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CONTROL OF WATER USE BY PEARL MILLET (*PENNISETUM TYPHOIDES*)

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SUMMARY

At Hyderabad, India, stands of pearl millet were grown after the monsoon (a) with no irrigation after establishment and (b) with irrigation as needed to avoid stress. Increases of dry matter and leaf area were determined by regular harvesting. The interception of radiation by the foliage, uptake of water from the soil and stomatal conductance were monitored. Before anthesis at 42 days after sowing (DAS), the rate of dry matter production and the transpiration rate in the unirrigated stand were about 80% of the corresponding rates for the irrigated control, mainly because of a smaller stomatal conductance from 30 DAS. After anthesis, the unirrigated stand grew little and used only 10% of the water transpired by the control. This large difference was partitioned between loss of leaf area and smaller stomatal conductance in the ratio of approximately 2:1. Radiation intercepted by foliage in the irrigated stand produced 2.0 g of dry matter per MJ compared with 2.5 g MJ^{-1} for the same variety growing in the monsoon, a difference consistent with a smaller stomatal conductance in drier air.

DROUGHT STRATEGIES

In the absence of rain or of irrigation, the growth of a crop can be sustained for a limited time by water stored in the soil. Equilibrium between the demand for water imposed by the atmosphere and the supply of water provided by the soil can be achieved in several ways. When the demand tends to exceed the supply, water stress in leaves may restrict their expansion and a larger fraction of the assimilate supply may then become available for extending the root system. Alternatively or additionally, stomatal control may restrict the rate of transpiration per unit of leaf area by decreasing the conductance of vapour from mesophyll cells to the air moving through foliage. Finally, in extreme stress, leaves may die and be lost by abscission.

These strategies - restriction of leaf area and reduction in leaf conductance - have different implications for crop growth during stress and after release from stress if water becomes available. Slower leaf expansion decreases the amount of radiation intercepted by foliage and so decreases the amount of dry matter

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produced per unit of radiant energy *incident* on the stand. The growth per unit of *intercepted* radiation is not necesssarily affected nor is the loss of water by transpiration per unit of intercepted radiation.

In contrast, a decrease in stomatal conductance induced by water stress must reduce the increase of dry matter per unit of *intercepted* radiation as well as the rate of water loss. Nevertheless, the loss of water per unit of dry matter gain is conservative when the intercellular concentration of CO_2 remains stable, as several workers have shown (e.g. Wong, Cowan and Farquhar, 1978).

Gregory and Squire (1979) presented a preliminary account of the growth of two adjacent stands of pearl millet, one growing on stored water and the other irrigated. We now extend the analysis to show how measurements of light interception and stomatal conductance can be interpreted in terms of strategies to conserve water.

MATERIALS AND METHODS

Crop, site and irrigation

The management of the crop and the programme of measurements was described fully by Gregory and Squire (1979). Pearl millet (*Pennisetum typhoides* S. & H., cv. BK 560) was grown at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, on a medium deep alfisol. Figure 1 shows the disposition and dimensions of the plots within

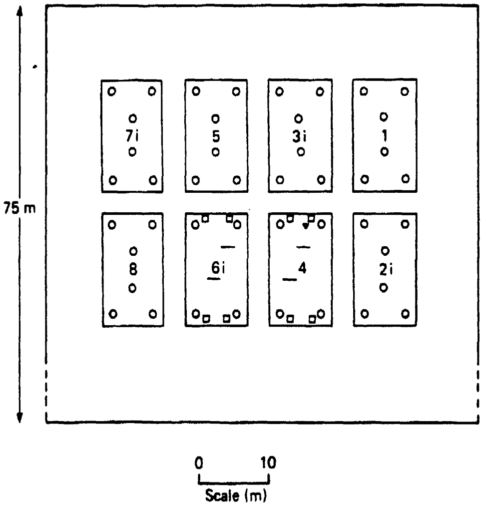

Fig 1. Disposition of the experimental plots and instruments. Irrigated plots are indicated by i and the instruments are tube solarimeter (—), neutron probe access tubes (○), tensiometers (□) and thermocouple psychrometers (△).

