigated, non-salinized (elite lines of) cowpea plants (Lush and Rawson 1979). We presume, therefore, that the mean rate of photosynthesis was near maximum for these growing conditions and would not have been increased by higher leaching fractions or by irrigation with non-saline water.

With decreased leaching fraction, leaf conductance declined (Fig. 1 and Table 2), leaf water and osmotic potential (Fig. 3) and leaf relative water content

**Table 1.** Carbon dioxide assimilation rates ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for cowpea leaves as a function of leaching fraction and time of day for normal and senescing leaves in 1980. Assimilation calculated after an ethanol extraction (ethanol) and after an ethanol and acid extraction sequence (total) are given

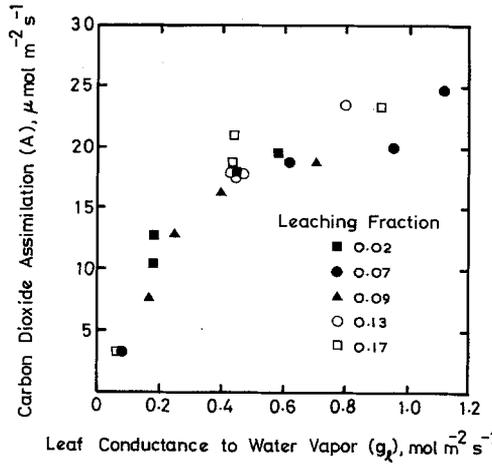
Leaching fraction	Ethanol extraction ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Total extraction ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
0.17	13.2	23.1
0.13	11.6	20.5
0.09	10.1	17.3
0.07	11.2	19.5
0.02	9.1	16.9
	N.S.	N.S.
Leaf status		
Normal	13.1	23.4
Senescing	8.9	15.5
	$P=0.026$	$P=0.015$
Time of day (h)		
10.00	11.8	19.5
11.30	11.2	20.5
14.00	10.0	18.4
	$P=0.040$	N.S.



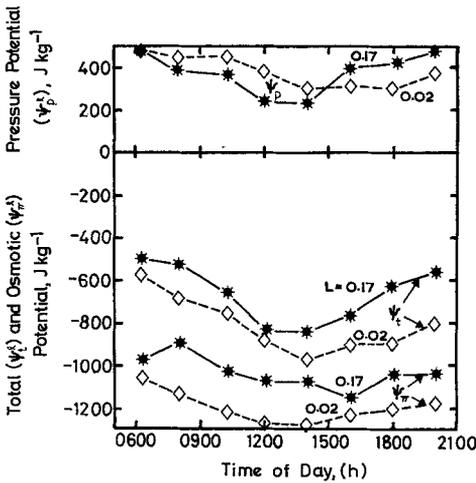
**Fig. 1.** Diurnal responses of leaf conductance to water vapor for cowpea measured with a steady-state porometer as a function of leaching fraction treatment (L) on 8 and 28 July 1981

(Fig. 4) also decreased leading to a reduction in A. It is likely that these responses were due to the reductions in  $\psi_s^2$  as L decreased.

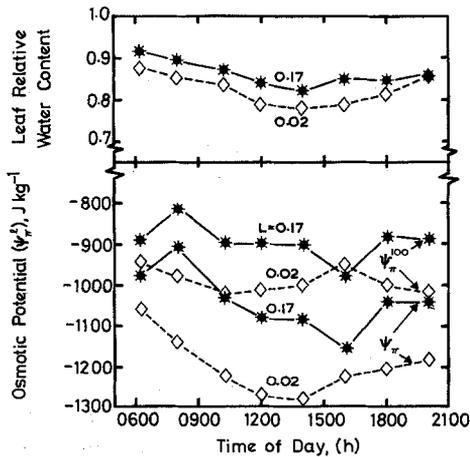
Decreased leaching reduced seed yield in this experiment (relative yields of 1.00, 0.87, 0.76, 0.64, and 0.35 for the L of 0.17, 0.13, 0.09, 0.07, and 0.02). Peak photosynthetic rates in cowpea and duration of high photosynthetic activity depends strongly upon the presence of the growing fruits, which act as sinks for



