Response to fertilizer nitrogen and water of post-rainy season sorghum on a Vertisol. 2. Biomass and water extraction

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(*Revised MS received 18 May 1998*)

SUMMARY

During rainless weather following a monsoon, sorghum (*Sorghum bicolor* cv. SPH–280) was grown on a Vertisol either unirrigated throughout growth or irrigated for 7 weeks after emergence and rainfed thereafter. Before sowing, ammonium sulphate was applied at six rates from 0 to 150 kg/ha N. Roots were sampled every 2 weeks to determine biomass and root length density as a function of depth. Every week, soil water content in all treatments was measured gravimetrically to a depth of 0·23 m and with a neutron probe from 0·3 to 1·5 m.

Below 0·45 m, volumetric water content was a negative exponential function of time after roots arrived and the maximum depth of extraction moved downwards at 2–5 cm per day. In the dry treatment, the extraction 'front' lagged behind the deepest roots by *c.* 12 days initially but the two fronts eventually converged. Irrigation delayed the descent of the extraction front by *c.* 20 days but thereafter it appeared to descend faster than without irrigation. Averaged over N rates, the time constant of the exponential function was inversely related to the root length density, l_v, decreasing with depth from about 20 to 10 days as l_v increased from 2·5 to 4·0 km/m³.

The biomass:water ratio was almost independent of N but increased from a mean of 5·3 g dry matter per kg water in the dry treatments to 6·9 g/kg with irrigation. When normalized by the seasonal mean difference in vapour pressure deficit within irrigated and unirrigated plots, the ratios were 13·1 and 13·3 kPa g per kg water, respectively.

INTRODUCTION

In a companion paper, Rego *et al.* (1998) analysed the response to nitrogen and water of sorghum cultivar SPH–280 grown in the Indian Deccan during the post-monsoon season. Response was interpreted in terms of three components: the interception of solar radiation; the efficiency with which intercepted radiation was used to generate biomass; and the fraction of biomass allocated to structural organs and to grain. All three components responded strongly to lack of water.

When the application of N was 30 kg/ha or more, absolute root mass at 33 days after emergence (DAE) was larger in unirrigated (dry) than in irrigated plots but leaf area and light interception were less. Both differences contributed to a larger root:shoot ratio and therefore to a more favourable balance between a 'supply' determined in part by the ability of roots to extract water and a 'demand' determined by the state of the atmosphere and by the response of stomata to that state.

This paper explores two hypotheses: (i) that in the absence of rain or irrigation, the supply of water can be related to (*a*) the rate at which the root system descended and (*b*) the rate at which water was extracted at a given depth once soil was penetrated by roots; and (ii) that the rate of growth was tightly coupled to the water supply. Analysis established which physiological parameters were most sensitive to differences in water and nitrogen and which were conservative.

METHODOLOGY

Agronomy

The sorghum cultivar SPH–280 was sown on a Vertisol at the ICRISAT Centre (17·5 °N, 78·5 °E) on 29 October 1988. Table 1 summarizes soil physical

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Table 1. *Soil physical properties as function of depth*

Horizon	Depth (cm)	Percentage distribution of particle size (mm)				Water content (vol. %)	
		Coarse sand (2·0–0·2)	Fine sand (0·2–0·02)	Silt (0·02–0·002)	Clay (< 0·002)	−0·033	−1·5 (MPa)
AP	0–16	18·3	25·3	16·3	40·1	38·0	21·9
B12	16–57	17·6	15·6	17·3	49·5	44·7	26·2
B13	57–118	8·9	10·0	20·4	60·7	44·4	27·3
B14	118–155	9·9	10·4	19·4	60·3	47·6	28·3

El Swaify *et al.* (1985).

properties. Plots of 10×10 m with six replicates received 0, 30, 60, 90, 120 or 150 kg/ha N applied as ammonium sulphate before sowing. To facilitate germination, all plots were given 30 mm of water through sprinklers. For each nitrogen rate, three replicates subsequently received 40 mm of irrigation three times at 18, 28 and 50 days after emergence (DAE) and the other three were not irrigated. Plants reached physiological maturity at *c.* 95 DAE and were harvested at 110 DAE.

From all plots, shoots were sampled every week and roots every 2 weeks at intervals of 0·15 m to a maximum depth of 2 m. To obtain root samples to a depth of 0·5 m, soil was removed from pits with a cross-section of 0.6×0.8 m that included eight plants. Deeper roots were obtained by extracting seven cores (diameter 4 cm) from below each pit. Roots and organic debris were separated from soil using the hydropneumatic elutriation system described by Smucker *et al.* (1982) and the length of roots in each sample was measured by scanning on a Delta-T Light Table (Harris & Campbell 1989). Further details of management and measurements are as given by Rego *et al.* (1998).

Weather and water

Weather was measured at a standard climatological station 540 m from the experimental site. Daily mean air temperature decreased from 25 °C at sowing to *c.* 20 °C at 100 DAE and there was a corresponding decrease in daily values of mean saturation vapour pressure deficit from *c.* 2·4 to 1·8 kPa over the same period. Rainfall was negligible: 2·3 mm in the first week of the trial and 6·7 mm at 32 DAE.

