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EFFECTS OF PLANTING DENSITY ON WATER USE AND PRODUCTIVITY OF PEARL MILLET (*PENNISETUM TYPHOIDES*) GROWN ON STORED WATER. II. WATER USE, LIGHT INTERCEPTION AND DRY MATTER PRODUCTION

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SUMMARY

Pearl millet was grown on stored water at Niamey, Niger, using three row spacings. Water extraction based on neutron probe readings was compared with crop transpiration using a porometer and allied measurements. Between 23 and 52 days after sowing, plants at the narrow and medium spacings used about 77 and 100 mm of water, respectively, and those at the wide spacing used between 59 and 75 mm. Estimates of seasonal crop evaporation from leaf resistances and from the green leaf area index (GLAI) of the crops were 103, 130 and 123 mm for the narrow, medium and wide spacings, respectively. The water use per unit of dry weight produced was similar for both narrow and medium spacings but water was used more efficiently in the wide spacing. Dry weight increased in proportion to intercepted radiation with the same efficiency (1.3 g MJ^{-1}) irrespective of spacing.

When a crop is grown in a dry area without irrigation, the rate at which roots extract water from the soil can be manipulated by changing either the planting density (Bond *et al.* 1964) or the planting arrangement, or both. At least in principle, this type of manipulation may increase the economic yield of the crop per unit of available water.

In a previous paper (Azam-Ali *et al.* 1984, subsequently referred to as Paper I) we presented measurements of the root and shoot growth of three populations of pearl millet (2.9, 5.8 and 11.5 plants per m^2) growing on stored water at the World Meteorological Office Agrhymet Centre, Niamey, Niger (13° 29′ N, 2° 10′ E) between October 1980 and January 1981. We now consider the interaction of water use and light interception on the growth of the shoots.

METHODS

Soil water

Sets of tensiometers (Webster, 1966) were installed in two plots of each row spacing (38, 75 and 150 cm) at depths of 10, 20 and 40 cm and at 20 cm intervals thereafter to 140 cm. The manometer stake was sited midway between the rows and the tensiometers installed in an arc of 50 cm radius around it. There

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was therefore a bias in favour of mid-row potentials in the wide spacing. Readings were taken early in the morning, to minimize heating, every 3 to 4 days throughout growth.

Volumetric water content was measured with a Wallingford neutron probe at 10 cm intervals from 10 to 180 cm depth. Aluminium access tubes were installed to a depth of 2 m on all plots shortly after sowing by augering a hole slightly smaller than the tube and then pushing in the access tube. Different numbers of access tubes were installed in each plot depending on the row spacing: one tube mid-row for the narrow spacing; one on a row and one mid-row for the medium spacing; and one on a row, one mid-row and one a quarter of the distance across a row for the wide spacing. The probe was calibrated in the field by taking cores of known volume from positions close to extra access tubes. As a result, water content at 20 cm and below was calculated from a single calibration but a separate calibration was used nearer the surface. Unfortunately, the probe broke during the later stages of crop growth and no readings were possible beyond 52 days after sowing (DAS).

Plant water loss

A Delta-T Devices automatic porometer was used to measure stomatal resistance to water transfer. The temperature difference between the leaf and the sensor was minimized by leaving the instrument in the shade of the crop between measurements and by holding the cup by the end furthest from the sensor. The porometer was left attached to the calibration plate and switched to the 'automatic' mode for at least 15 minutes before each series of measurements.

Measurements of stomatal conductance were normally made twice weekly between 23 and 58 DAS. Readings were usually made at 0800, 1200 and 1600 h but occasionally there were additional measurements at 1000 and 1400 h. In two periods (37–40 DAS and 51–54 DAS), readings were taken over four consecutive days to enable comparison of estimated evaporation based on porometry with water use measured with a neutron probe (Azam-Ali, 1983).

Concurrently with measurements of stomatal resistance (r_s), boundary layer resistance (r_a) was also measured using artificial, blotting-paper 'leaves'. Wet and dry bulb temperatures of the air above the canopy measured with an Assmann psychrometer and leaf temperature measured with a copper-constantan thermocouple, were combined with the resistances to calculate evaporation per unit area of leaf (E) using the relation

$$E = \frac{x_1 - x_2}{r_s + r_a} \qquad (1)$$

where x_1 is the saturation vapour concentration at leaf temperature and x_2 is the vapour concentration in the ambient air. Evaporation from the whole crop can be found by multiplying the above value by the green leaf area index

(GLAI) of the whole crop. Full details of the technique are given by Azam-Ali (1983).