Table 1. *Ten-day averages of temperature (T) and saturation deficit (SD) and totals of evaporation and insolation measured at ICRISAT meteorological station*

Age of millet crop (DAS)†	T (°C)	SD (kPa)	Evaporation Class A Pan (mm)	Insolation (MJ m^{-2})
1-10	25.4	2.62	54	19.3
11-20	24.5	3.04	57	18.4
21-30	25.0	2.66	56	17.3
31-40	24.4	1.77	42	13.0
41-50	25.1	2.06	41	13.6
51-60	20.8	2.63	47	16.4
61-68	19.3	2.26	37	16.8

† Days after sowing.

a 0.5 ha field. Seeds were sown on 13 October 1977 in rows 37.5 cm apart. All plots were given 15 mm of water from overhead spraylines on the second and third days after sowing (DAS). Ten days later (13 DAS), the plants were thinned to 10 cm apart and given 20 mm of irrigation. Thereafter, four of the plots (the dry crop) received no water apart from a few millimetres of rainfall in scattered showers so that plants grew on stored water and were increasingly stressed. The other four plots received 30 mm of irrigation on each of 30, 42 and 58 DAS which was sufficient to re-wet the soil to a matric potential of about −0.05 MPa on each occasion. Table 1 summarizes the weather during the experiment.

Crop growth

Plants were sampled weekly from all plots except numbers 4 and 6 which were reserved for instrumentation. Samples comprised all the shoots from adjacent 1 m lengths of three rows, giving approximately 30 plants per plot and 90 plants per treatment on each occasion. Leaf areas were determined for three layers of the canopy (0-30 cm, 30-60 cm and above 60 cm above the soil), together with the areas of the stems (leaf sheaths). Dry weights were measured after drying the harvested material in an oven at 70°C for at least 24 h.

Intercepted radiation

Total radiation intercepted by the stands was measured using five tube solarimeters (Szeicz, Monteith and dos Santos, 1964). One was mounted on a stand above the canopy and four were placed at ground level in plots 4 and 6 as two sets of two, each set spanning five rows. The output of each solarimeter was measured on a millivoltmeter every hour from sunrise to sunset on two days a week during periods of clear sky or uniform cloud. The mean of the four readings was used to derive the hourly fractional radiation interception. Absolute values of intercepted radiation were then estimated from records of irradiance obtained with a pyranometer sensor (Lambda Instruments) at the ICRISAT meteorological station. On those days when intercepted radiation was not measured, fractional interception was estimated by interpolation.

Leaf and canopy conductance

Leaf conductance was measured with a diffusive resistance porometer (Delta-T Devices, Mark II) every three or four days between 25 and 67 DAS. Measurements were concentrated between 1000 and 1600 local time, and on two days they were made hourly from sunrise to sunset. Conductance was measured on four types of foliage: laminae within 0 to 30 cm, or 30 to 60 cm, or above 60 cm above the ground; and the leaf sheaths. Usually five measurements were made on different plants in each type of foliage. Conductances of adaxial and abaxial surfaces were measured in the central third of each lamina and were summed to give a value of leaf conductance. Squire (1979) gave further details of the method of measuring leaf conductance of this species and the calculation of canopy conductance from the sum of the products of mean leaf conductance and leaf area index (LAI) of each type of foliage.

Soil water content

Soil water content was measured using a combination of gravimetric sampling and neutron probing. Twenty-two access tubes, arranged systematically (Fig. 1), were installed to a depth of 2 m in both dry and irrigated plots. The volumetric moisture content of the soil below 0.3 m was monitored about every 2 weeks at 15 cm intervals down to 1.8 m with a Troxler neutron probe. For the surface layers, a 5 cm diameter core was extracted within 1 to 1.5 m of each access tube to a depth of 0.22 m. Each core was divided at 0.1 m, both parts were weighed, dried at 105°C for two days and reweighed. The volumetric water content of the 0 to 10 and 10 to 22 cm layers of the profile was calculated using a pre-determined bulk density.

Soil water potential

Four groups of tensiometers were installed in each of plots 4 and 6 at depths of 15 (plot 6 only), 30, 60, 90, 120 and 150 cm. Every two days from 28 DAS, readings were taken early in the morning to minimize heating effects. One set of thermocouple psychrometers (Wescor PT-51) was installed in plot 4 at depths of 15, 30, 45, 60 and 75 cm. A 10 cm diameter hole was made in the soil and the psychrometers were pushed horizontally into undisturbed soil at the desired depths. The soil removed from the hole was replaced. The wet-bulb depression of the psychrometers was read with a microvoltmeter and the manufacturer's calibration of the psychrometers was used to obtain soil water potential.

Evaporation of water from the soil surface

The loss of water directly from the soil surface was measured by weighing trays filled with soil. The trays were aluminium with an area of 20 x 40 cm and a depth of 9 cm. They were filled to the rim with soil removed from between the rows in plots 3, 4 and 6 to form holes of the same geometry as the trays. The sides of the holes were lined with polythene and the trays were carefully inserted so that the soil within them was flush with the surrounding soil. The trays were weighed daily between 20 and 29 DAS and again between 60 and 69 DAS.