The soil was a deep Vertisol with clay increasing from *c.* 40 % near the surface to *c.* 60 % in the layer from 1 to 2 m deep that was eventually permeated by roots (Table 1). There was a corresponding increase in water content with depth but the amount of water held between conventional limits of −0·033 and −1·5 MPa changed little to a depth of 2 m.

Two neutron-probe access tubes were installed in each plot and an IH II probe (Didcot Instruments Ltd) was used to monitor changes of volumetric soil water content at 0·15 m intervals from 0·3 to 1·5 m. The probe was calibrated earlier against the volumetric water content of soil samples taken from this range of depth. Water content above 0·3 m was determined gravimetrically. Total loss of water by evaporation and transpiration from each plot was estimated as $\delta M + I + P$ where δM is the decrease of water in the soil profile to a depth of 1·5 m between observations (7 days on average), I is irrigation for the same period (if any) and P is precipitation.

Psychrometers, screened and aspirated in a double-walled tube, were installed at the centre of each plot to obtain records of temperature and vapour pressure and were raised each week to the approximate height of the second fully-expanded leaf. These measurements were checked each week against an Assmann psychrometer.

EXTRACTION ANALYSIS

The following procedure for the analysis of water extraction by a descending root system (Monteith 1986) was successfully applied to sorghum by Robertson *et al.* (1993 *a, b*) and to sunflower by Meinke *et al.* (1993). It is based on the suggestion by Passioura (1983) that water 'available' to roots at depth z and time t can be expressed as

$$\theta(z, t) = \theta_a(z) \exp[-t/\tau(z)] \qquad (1)$$

where $\tau(z)$ is a time constant changing with depth and $\theta_a(z)$ is the (maximum) water available when roots reach depth z at $t = 0$. (This quantity is sometimes estimated as the difference in water content corresponding to a difference in water potential between conventional limits of field capacity and permanent wilting point but the less arbitrary procedure adopted here is described later.)

When Eqn (1) is valid, $\ln[\theta(t)]$ obtained from sequential measurements can be regressed against
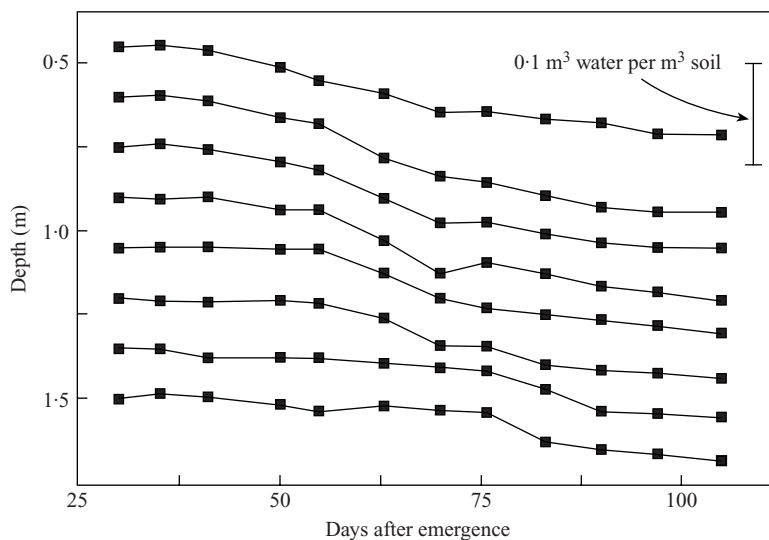
Fig. 1. Change of relative water content with time at eight depths averaged over three unirrigated plots receiving 150 kg/ha N. Depth (0·45–1·50 m) is given by the position of extreme left-hand points. For each set of points corresponding to a fixed depth, a decrease of 0·1 m³ water per m³ soil corresponds to 0·3 m on the depth scale (see secondary scale top right).

time (elapsed since $\theta = \theta_a$) to obtain $-\tau$ as an inverse slope. Passioura (1983) suggested that τ could be assumed inversely proportional to root length density. The validity of this scheme for the extraction of water by a uniform stand can be examined for any layer of soil containing roots and within which changes of water content are determined predominantly by extraction. The analysis was therefore confined to depths below 0·45 m, assumed to be beyond the influence of evaporation from the soil surface. For irrigated plots, the analysis was also confined to the period after the final irrigation at 50 DAE.

Figure 1 presents an example of the decrease in water content with time in the unirrigated treatment supplied with N at 150 kg/ha. Each set of 12 points (joined by lines) represents the change in water content with time at a fixed depth. That depth is given by the position of the earliest measurement plotted in each set (i.e. at 30 days after emergence). The uppermost set therefore refers to measurements at 45 cm and successive sets refer to depths at intervals of 15 cm down to 150 cm. At a given depth, the decrease of water content with time is plotted as a slow increase in an apparent depth. This can be read from the y-axis and then converted to water content by using the factor 0·1 m³ water per m³ soil for an apparent difference in depth of 30 cm (see secondary scale top right in Fig. 1).