**Fig. 2.** Relationship of carbon dioxide assimilation to leaf conductance to water vapor for cowpea leaves at different leaching fractions. Data are for one set of measurements on senescing leaves



**Fig. 3.** Diurnal courses of leaf total water potential ( $\Psi_t^l$ ), osmotic potential ( $\Psi_\pi^l$ ), and pressure potential ( $\Psi_p^l$ ) for cowpea at leaching fractions (L) of 0.17 and 0.02



**Fig. 4.** Diurnal courses of leaf relative water content and osmotic potential as measured ( $\Psi_\pi^l$ ) and as corrected to full turgor ( $\Psi_\pi^{100}$ ) for cowpea at leaching fractions (L) of 0.17 and 0.02

CO<sub>2</sub> assimilate (Herridge and Pate 1977; Lush and Rawson 1979). Differences in fruit loading can therefore account for part of the reduction in the rates of photosynthesis observed here.

Measurements of A (Table 1) made on 18, 21, 28 August, were significantly ( $P=0.05$ ) lower on the last date. This reduction in A occurred even though leaves appeared to be bright, glossy, green, and healthy. Leaf senescence begins in cowpea about 70 days after planting depending upon cultural and environmental conditions (Turk et al. 1980) and senescence and abscission of leaves progresses rapidly with the onset of seed development (Herridge and Pate 1977). The final day of measurement was 76 days after planting and leaves lower in the canopy were beginning to abscind. The effects of time of day on A were minimal (Table 1) with no statistically significant effects.

#### *Partitioning of Assimilates*

The analytical procedure partitions the immediately-fixed <sup>14</sup>CO<sub>2</sub> into ethanol-soluble and ethanol-insoluble fractions. The ethanol-soluble extract was assumed to contain low molecular weight sugars and other ethanol soluble products while the hot acid extract (ethanol-insoluble) was presumed to hydrolyze starch. Any incorporation of <sup>14</sup>CO<sub>2</sub> immediately into structural compounds would not be hydrolyzed by the hot acid extraction. The leaf disc, however, remained in the acid solution at the time of counting, so that any <sup>14</sup>CO<sub>2</sub> incorporated into structural compounds would contribute to the counts obtained depending upon the degree of quenching within the remnants of the leaf disc.

The mean values before and after acid extraction indicate that about 45% of the <sup>14</sup>C was incorporated rapidly into ethanol-insoluble compounds (Table 1). The amount of ethanol-soluble assimilate in the leaves from senescing plants was reduced significantly ( $P<0.05$ ) compared with non-senescing plants (Table 1). The proportion of ethanol-soluble to total assimilate remained constant at around 56% in both sets of leaves. There was no significant effect of leaching fraction on the amount of ethanol-soluble assimilate or total assimilate.

The amount of ethanol-soluble assimilate showed a significant ( $P<0.05$ ) response to time of day with significantly lower amounts in the afternoon compared with the two morning samplings. In addition there was a significant ( $P<0.05$ ) interaction between time of day and leaching fraction. At a leaching fraction of 0.17, the proportion of ethanol-soluble assimilate increased during the day; with  $L=0.13$  there was no change during the day and with leaching fraction treatments of 0.09, 0.07, and 0.02 there was a linear decline over time in the amount of ethanol-soluble assimilate during the day.

Prior to senescence, the partitioning changed very little during the day, with the insoluble fraction tending to be slightly higher at midday compared to morning or afternoon. In senescing plants the insoluble fraction increased from about 38% of the total in the morning to 48% in the afternoon. Shimshi (D. Shimshi, personal communication) has shown the proportion of ethanol-soluble to ethanol-insoluble <sup>14</sup>C increases with increasing water stress on potatoes and with increasing salinity stress in mature corn but not young corn. The results for corn and potatoes were the reverse of that for cowpea in that increasing stress reduced the fraction of <sup>14</sup>CO<sub>2</sub>

being incorporated into ethanol-insoluble compounds. Apparently the distribution of  $^{14}\text{CO}_2$  into different fractions varies with plant species, age of plant or stage of development, and environmental conditions.