MEASUREMENTS

Dry matter production and intercepted radiation

The fraction of solar radiation intercepted by the foliage (Fig. 2) closely reflected the growth and decay of leaf area described in earlier publications (Gregory and Squire, 1979; Squire, 1979). A maximum interception of 0.75 was achieved by the irrigated crop on 40 DAS; the fraction intercepted then decreased slowly until 60 DAS. In the dry crop, fractional interception began to decline soon after reaching a maximum of 0.65 at 40 DAS.

The crops were similar in dry weight before the irrigation on 30 DAS, but the irrigated crop was somewhat heavier than the dry one at the two subsequent harvests. The dry crop reached its maximum weight at 47 DAS and then stopped growing while the irrigated crop continued to grow. Figure 3 shows the relation between the standing dry weight of both crops and accumulated intercepted radiation. Only the weight of the shoots is shown although roots did contribute significantly to total plant weight during early growth (Gregory and Squire, 1979). Before anthesis (about 45 DAS), the dry matter produced per unit of radiation intercepted was similar for the two crops (1.96 g MJ^{-1} and 1.70 g MJ^{-1} for irrigated and dry crops, respectively). After anthesis the efficiency of the irrigated crop decreased to 0.91 g MJ^{-1}.

Adaxial and abaxial leaf conductance

Figure 4 shows the relations between the conductance of the upper layer of leaves in the canopy and irradiance before (a and b) and after (c and d) anthesis. Conductances of the dry crop after anthesis are not included because they

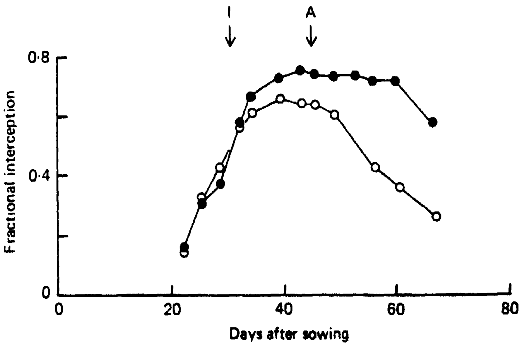

Fig. 2. Changes in fractional interception of total irradiance of the irrigated (●) and dry (○) stands. Arrows show the first irrigation (I) and 50% anthesis (A).

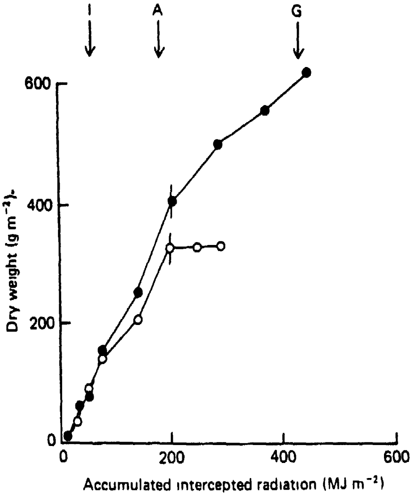

Fig 3. Dry matter production in relation to accumulated intercepted radiation in (●) irrigated and (○) dry stands. The arrows show the time of (I) first irrigation, (A) 50% anthesis and (G) the end of grain filling. The symbols are means of two plots ± standard errors.

were usually less than 0.15 cm s^{-1} at all values of irradiance. The four figures also illustrate differences in the response of adaxial and abaxial surfaces to both irradiance and soil water.

Before anthesis, the *adaxial* conductance increased linearly with irradiance and was similar for both stands (Fig. 4a). A constant relation was observed on 7 days between 32 and 48 DAS over a broad range of air temperature (23° to 31°C) and saturation deficit (0.5 to 3.0 kPa). This relation was not stable because conductance sometimes decreased by up to 50% for one or two hours around noon when irradiance exceeded 700 W m^{-2}. (The corresponding points have been omitted from Fig. 4a for clarity).

In contrast, the *abaxial* conductance of irrigated and dry crops responded differently to irradiance (Fig. 4b). The shape of the relation was less well defined than for the other surface. The smaller conductances of the dry crop were caused by the prevailing environment: the triangular symbols on Fig. 4b show the response of the abaxial surface when the soil was wetted by a light shower of rain; the adaxial surface did not respond.

In general, the stomatal response of the middle layer of leaves was similar to that of the abaxial surface of the upper layer: conductance was larger in the irrigated than in the dry crops at all values of irradiance and was also more sensitive to atmospheric humidity (Squire, 1979). In summary, before anthesis, only the adaxial surface of the upper leaves seemed insensitive both to a drying soil and to a range of saturation deficit.