Before roots arrived at a specific depth, apparent changes of θ from week to week were small and random so that a well-defined mean value could be obtained for $\theta_{max}(z)$, the initial water content at depth z. A mean minimum water content $\theta_{min}(z)$ was

determined in a similar way from measurements after extraction appeared to have ceased, usually *c*. 40 days after it began at a given depth. To use Eqn (1), the maximum amount of water effectively available at depth z, $\theta_a(z)$, was assumed to be $\theta_{max}(z) - \theta_{min}(z)$. The actual amount available at time t was taken as $\theta(z, t) - \theta_{min}(z)$.

To fit Eqn (1), the vertical depth scale was left unaltered but the vertical local scale was changed to the logarithm of the fractional water content, i.e. the value of

$$p = \ln\left[\{\theta(z, t) - \theta_{min}(z)\} / \{\theta_{max}(z) - \theta_{min}(z)\}\right] \quad (2)$$

In Fig. 2, a fractional water content of 0·5 gives $p = \ln 0·5 = -0·69$ and corresponds to 6·9 cm on the depth scale. For each depth and nitrogen rate, p was calculated for all measurements defining straight lines with descending slopes (identified by full points in Fig. 2). Small values of $\theta(z, t) - \theta_{min}(z)$ were excluded from the analysis because corresponding estimates of p were very scattered. In the dry treatment, analysis covered all six rates of N from the arrival of the extraction front at the highest depth of measurement (*c*. 40 DAE).

With increasing depth, θ_{max} increased slightly but there was a much larger increase of θ_{min} with the consequence that $\theta_a(z)$ decreased from *c*. 0·084 m³/m³ at 0·45 m to 0·056 m³/m³ at 1·5 m. Figure 3 shows water content limits for the dry treatments averaged over six rates of N and plotted as a function of depth. Standard errors were small – reassuring evidence for the uniformity of the soil profile across the site. The figure also shows the relation between water content
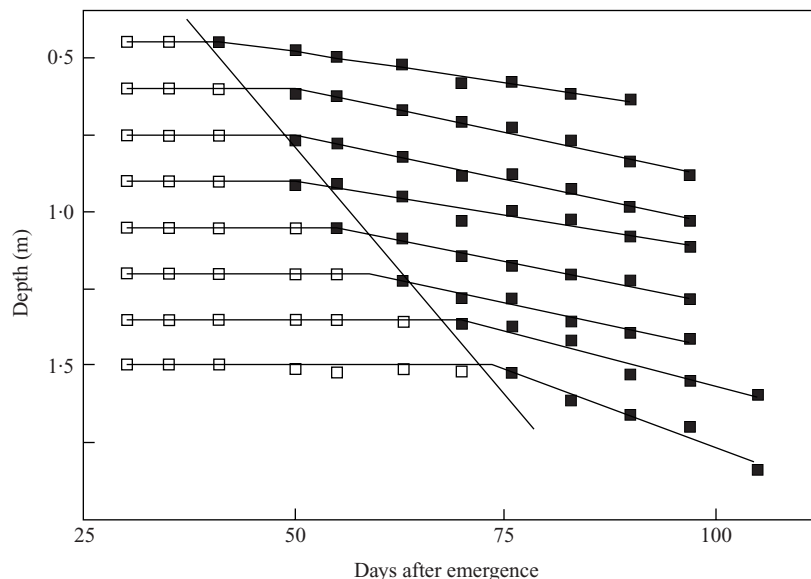
Fig. 2. As Fig. 1 but with the logarithm of relative water content (p) plotted against time (see Eqn (2)). A difference in water content corresponding to $p = -0.69$ is equivalent to 6.9 cm on the apparent depth scale (see text). Open points precede the apparent onset of extraction. Full points were fitted to Eqn (1) (thin lines). The diagonal line is the estimated position of the extraction front.
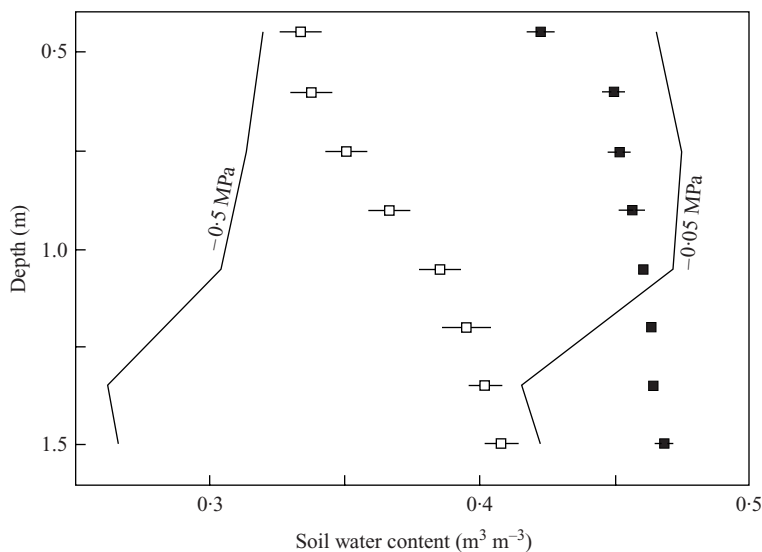