Interception of solar radiation

Fourteen solarimeters (Delta-T Devices), approximately 1 m long, were placed at ground level across the rows. In order to span five rows of each spacing, the wide, medium and narrow stands had eight, four and two solarimeters, respectively, placed end to end. Because of the prevalence of dust thoughout the season, the solarimeters were regularly wiped clean with a damp cloth. Output from the solarimeters was monitored on six integrators housed in a shaded position adjacent to the field site and powered by a 12 volt battery. Daily values of incident radiation were recorded between 16 and 73 DAS.

One solarimeter mounted above the canopy was calibrated against a standard Kipp solarimeter situated at the meteorological site about 100 m from the field. All the others were calibrated against the instrument above the canopy and against the Kipp solarimeter both before and after exposure. The intercepted radiation of each stand was obtained as the difference between solarimeter measurements above and below the canopy.

RESULTS

Soil water

At 16 DAS, the tensiometers indicated that the irrigation equipment had provided a uniform distribution of water over the experimental area. Subsequent changes in volumetric water content with time showed differences in both the amount and pattern of water extraction by crops at the three spacings (Fig. 1).

Over the period of measurement, soil under the narrow and medium spacings lost approximately the same quantity of water; from 30 to 120 cm depth the water content decreased by about 7%. Under the wide spacing, the loss was about 6% in the same layer. In all crops, most water was lost during the first seven day period, with smaller losses in each succeeding period. From 37 DAS onwards, no water was lost from the top 30 cm but the loss of water below this depth differed between crops. Beneath the narrow and medium spacings, the soil dried to an almost constant water content of 4% between 40 and 120 cm, but beneath the wide spacing the amount of drying decreased with depth.

Before the amount of water used by crops could be calculated from the changes in volumetric water content in Fig. 1, drainage and evaporation had to be assessed. However, because water contents in all soil layers changed continuously throughout the experiment, it was impossible to detect systematic discontinuities of the type which usually allow this distinction (Gregory *et al.* 1978).

The separation of drainage and evaporation was first attempted using the

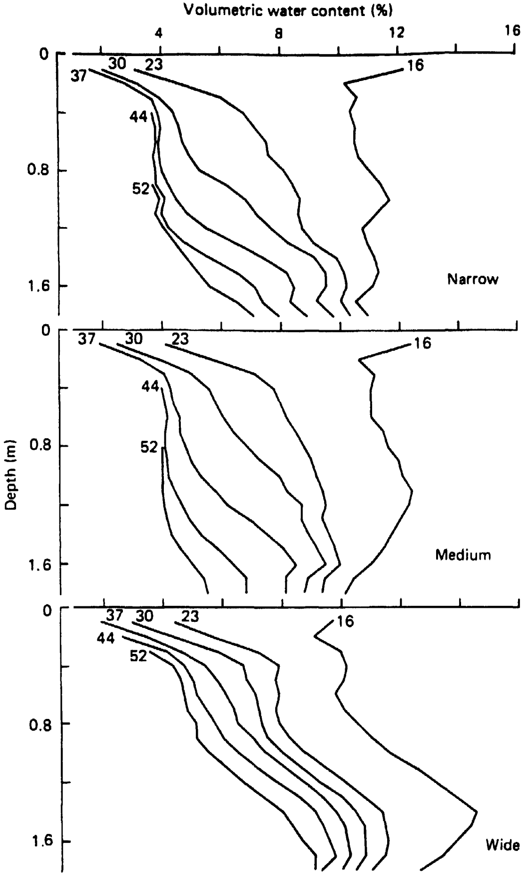

Fig. 1. Changes in volumetric water content with time beneath millet crops. Days after sowing are shown against each line; lines are drawn only at depths where changes in water content occurred.

depth at which the potential gradient, as measured with tensiometers, was zero, implying that the vertical flux of water was zero. This analysis produced values for drainage ranging from one-third of the total change in storage (narrow spacing) to two-thirds (wide spacing). Such large losses by drainage are implausible, particularly as they occurred throughout the growing period. As it was unlikely that sandy soil would continue to lose a substantial amount of water by drainage up to 30 days after irrigation, systematic error was suspected. We now believe that the location of the tensiometers in mid-row gave a serious underestimate of the depth of the zero flux plane particularly in the medium and wide spacing. We therefore assumed arbitrarily that the depth of zero flux measured by tensiometers was valid until 23 DAS and that no further drainage occurred after this date. Table 1 shows the total water use and abstraction from different soil layers estimated in this way.

Between 16 and 52 DAS, evaporation from the narrow and medium spacings was similar and was about 50% greater than from the wide spacing. Substantial amounts of drainage occurred between 16 and 23 DAS to give water contents in the deeper soil layers of about 9 to 10%, this corresponds well with 'field capacity' given by the moisture characteristic curve at a potential of 5 kPa. During the first seven days of measurements, and particularly in the wide and medium spacings, water was lost mainly by evaporation from the soil surface. After the first week, however, measurements on an adjacent, fallow plot showed that evaporation directly from the soil was minimal so that, from 23 DAS at least, the values shown in Table 1 can be ascribed to transpiration alone.