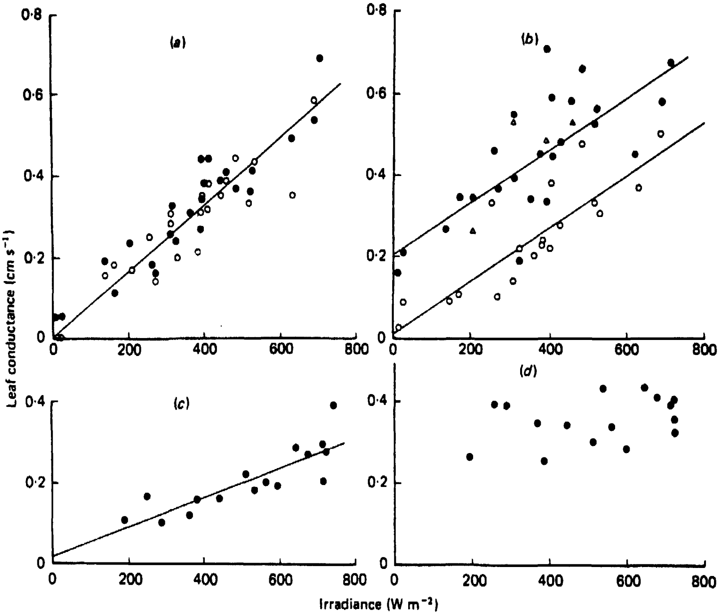

Fig. 4. Relations between leaf conductance in the upper layer of leaves and irradiance measured above the foliage in (●) irrigated and (○) dry stands: (a) adaxial (upper) leaf surface, before anthesis (32 to 48 DAS); (b) abaxial (lower) surface, before anthesis; (c) adaxial, after anthesis (56 to 67 DAS); (d) abaxial, after anthesis. The triangular symbols are explained in the text.

After anthesis, the relation between conductance and irradiance for the adaxial surface was still linear, but the slope was reduced by half (Fig. 4c). For the abaxial surface (Fig. 4d) there was no increase in conductance with irradiance above 200 W m^{-2}, but no measurements were made below this irradiance. The ranges of air temperature and saturation deficit after anthesis did not exceed the limits of their respective ranges during the vegetative period.

Canopy conductance (g_c)

Figure 5 shows temporal changes in g_c of both stands. The dashed line is based on the observation that leaf area was negligible until the canopy began to expand rapidly at about 16 DAS. Until about 45 DAS, the conductance of the dry crop ranged from 0.6 to 0.8 cm s^{-1}. The sharp decline in g_c after 45 DAS was caused initially by a fall in the conductance of individual leaves followed by a decline in leaf area. Leaf area and fractional light interception decreased more slowly. In contrast, the conductance of the irrigated crop was more variable in response to variable weather and possibly as a consequence of sampling errors. After 45 DAS it declined to more steady values around 0.8 cm s^{-1}.

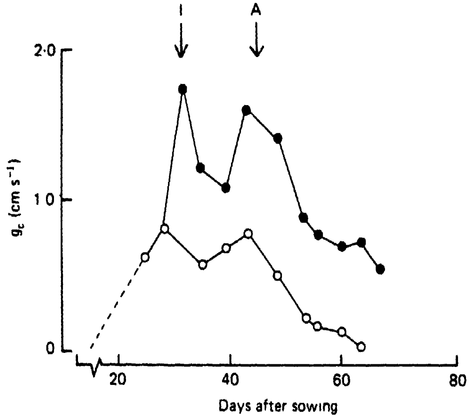

Fig. 5. Seasonal variation in canopy conductance (g_C). Each point is the mean of (usually) four estimates of g_C made between 0900 and 1600 local time. Arrows indicate irrigation (I) or 50% anthesis (A) and ●, the irrigated stand and ○, the dry stand.

Changes in soil water status

Figure 6 shows changes in the volumetric water content of soil profiles beneath dry and irrigated crops. During the first period of measurements (18 to 28 DAS), the two crops were growing under identical conditions; water content decreased in the upper 0.45 m of the profile but there was a gain (13.3 mm) of water below 0.45 m (Fig. 6a). A total of 17.5 mm of rain fell during this period and so the accretion of water below 0.45 m may represent net accumulation by drainage. After 28 DAS, the dry crop depleted water throughout the profile to 1.5 m while the pattern of extraction for the irrigated crop was different for each period of measurement. The water content under the dry crop remained almost constant after 53 DAS but water was lost from the irrigated crop until it was harvested.