Fig. 3. Mean maximum (■) and minimum (□) water contents observed at each depth, averaged over unirrigated treatments at six application rates of N. Bars are standard errors. Full lines correspond to water content measured in the laboratory at potentials of -0.05 and -0.5 MPa.

and depth for arbitrary values of soil water potential (-0.05 and -0.5 MPa) obtained from cores previously extracted from a nearby site and equilibrated at fixed values of suction on a pressure-membrane system (Krantz *et al.* 1976). Values of $\theta_a(z)$ were much smaller than would be predicted from conventional estimates of water 'available' to a lower limit of -1.5 MPa. A possible explanation is that a relatively small gradient of water potential in the taproot may have prevented upper roots from drying the surrounding soil to a potential below that of water becoming accessible to deeper roots.

Table 2. *Parameters derived from the extraction equation* $\theta(z,t) = \theta_a(z) \exp\{-(t_i - z/(u)/\tau(z)\}$. *See text for explanation of symbols and parameters*

Parameters	Nitrogen (kg/ha)					
	0	30	60	90	120	150
	Unirrigated					
t_i	25 ± 7.5	30 ± 5.1	26 ± 9.1	30 ± 11.0	27 ± 6.2	26 ± 8.3
u (cm/d)	2.6 ± 0.29	3.3 ± 0.25	3.2 ± 0.46	3.6 ± 0.61	3.4 ± 0.33	3.2 ± 0.43
r^2	0.93	0.97	0.89	0.85	0.95	0.90
τ (d)	14.5 ± 4.14	15.7 ± 3.12	16.0 ± 4.84	13.5 ± 2.81	13.4 ± 5.10	17.8 ± 4.44
	Irrigated					
t_i	52 ± 26.8	49 ± 18.8	46 ± 8.8	43 ± 10.7	49 ± 12.0	50 ± 11.6
u (cm/d)	5.6 ± 1.74	4.5 ± 0.99	3.9 ± 0.41	3.9 ± 0.52	4.7 ± 0.62	4.9 ± 0.67
r^2	0.64	0.78	0.94	0.89	0.89	0.90
τ (d)	13.4 ± 6.6	20.0 ± 6.09	16.2 ± 8.07	19.3 ± 5.17	20.4 ± 15.5	17.5 ± 4.63

Linear regressions of p against time during the main period of extraction yielded two parameters: $-1/\tau(z)$ from the slope of the regression at each depth; and the time $t_i(z)$ at which extraction started at each depth as defined by the intersections of the straight lines $p = 0$ ($\theta = \theta_{max}$) and the sloping lines $p = p(t)$ (see Fig. 2). In general, $t_i(z)$ appeared to increase linearly with depth implying that a constant velocity (u) could be assigned to an extraction front; but in some treatments the front may have descended somewhat faster at intermediate depths as Angus *et al.* (1983) found for a range of dryland crops. The value of u was obtained from the regression equation:

$$z_f(t) = u(t - t_i) \tag{3}$$

where t_i is the apparent time when the front began to descend from the soil surface.

Table 2 summarizes this analysis and includes the correlation coefficient (squared) for the regression of z_f on time. Standard errors were larger and correlation coefficients were smaller in the irrigated than in the dry treatments. Unavoidably, the application of water was not perfectly uniform and redistribution within the profile was probably irregular vertically because of the presence of cracks and large pores.

For the five treatments receiving nitrogen, none of the parameters appear to change systematically with the application rate. For zero application, however, the extraction front velocity in the dry treatment was anomalously small (2.6 ± 0.29 cm/day as compared with a mean of 3.34 ± 0.15 cm/day for the other five N rates). Conversely, the velocity in the irrigated zero N treatment was anomalously large (5.6 ± 1.74 cm/day as compared with 4.38 ± 0.41 cm/day for the other rates). The relatively rapid descent of the extraction front in this treatment is consistent with the large root:shoot ratio reported by Rego *et al.* (1998), possibly associated with a loss of mineralized N.

Observations made on Table 2 are further supported by the plot of data in Fig. 4 where the depth of the extraction front, estimated from Eqn (3), is plotted against time. The descent of the front was effectively independent of N (when applied) but was delayed by irrigation. Extrapolation below the lowest depth of measurement (1·5 m) implies that, irrespective of treatment, the front reached 2·1–2·2 m at physiological maturity (*c.* 95 DAE). Independent confirmation that roots reached this depth is provided later.