#### *Leaf Conductance to Water Vapor*

Leaf conductance to water vapor varied linearly with leaching fraction (Table 2) ( $P < 0.05$ ) over an almost two-fold range. Mean values for leaves on non-senescent and senescing plants were  $0.53$  and  $0.55 \text{ mol m}^{-2} \text{ s}^{-1}$ , respectively, indicating no effect of senescence. There was no effect of time of day ( $P < 0.05$ ). However, there was an interaction ( $P < 0.05$ ) between time of day and whether leaves were on normal or senescing plants (Table 2). In non-senescent plants  $g_1$  increased linearly from 10.00 until 14.00 h but declined to 14.00 h in senescing plants. The linear increase in  $g_1$  to 14.00 h was also shown by measurements with a steady-state porometer. The decline in leaf conductance in senescing leaves could be a major factor contributing to the lower value of  $A$  in these leaves (Table 1). The values of  $g_1$  (Table 2) do not include any boundary layer conductance of the leaf clamp.

On one day of measurement for leaves of senescing plants, concurrent measurements of  $g_1$  were made with a transit-time diffusion porometer (Li-Cor Inc. L165 Lincoln, Nebraska). Each measurement was made on the leaflet opposite that used for the DIPA. Values of  $g_1$  from the DIPA were always higher than those obtained from the transit-time porometer although agreement between the two methods was good at values of  $g_1$  below  $0.1 \text{ mol m}^{-2} \text{ s}^{-2}$ . However, as  $g_1$  increased the difference between the two values increased. Johnson et al. (1979) have also reported  $g_1$

**Table 2.** Leaf conductance to water vapor ( $g_1$ ,  $\text{mol m}^{-2} \text{ s}^{-1}$ ) and carbon dioxide ( $g'$ ,  $\text{mmol m}^{-2} \text{ s}^{-1}$ ) for cowpea as a function of leaching fraction and time of day for normal and senescing leaves during 1980

Leaching fraction	Water vapor $g_1$ ( $\text{mol m}^{-2} \text{ s}^{-1}$ )	Carbon dioxide $g'$ ( $\text{mmol m}^{-2} \text{ s}^{-1}$ )
0.17	0.75	77.5
0.13	0.59	69.8
0.09	0.45	56.6
0.07	0.48	66.4
0.02	0.43	54.8
	$P = 0.03$	N.S.
Leaf status		
Normal	0.53	78.4
Senescing	0.55	51.7
	N.S.	$P = 0.007$
Time of day (h)		
10.00	0.50	64.9
11.30	0.54	68.0
14.00	0.58	62.1
	N.S.	N.S.

values measured with the DIPA to be higher than those measured with a transit-time porometer at values of  $g_1$  above  $0.12 \text{ mol m}^{-2} \text{ s}^{-2}$ . The values of  $g_1$  from the DIPA are lower than those from the steady state porometer (Fig. 1) although they cannot legitimately be compared as they were separated in time.

The maximum values of  $g_1$  measured with the DIPA in these field-grown cowpeas were up to three times higher than the maximum values reported for wheat and corn in a green house (Ramos et al. 1982) and salinized corn in a greenhouse (D. Shimshi, personal communication). The maximum value of  $g_1$  measured,  $1.6 \text{ mol m}^{-2} \text{ s}^{-2}$ , occurred on one individual leaf in the 0.17 leaching fraction treatment. Thus, under these experimental and environmental conditions, cowpea was able to maintain both high assimilation rates and high values of  $g_1$ .

Diurnal measurements of  $g_1$  measured with a steady-state porometer in 1981 are presented in Figure 1. The diurnal pattern is similar for both leaching fraction treatments which were measured but  $g_1$  of low leaching was only about half that of high leaching. It is noteworthy that on 8 July partial stomatal closure began at midday and  $g_1$  remained stable for 4 to 5 h during the afternoon for both leaching treatments. The diurnal pattern for 28 July was more typical,  $g_1$  increased steadily but more slowly than on 8 July, reaching maximum values in the afternoon followed by a steady decline for the remainder of the day.