Hydraulic potentials derived from the tensiometers were referenced to the soil surface and Fig. 7 shows profiles under the irrigated crop on selected days. Although irrigation maintained potentials greater than −0.08 MPa throughout the profile until 69 DAS, the repeated cycles of soil drying can be clearly distinguished. These profiles of potential are useful for determining the direction of water movement in the soil: the depth of zero flux indicates the boundary between drainage and evaporation (Williams and McGowan, 1980). At 29 DAS, for example, the potentials at 0.6 and 1.2 m were smaller than that at 0.9 m, so that water below 0.9 m must have been moving downwards (i.e. 0.9 m is the depth where the flux is zero). Before the first and second irrigations (30 and 42 DAS), the depth of zero flux was 0.9 m, but it changed to 1.2 m from about 57 DAS.

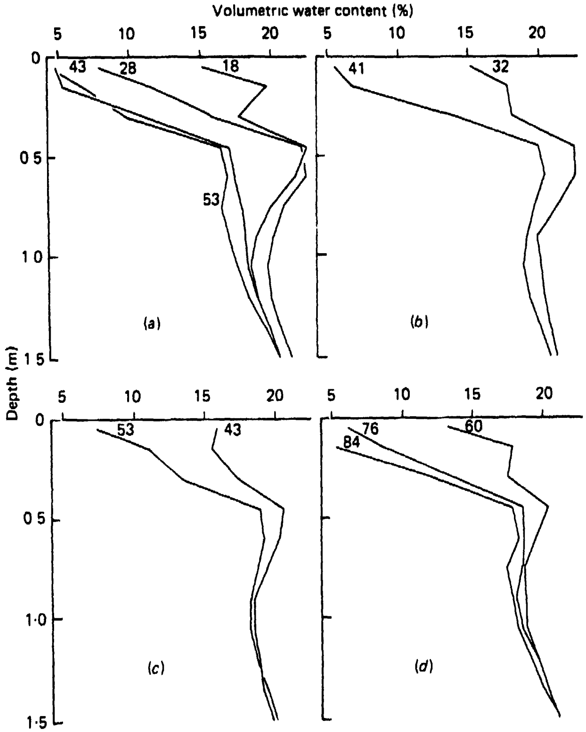

Fig. 6. Changes in the volumetric water content of the soil for the dry stand (a) and the stand irrigated at 30 DAS (b), 42 DAS (c) and 58 DAS (d). The number accompanying each line indicates DAS.

The soil dried rapidly under the dry crop and by 32 DAS, the surface layers were drier than −0.08 MPa. Figure 8 shows soil water potentials under the dry crop measured with thermocouple psychrometers. The top soil layer (psychrometer at 15 cm) dried continuously throughout the period of measurement, reaching a potential of −4.4 MPa by 80 DAS; potentials at the other depths decreased until about 60 DAS then remained almost constant. Slow evaporation of water from the soil surface is thought to have been responsible for the continual decrease in potential at 0.15 m, and the unchanging potentials below that depth are consistent with evidence from the neutron probe.

Use of water by the crops

Transpiration (T) was estimated as a residual in the water balance equation:

$$T = S + P - E - D \qquad (1)$$

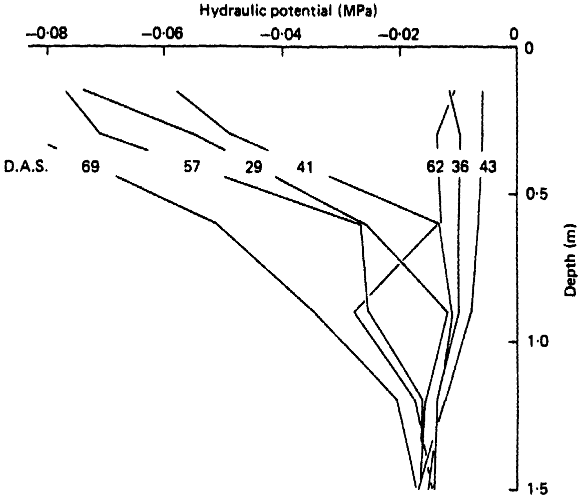

Fig. 7. Changes in hydraulic potential beneath the irrigated stand. The number accompanying each line indicates DAS.

where S is the depletion of soil water storage; P, rainfall; E, evaporation from the soil surface; and D, drainage (run-off was zero). Drainage was separated from E plus T by identifying the depth of zero flux. For example, for the irrigated crop between 32 and 41 DAS, the change in S below 0.9 m was attributed to drainage.