Comparison of extraction and root fronts

The position of the extraction front can be compared with the maximum depth of rooting estimated from the change in root length density with time at each depth. The depths plotted in Fig. 4 are averages for the five fertilized treatments (dry and irrigated) based on the time when the measured root length density first exceeded an arbitrary minimum of 1 km/m³.

In the dry treatment, the extraction front lagged behind the root front by *c.* 10 days for the first 60 days but the position of the points at 59 and 74 DAE suggests that the descent of the root front may have slowed during the latter stages of growth, allowing the extraction front to catch up. In the irrigated treatment, the gap between the root and extraction fronts appeared to narrow throughout the second half of the season. Robertson *et al.* (1993*b*) also found that the extraction front in stands of sorghum lagged behind the root front initially but then descended somewhat faster.

The difference in behaviour of the root and extraction fronts can be explored further through an expolinear equation (Goudriaan & Monteith 1990). The equation was originally used to describe measurements of biomass as a function of time (t), at least when there is little change in climate over the growing season. It can also be applied to individual organs such as leaves, stems and roots. The initial growth rate of each of these organs, unrestricted by com-
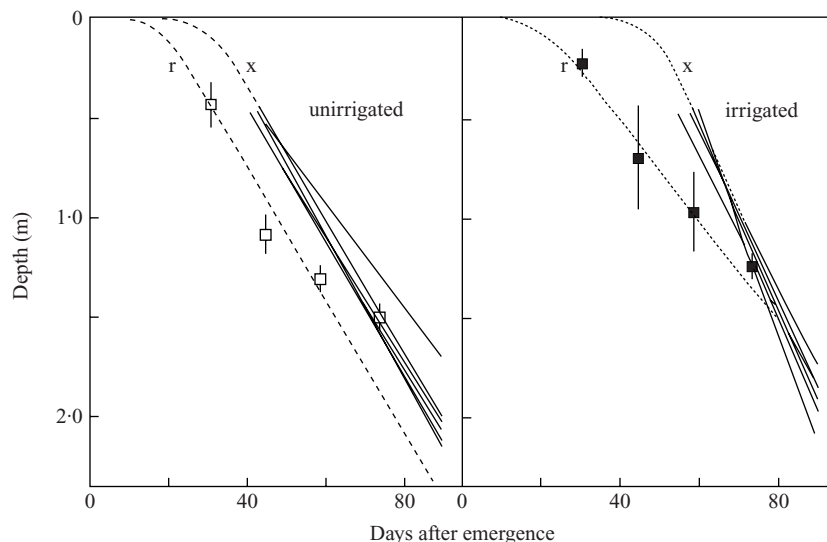
Fig. 4. Squares: approximate depth of root front with time averaged over levels of N as estimated from measurements of root length density in unirrigated (□) and irrigated (■) stands. Full lines: position of extraction front estimated from parameters in Table 2 (the outlier in the unirrigated treatment corresponds to zero nitrogen application). Dashed lines: position of root (r) and extraction (x) fronts estimated from expolinear equation (Eqn (4)).
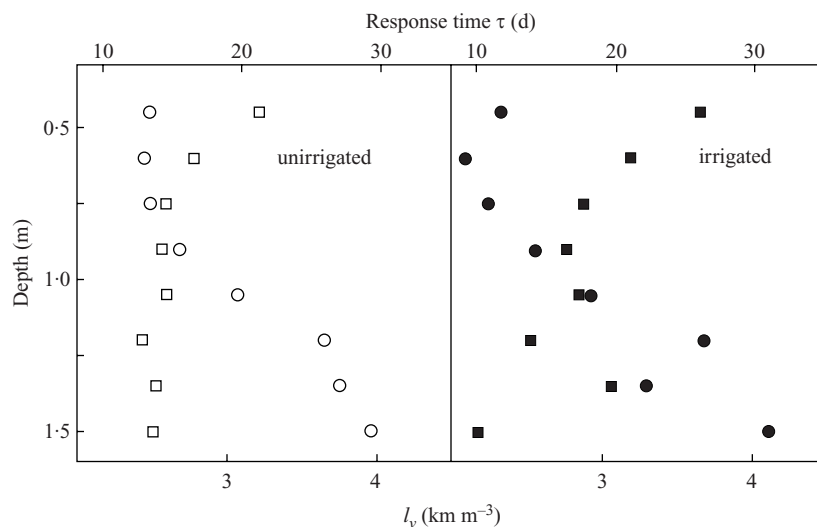

Fig. 5. Root length density l_v (circles) and response time τ (squares) averaged across N levels and plotted against depth in unirrigated ($\bigcirc, \square$) and irrigated ($\bullet, \blacksquare$) plots.

petition between neighbouring plants, is proportional to their mass (W) implying that the relative growth rate [$R_m = (\mathrm{d}W/\mathrm{d}t)/W$] is effectively constant. As time proceeds, however, the relative growth rate decreases because of competition but the absolute growth rate $\mathrm{d}W/\mathrm{d}t$ increases until it reaches a constant maximum value determined by the availability of resources such as light, water and nutrients.