#### *Relationship Between A and $g_1$*

The relationship between the values of A and  $g_1$  measured with the DIPA is shown in Figure 2 for one set of measurements when the leaves were senescing. Clearly, there was a wide spread in the values of A and  $g_1$  among the different leaching fractions. The relationships for the two data sets were  $A=5.62 (g_1)^{0.24}$  for non-senescent leaves ( $r^2=0.67$ ) and  $A=5.62 (g_1)^{0.55}$  for leaves on senescing plants ( $r^2=0.77$ ). Senescence altered the relationship between A and  $g_1$  with lower assimilation rates for any value of  $g_1$ . However, the form of the relationship was the same for both sets of data and was similar to those reported for other species (Johnson et al. 1979; Ramos et al. 1982), but covers a much broader range of values of  $g_1$ .

#### *Leaf Conductance to Carbon Dioxide*

Values of total leaf conductance to CO<sub>2</sub> ( $g'$ ) were calculated as described from the data for A and  $g_1$  (Table 2). There was a significant ( $P < 0.05$ ) linear interaction between time of day and leaching fraction. At leaching fractions of 0.17 and 0.13,  $g'$  increased linearly during the period 10.00 to 14.00 h. At leaching fractions of 0.09, 0.07, and 0.02,  $g'$  decreased approximately linearly over the period. This interaction was not evident in  $g_1$  suggesting that high salt had an effect on carbon assimilation in addition to stomatal effects.

#### *Water Relations*

During 1981, psychrometric measurements of water potential were taken twice before the onset of senescence. Although measurements in July tended to be higher than those in early August, average values for the two sampling periods are presented in Figure 3. Based on daily averages, both total leaf water potential ( $\psi_t^1$ )

and leaf osmotic potential ( $\psi_{\pi}^1$ ) were 100 to 200 J kg<sup>-1</sup> higher in July than in August for L of 0.17 but only higher by 50 J kg<sup>-1</sup> or less for the 0.02 leaching treatment.

In general, the diurnal course of total water potential and its components were similar to that of other species. During the morning,  $\psi_t^1$  and  $\psi_{\pi}^1$  for L=0.17 declined steadily, reaching minimum values in the early afternoon. Recovery began in late afternoon. Values of  $\psi_t^1$  and  $\psi_{\pi}^1$  for L=0.17 were statistically ( $P < 0.05$ ) higher than those for L=0.02 by 100 to 200 J kg<sup>-1</sup>. Of note is the small change in  $\psi_{\pi}^1$  during the day compared to  $\psi_t^1$ . Of particular interest was the diurnal course of  $\psi_p^1$ . Although  $\psi_p^1$  was essentially equal for both leaching fractions early in the morning,  $\psi_p^1$  dropped more rapidly for the 0.17 leaching treatment than for 0.02; and also recovered more quickly in the afternoon. The result was an average daily value of 380 J kg<sup>-1</sup> for  $\psi_p^1$  in both leaching treatments. The importance of the difference in diurnal response of  $\psi_p^1$  to leaching is not known; but coupled with the diurnal differences in  $\psi_{\pi}^1$ , results in  $\psi_t^1$  for L=0.17 being only about 100 J kg<sup>-1</sup> higher than for L=0.02 in the morning but more than 200 J kg<sup>-1</sup> higher in the late afternoon.

Calculating osmotic potential at full turgor ( $\psi_{\pi}^{100}$ ) by utilizing leaf relative water content (RWC) values, showed that diurnal variation in  $\psi_{\pi}^1$  was caused by changes in RWC, and not by solute accumulation (Fig. 4). RWC values for L=0.17 were consistently about 3% higher than values for L=0.02. Average daily values of  $\psi_{\pi}^{100}$  were -890 J kg<sup>-1</sup> and -999 J kg<sup>-1</sup> for leaching fractions of 0.17 and 0.02, respectively. This suggests a long term osmotic adjustment of about 100 J kg<sup>-1</sup> induced by the different salt concentrations in the soil.

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