The measurements of evaporation from trays filled with soil confirmed that cumulative water loss from bare soil was a linear function of the square root of time from the last wetting of the surface (Ritchie, 1972). When there was a partial or complete canopy, measured values of E agreed closely with calculations using an empirical formula:

$$E = fE^* \qquad (2)$$

where f is the fraction of irradiance reaching the soil and E^* is $E_0/(t + 1)$, E_0 being open pan evaporation, and t the number of days without significant rainfall. As measured and calculated values agreed closely, E was obtained using Equation 2.

Table 2 shows the detailed soil water balance calculated for neutron probe readings taken to a depth of 1.8 m. In the irrigated crop, the rate of transpiration in a period which included irrigation was estimated by multiplying the measured E_0 for that period by an estimated value of T/E_0 obtained by interpolation. This method gave a total of 153 mm (from 18 DAS) which compares well with an approximation of 147 mm obtained using a simple proportional

Table 2. *Soil water balances for dry and irrigated crops (see text for explanation of symbols)*

DAS of millet	E_o (mm)	E^* (mm)	f	P (mm)	S (mm)	D (mm)	E (mm)	T (mm)	$(E + T)/E_o$
				Dry crop					
18–27	52.1	16.3	0.7	17.5	7.3	0.0	11.4	13.4	0.48
28–42	67.0	14.0	0.35	10.3	51.1	9.9	4.9	46.6	0.77
43–52	39.7	3.6	0.40	2.0	7.6	0.0	1.4	8.2	0.24
53–62	49.3	1.5	0.6	0.0	1.4	0.0	0.9	0.5	0.03
Water transpired = 68.7 mm									
				Irrigated crop					
18–27	52.1	16.3	0.7	17.5	7.3	0.0	11.4	13.4	0.48
32–40	38.3	12.0	0.35	4.6	47.4	7.5	4.2	40.3	1.16
43–52	39.7	12.3	0.25	2.0	26.9	0.5	3.1	25.3	0.72
60–75	73.5	11.6	0.4	0.0	30.0	−0.5	4.6	25.9	0.42
76–83	37.2	1.7	0.6	0.0	15.6	1.1	1.0	13.5	0.39
Water transpired = 153 mm (includes 35 mm estimated for the missing periods)									

correction for missing days. The sum of evaporation of water from the soil surface and from the plants (E + T) was less than open pan evaporation at all times except for the irrigated crop after the first irrigation. The water use efficiency, based on transpiration alone, was 255 g water per g dry matter for the irrigated crop, and 220 for the dry crop; based on E + T, the efficiencies were 296 and 278 for the irrigated and dry crops, respectively.

Table 3 shows the mean rates of water extraction at different depths in relation to root density (root length per unit volume) for the dry crop around anthesis. Before anthesis (45 DAS), drying was confined to the upper 1 m of soil and most water was withdrawn from the top 0.6 m of the profile, i.e. from that soil which contained most of the roots. After 43 DAS, the rate of water loss from the soil above 0.67 m decreased rapidly (to about 0.1 mm d^{-1}) while at depths between 0.67 and 1 m the rate remained unchanged and additional

Table 3. *Rooting density and water use of the dry millet crop in different soil layers shortly before growth ceased*

Depth increment (m)	Root density ($cm\ cm^{-3}$)	Transpiration rate ($mm\ day^{-1}$) 28–43 DAS	Transpiration rate ($mm\ day^{-1}$) 43–53 DAS
0–0.22	0.65	1.09	−0.12
0.22–0.37	0.64	0.47	0.15
0.37–0.52	0.68	0.53	0.08
0.52–0.67	0.15	0.51	0.08
0.67–0.82	0.03	0.29	0.23
0.82–0.97	0.02	0.20	0.18
0.97–1.12	not measured	0	0.11
1.12–1.27	"	0	0.11
> 1.27	"	0	0

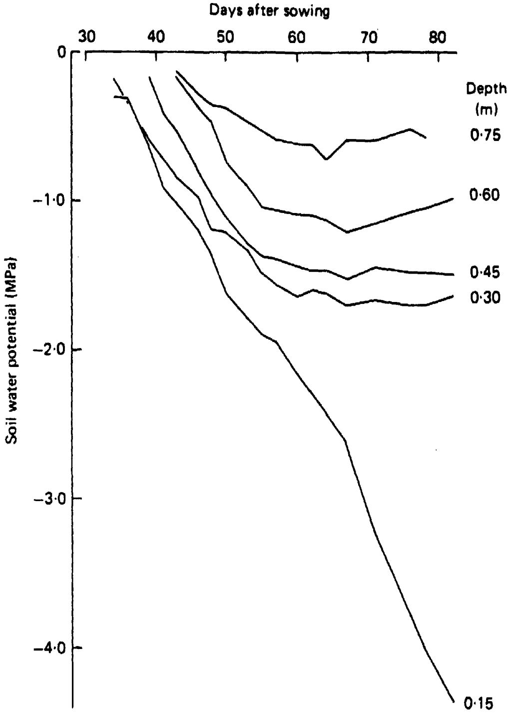

Fig. 8. Changes in soil water potential beneath the dry stand.

water was extracted below 1 m. Nevertheless, despite the increased uptake of water from deeper in the soil, the total extraction rate was only 1 mm d^{-1}, about 0.25 of open pan evaporation.