In this application, the depth z_f achieved by either root or extraction front at time t after emergence can be expressed as:

$$z_f = (u/R_m)\ln[1+\exp\{R_m(t-t_i)\}] \qquad (4)$$

where R_m is the maximum relative growth rate of roots with units of d^{-1}, u (cm/d) is the constant (maximum) velocity of either front and t_i is the apparent time when either front started to descend.

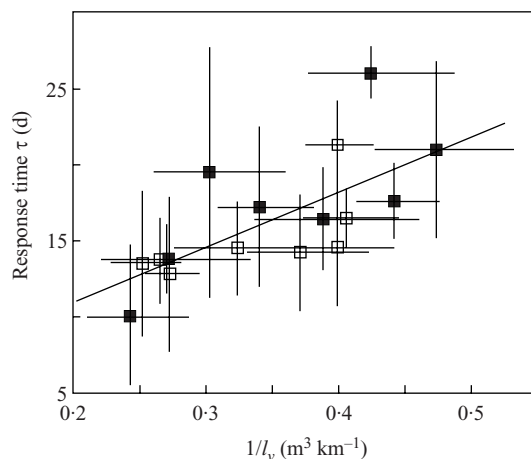A mean value of $R_m = 0.29\ \mathrm{d}^{-1}$ was obtained for

Fig. 6. Mean response time at each depth as a function of mean reciprocal root length density (l_v) at that depth for unirrigated (□) and irrigated (■) plots. The regression fitting coordinates for eight depths and both treatments is $\tau = [(37 \pm 10)/l_v] + (3 \cdot 6 \pm 3 \cdot 6)$. Error bars are standard errors obtained by averaging τ and $1/l_v$ over all treatments at each depth.

both dry and irrigated treatments by plotting the logarithm of root biomass as a function of time. Mean values of u and t_i for the extraction front were obtained by averaging values across N levels. Corresponding values for the root front (not well defined by measurements of root length density) were estimated by inspection of the points plotted in Fig. 4. Table 2 contains these parameters. Without irrigation, the root and extraction fronts descended at approximately the same rate (*c.* 3·3 cm/d) (see Fig. 4). With irrigation, the root front descended somewhat more slowly and the descent of the extraction front was delayed by *c.* 3 weeks.

Time constant and root length density

At a specific depth, the root length density, like the extraction velocity, appeared to respond to irrigation but not to nitrogen and values of l_v were therefore averaged across all rates of N application to reduce scatter. Contrary to reports for many other species (e.g. de Willigen & van Noordwijk 1987) but consistent with measurements on sorghum by Merrill & Rawlins (1979), the value of l_v, averaged over time, increased with depth from about 2·5 km/m³ at 0·6 m to 4·0 km/m³ at 1·5 m in the irrigated treatment (Fig. 5). Consistent with this increase, the mean time constant τ decreased over the same range of increasing depth and the rate of decrease was somewhat faster with irrigation, behaviour consistent with faster transpiration from irrigated plots.

To test Passioura's (1983) hypothesis that τ and l_v may be inversely related, τ was plotted against the
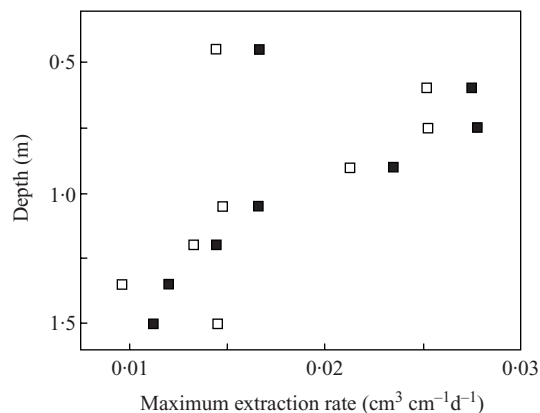

Fig. 7. Maximum rate of extraction per unit length of root as function of depth estimated from root length density and response time in unirrigated (□) and irrigated (■) treatments.

reciprocal of mean l_v for each depth below 45 cm and a linear regression was fitted to all points in Fig. 6 (see legend). The coordinates of the regression are within the standard error for almost every point. Because the constant term in the regressions is small, the product of τ and l_v could be treated (at least within the observed range of l_v) as independent of water and nitrogen regimes at *c.* $4 \cdot 0 \times 10^4$ d/m² consistent with a value of $4 \cdot 2 \times 10^4$ d/m² reported by Robertson *et al.* (1993 *a*) as the mean for a series of sorghum trials.

Extraction per unit length of root

Differentiating Eqn (1) with respect to time and setting $t = 0$ gives the initial (maximal) rate of extraction at depth z as $\theta_a(z)/\tau(z)$ and the maximal extraction per unit length of root is therefore

$$E_m(z) = \theta_a(z)/\{\tau(z)l_v(z)\} \qquad (5)$$

Figure 7 shows that in a layer extending from *c.* 0·60 to 0·75 m deep, extraction achieved a maximum rate of *c.* 0·025–0·028 cm³/d per cm of root, a range close to the upper limit of 0·03 cm³/d per cm suggested by Ritchie (1985) and reported by Robertson *et al.* (1993 *b*). Both above and below this layer the rate was substantially less, implying that the potential rate of water supply exceeded the demand.

TRANSPIRATION AND BIOMASS

Extrapolation procedure

Rego *et al.* (1998) showed that total biomass was strongly correlated with the accumulated interception of solar radiation by foliage. With irrigation, the production of biomass per unit of intercepted radiation was almost independent of nitrogen application rate > 30 kg/ha. This response might be interpreted as evidence that biomass production was driven by
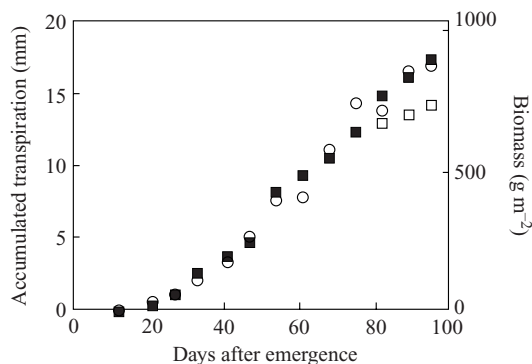
Fig. 8. Increase in biomass and in accumulated extraction of water as functions of time from emergence (unirrigated stand, 30 kg N/ha). A calculated ratio of 5·18 g/kg was used to match the scales of the vertical axes for water (left) and biomass (right) so that the water measurements corrected for extraction below 1·5 m (■) and biomass measurements (○) are coherent. Open squares (□) are measurements of accumulated extraction to 1·5 m only (see text).
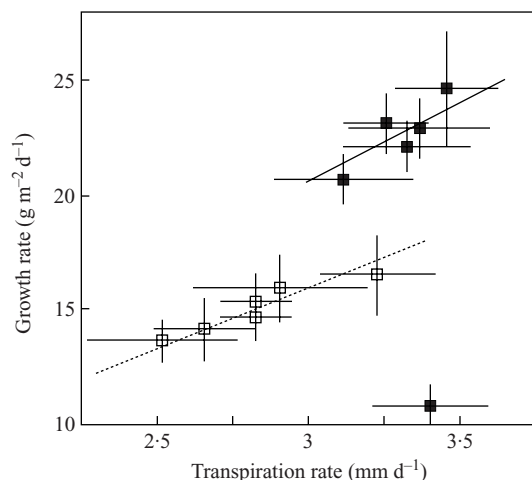

Fig. 9. Mean crop growth rate for each N level estimated from 41 to 82 DAE plotted as a function of mean transpiration rate for the same period for the unirrigated (□) an irrigated (■) treatments. Lines correspond to mean biomass/water ratios of 5·31 (±0·13) g/kg and 6·82 (±0·17) g/kg for unirrigated and irrigated treatments respectively. (The full square at bottom right is the anomalous irrigated, zero-nitrogen treatment (see text).)

the availability of radiant energy to leaves rather than by the availability of water to roots. To explore this hypothesis, biomass accumulation was correlated with accumulated transpiration using the following procedure.

The total water loss from the soil surface down to the extraction front was estimated by adding com-ponents from (i) gravimetric measurements for the upper 0·23 m layer of soil and (ii) neutron probe measurements from 0·3 to 1·5 m (accounting nominally for depths between 0·23 and 1·65 m and assuming neutron moderation in a 0·15 m diameter sphere). Because soil water and biomass were measured on different days for logistic reasons, it was convenient to estimate cumulative water loss E on days when plants were harvested to determine cumulative biomass (W). This was achieved by linear interpolation of E between dates of measurements.

In all treatments, total biomass W increased linearly with accumulated evaporation during the main period of growth. Regressions of W on E for measurements between 41 and 82 DAE inclusive gave the biomass:water ratio (discussed later) as a slope, dW/dE. Biomass could therefore be expressed as

$$W = (dW/dE)(E - E_s) \qquad (5)$$

where E_s, the intercept of the regression line on the evaporation axis, was interpreted as the amount of water lost by evaporation from the soil surface.

In the unirrigated treatment, the soil surface was extremely dry from *c.* 15 DAE onwards and in the irrigated treatment, shading by foliage and absorption by roots near the soil surface both constrained direct evaporation from about the same date. Values of E_s were uncorrelated with nitrogen rates and ranged from 4·8 to 4·9 cm in the unirrigated and from 8·2 to 9·4 cm in the irrigated plots.

In Fig. 8, accumulated total biomass and accumulated transpiration for one treatment are plotted as functions of time over the whole season with vertical scales adjusted to demonstrate the congruence of growth and transpiration, at least until *c.* 80 DAE Thereafter, although biomass continued to accumulate at an almost constant rate as plants approached physiological maturity, the rate of extraction of water, as originally estimated, appeared to decline in all treatments (open squares). As it is highly improbable that the biomass:water ratio increased substantially during the final stages of growth, this anomaly was ascribed to an underestimate of transpiration because of the arbitrary choice of 1·65 m as a maximum depth for assessing the uptake of water.