DISCUSSION

Comparison of stands

The stands of millet grew at the same rate initially and differences in the amount of radiation intercepted by the foliage were not apparent until 30 DAS. By anthesis (45 DAS) the fraction of radiation intercepted by the irrigated crop was about 0.15 more than by the dry crop but integrated over the whole period from emergence to anthesis the difference was only about 0.02 (i.e. from 0.45 to 0.43; Fig. 2). In the period before anthesis, there was a more significant difference in the amount of dry matter produced per unit of radiation intercepted which was about 20% less in the dry crop (Fig. 3). This difference is consistent with the smaller canopy conductance of the dry crop shown in Fig. 5.

After anthesis, the *irrigated* crop continued to extract water from the soil (Fig. 8), albeit at a smaller rate, probably because of the effect of senescence on leaf conductance (Fig. 4). The efficiency of storage of solar energy was also reduced to about 50% of its value before anthesis. In marked contrast, the measured growth of the *dry* crop after anthesis was effectively nil (Fig. 3): growth of the panicle was matched by an equivalent decrease in stem weight which is circumstantial evidence for retranslocation of stored assimilates (Gregory and Squire, 1979).

At harvest, the dry weight of the dry stand (312 g m^{-2}) was 52% of the corresponding figure for the irrigated stand, somewhat larger than the figure of 46% for the relative transpiration (Table 2). However, since figures for both dry matter production and evaporation are uncertain to at least ± 10%, the difference between these percentages may not be real.

Stomata played an essential role in balancing water supply and demand during vegetative growth. Near the top of the canopy, the abaxial conductance was smaller in the dry crop and stomata on both surfaces of older leaves responded to saturation deficit and soil water stress as reported by Squire (1979). Stomata on the adaxial surfaces of upper leaves showed little response to soil water supply (Fig. 4) and were insensitive to the variations in saturation deficit that occurred before anthesis (cf. Henson, Alagarswamy, Bidinger and Mahalakshmi, 1982). However, it is significant that even the irrigated stand did not grow as well as expected from measurements on the same cultivar of millet growing in the monsoon season when the air is more humid. Reddy and Willey (1981) reported an efficiency of 2.5 g MJ^{-1} before anthesis compared with the figure of 1.96 g MJ^{-1} for the irrigated stand studied here. This difference may be a consequence of smaller stomatal conductances in drier air. (At Hyderabad, the mean maximum saturation deficit during the monsoon is of the order of 1.5 kPa compared with 2 to 3 kPa in the months following the end of the monsoon). At about 50 DAS, leaf conductance of the dry crop dropped sharply. Table 3 and Fig. 8 show the state of water in the soil that was associated with this stomatal response. The water above 0.5 m, at potentials less than 1.4 MPa, was not exhausted despite a large concentration of roots; water at greater potentials deeper in the soil was unavailable because roots were scarce.

Comparison of processes

The measurements reported in this paper can be manipulated to estimate the extent to which a crop growing on stored water responds to a progressive reduction in water supply partly by stomatal closure and partly by developing and maintaining a smaller leaf area.

It has been shown here that the amount of dry matter produced by the two stands of millet was nearly proportional to the amount of water they transpired and that before anthesis each stand produced an amount of dry matter that could be related to the radiation intercepted by the canopy. It follows that the amount of water transpired by each stand before anthesis (T) can also be related to intercepted radiation (S_i). Writing the relation as:

$$T = kS_i \tag{3}$$

the constant of proportionality k will depend on weather (the same for both stands) and on stomatal conductance (shown to depend on the availability of water). Using the symbol δ to denote the difference between stands, the differential form of Equation 3 is:

$$\delta T/T = \delta k/k + \delta S_i/S_i \tag{4}$$

Of the three terms in this equation, $\delta T/T$ was measured with the neutron probe and $\delta S_i/S_i$ with solarimeters. The term $\delta k/k$, which depends on the relative difference of stomatal behaviour, can therefore be derived as the residual term in Equation 4. Estimated in this way, however, it is subject to large errors when δT and δS_i are small differences between large quantities or when $\delta k/k$ is itself a small fraction.

The fraction $\delta k/k$ can be determined more confidently from measurements of leaf conductance with a porometer combined with measurements of leaf area index to give the canopy conductance g_c (Squire, 1979). It can be shown from the Penman-Monteith formula (Monteith, 1981) that the rate of transpiration of a crop is inversely proportional to the function $[\Delta + \gamma(1 + g_a/g_c)]$. The parameters Δ and γ are the rate of change of saturation vapour pressure with temperature and the psychrometer constant in the same units; g_a is the aerodynamic conductance of the canopy, a function of windspeed and surface roughness.

Table 4 shows the outcome of applying this type of analysis both to the vegetative phase of growth when k is expected to depend mainly on g_c and to the period after anthesis when the interception of a significant fraction of radiation by stems and other transpiring tissue is probably responsible for a decrease of k with time, superimposed on the effects of stress and senescence on stomatal behaviour. The figures in parentheses are the uncertainty in each fraction assuming an arbitrary value of 5% for random errors of measurements. When $\delta k/k$ is derived from Equation 4, it appears that the difference in transpiration ascribed to stomata is three times larger than differences ascribed to a smaller leaf area before anthesis and about 1.5 times as large after anthesis. The uncertainty of these figures is considerable, however.

Calculation of $\delta k/k$ from conductances proceeds as follows. For the irrigated stand, the mean value of g_c before anthesis (20 to 45 DAS) is 0.86 cm s^{-1} compared with 0.85 cm s^{-1} from anthesis to 65 DAS (Fig 5). Corresponding figures for the unirrigated stand are 0.50 and 0.17 cm s^{-1}, respectively. Putting Δ = 0.19 kPa K^{-1} at 25°C, γ = 0.066 kPa K^{-1} and choosing g_a = 3 cm s^{-1} as a representative value for a tall crop exposed to a mean windspeed of 4 m s^{-1}, relative rates of transpiration before and after anthesis are 0.75 and 0.34. Correspond-

Table 4. *Analysis of contributions made by differences in leaf area and in stomatal resistance to the reduction of transpiration in the dry stand of millet (figures in parentheses are the uncertainty associated with each fraction assuming an uncertainty of 5% in T, S_i or g_c)*

	Before anthesis		After anthesis	
Factor	Irrigated	Dry	Irrigated	Dry
Transpiration (mm)	72	60	79	9
$\delta T/T$		0.17 (0.06)		0.89 (0.01)
Mean fractional light interception	0.45	0.43	0.71	0.47
$\delta S_i/S_i$		0.04 (0.02)		0.34 (0.05)
Fractional difference in transpiration ascribed to stomata $\delta k/k$		0.13 (0.09)		0.55 (0.05)
Fractional difference in transpiration calculated from g_c		0.25 (0.04)		0.66 (0.02)

ing values of 0.25 and 0.66 for the fractional *difference* in transpiration are compatible with the values estimated from Equation 4, confirming the conclusion that stomatal closure was a more important mechanism for saving water than the reduction in leaf area.

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REFERENCES

Gregory, P. J. & Squire, G. R. (1979). Irrigation effects on roots and shoots of pearl millet. *Experimental Agriculture* 15:161-168.

Henson, I. E., Alagarswamy, G., Bidinger, F. R. & Mahalakshmi, V. (1982). Stomatal response of pearl millet. *Plant, Cell and Environment* 5:65-74.

Monteith, J. L. (1981). Evaporation and surface temperature. *Quarterly Journal of the Royal Meteorological Society* 197:1-27.

Reddy, M. S. & Willey, R. W. (1981). Growth and resource use studies in an intercrop of pearl millet/groundnut. *Field Crops Research* 4:13-24.

Ritchie, J. T. (1972). Model for predicting evaporation from a row crop. *Water Resources Research* 8:1204-1213.

Squire, G. R. (1979). The response of stomata of pearl millet to atmospheric humidity. *Journal of experimental Botany* 30:925-933.

Szeicz, G., Monteith, J. L. & dos Santos, J. M. (1964). Tube solarimeter to measure radiation among plants. *Journal of applied Ecology* 1:169-174.

Williams, J. B. & McGowan, M. (1980). The water balance of an agricultural catchment. *Journal of Soil Science* 31:217-230.

Wong, S. C., Cowan, I. R. & Farquhar, G. D. (1978). Leaf conductance in relation to assimilation in *Eucalyptus pauciflora. Plant Physiology* 62:670-674.