It is probable that roots continued to descend at a constant rate even after anthesis (Duncan *et al.* 1981) eventually reaching a predicted depth of *c.* 2·1 m at 95 DAE (Fig. 4). Water extracted between 1·5 and 2·1 m was therefore estimated by using an integrated form of Eqn (1) that includes the extraction velocity determined in the upper part of the profile, the time constant at 1·5 m, and an assumed value of 0·02 m^3/m^3 for θ_a. The scale of correction can be judged from the vertical distance between the open squares in Fig. 8 and the corresponding corrected values above them (closed squares) which are consistent with the biomass:water ratio obtained earlier in the season.

Determination of biomass: water ratio

In Fig. 9, growth rates are plotted against transpiration rates with standard errors obtained from the regressions. Within each water treatment, the dependence of the ratio on nitrogen rate, if it existed, was obscured by errors of measurement and mean ratios were 5.31 ± 0.13 and 6.82 ± 0.17 g dry matter per kg water for the dry and irrigated plots respectively.

In principle, the biomass: water ratio is inversely proportional to the mean difference of vapour pressure across the bulk resistance to diffusion offered by stomata. However, because this gradient is very difficult to measure, the daily mean vapour pressure deficit (VPD) at screen height is often used as a surrogate (Tanner & Sinclair 1983). In this trial, the values of VPD measured near the top of the canopy and meaned over the whole period were 2.5 and 1.9 kPa for the dry and irrigated treatments respectively. Because of mixing of air between the two types of plot, the effective difference of VPD between treatments was probably smaller than these figures suggest. Nevertheless, multiplying the biomass: water ratios already cited by the mean measured VPDs yielded consistent normalized ratios of 13.1 kPa g dry matter per kg water (unirrigated) and 13.3 kPa g per g dry matter (irrigated). Both ratios are close to the value of 13.8 kPa per kg obtained by Tanner & Sinclair (1983) from measurements by Teare *et al.* (1973).

CONCLUSIONS

At least for a simple climate and soil profile, the exponential equation appears to be a valid and useful algorithm for obtaining parameters that describe the downward movement of an extraction front at a constant or almost constant rate (u) and, at a given depth, the dependence of extraction rate on time (τ). In this trial, the magnitudes of u and τ depended on water supply but not on the application of nitrogen over the range explored. The range of values for u in the irrigated treatment (3.9–4.9 cm/d excluding the zero N treatment) was similar to the range reported by Robertson *et al.* (1993*a*) for two Australian cultivars on an Oxisol (3.3–4.9 cm/d) but the time constants in our Vertisol trial covered a smaller range (13.4–20.4 d for both irrigated and dry treatments compared with 7–20 d). Part of this difference may be a consequence of the greater availability of extractable water in the Vertisol; 0.06–0.09 m^3/m^3 (see Fig. 3)

compared with 0.04–0.05 m^3/m^3 over a comparable range of depths on the Oxisol.

Relations between root front velocity, root length density and the extraction time constant may be worth exploring as a basis for matching cultivars to soil type as well as to climate. At a site where the water-holding capacity of the soil was small or rainfall was erratic, early growth would be favoured by a root system that descended rapidly (relatively large u) to make water available from the whole profile early in the season. To conserve water for subsequent reproductive growth, however, laterals should permeate the soil slowly (relatively small l_v). Conversely, with reliable rainfall, consistently good yields could be achieved with smaller values of u and l_v that would allow potential rates of transpiration and growth to be maintained with minimal root biomass.

In the irrigated treatment, the biomass: water ratio was effectively independent of nitrogen (> 30 kg/ha). Without irrigation, the ratio was somewhat smaller in the plots that received most nitrogen, developed more leaf area, used water faster and therefore experienced more stress while grains were filling. In environments where this phenomenon is common, the relation between leaf expansion and root proliferation may be an appropriate index for cultivar selection.

In an almost rainless environment and for a specific cultivar, there will often be an optimum maximum leaf area determined (i) by a demand for water established by climate; and (ii) by water supply determined partly by soil storage and partly by the extent of the root system. Predicting optimum leaf area and root length from genetic and environmental information remains a major challenge but the systematic behaviour of the cultivar described in this paper suggests that it may be possible to tackle the problem by matching fertilizer application and population with water availability.

The stability of the biomass: water ratio in a given environment is mainly a consequence of the conservatism of the effective internal concentration of CO_2 of foliage (treated as 'big leaf') (Tanner & Sinclair 1983). In this trial, crop growth rate, normalized by VPD (a measure of water demand) was proportional both to the rate at which radiation was intercepted and to the rate at which water was extracted. These relations imply both that the effective internal CO_2 concentration of leaves was, in effect, independent of their water and nitrogen status; and also that the conductance of canopies was proportional to the fraction of incident radiation that they intercepted.

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