Because the soil water content at 180 cm decreased throughout the experiment, upward movement or extraction of water must have occurred from

Table 1. *Water use (mm) by millet crops from different soil layers*

	Depth (cm)					
DAS	0–40	41–80	81–120	121–160	> 161	Total
			Narrow			
16–22	27.3†	0	0	0	0	27.3
23–29	7.7	10.8	6.4	2.9	1.5	29.3
30–36	1.6	3.8	8.8	5.8	4.3	24.3
37–43	1.2	0.7	2.9	6.5	5.7	17.0
44–51	0.1	0.1	0.7	4.0	4.1	9.1
Total	38.0	15.4	18.8	19.2	15.6	107.0
			Medium			
16–22	17.7†	0	0	0	0	17.4
23–29	8.6	8.4	5.1	2.7	1.0	25.8
30–36	3.6	6.9	9.6	5.4	1.6	27.0
37–43	1.2	1.9	5.0	8.6	9.7	26.4
44–51	0.4	0.1	1.5	4.5	12.2	18.7
Total	31.7	17.3	21.2	21.2	24.5	115.3
			Wide			
16–22	11.4†	0	0	0	0	11.4
23–29	6.3	3.0	2.9	3.1	1.2	16.5
30–36	4.9	3.5	2.2	2.6	2.0	15.2
37–43	1.8	3.8	3.7	2.8	2.1	14.2
44–51	1.2	2.0	4.0	4.2	1.9	13.3
Total	25.6	12.3	12.8	12.7	7.2	70.6

† Water loss from the soil surface is likely to be a substantial component of these values.

below this depth. An estimate of this water content was obtained graphically by selecting an appropriate mean water content (e.g. 10% for the narrow spacing) at 23 DAS for all layers deeper than 160 cm. When profiles of water content obtained later were extrapolated to this value, maximum depths of extraction estimated at 52 DAS were 240, 260 and 220 cm for narrow, medium and wide spacings, respectively. The corresponding amounts of water depleted from soil deeper than 180 cm were calculated as 8.8, 16.6 and 2.9 mm.

Table 1 shows that more water was taken from deeper in the profile as growth proceeded, but there were differences between crops in the quantity and time of use of these deep reserves of water. The narrow and medium spacings used similar amounts of water from each soil layer but the medium spacing exploited more water from below 160 cm. In contrast, the wide spacing did not use as much water from any soil layer and its use of water deep in the profile was limited.

Transpiration

In Fig. 2 the estimated rate of transpiration based on porometer measurements is plotted for ten days between 23 and 54 DAS (points under line a). When the individual components of Equation 1 are considered, the green leaf area index (GLAI) emerges as the main determinant of the transpiration rate (Azam-Ali, 1983). It was therefore possible to estimate transpiration from GLAI before and after the period when the porometer was used (points under lines b). An estimate of the total amount of water lost from each stand over the whole growing season was obtained by integrating the area under each curve in Fig. 2. Since little transpiration occurred outside the period when the porometer was used, the error introduced from the correlation between transpiration rate and GLAI was small.

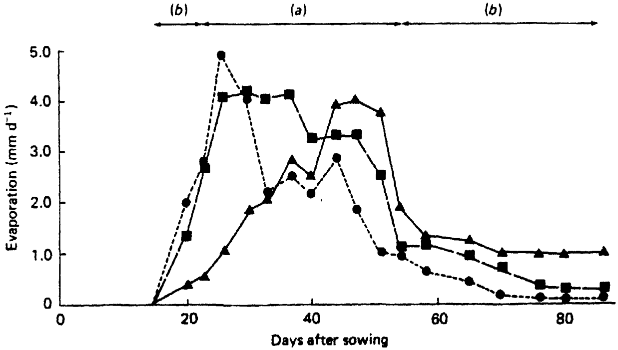

Fig. 2. Evaporation estimated (a) from porometry and (b) from green leaf area index for millet at three spacings: ● narrow, ■ medium and ▲ wide.

Figures for seasonal crop water use, obtained from porometry and associated measurements, were 103, 130 and 123 mm for the narrow, medium and wide spacings, respectively.

Water use ratio

In Fig. 3a the amount of above ground dry matter which accumulated before leaf senescence became pronounced (i.e. up to 52 DAS) is plotted against the accumulated loss of water estimated from stomatal conductances and allied measurements. The slope of the relation between dry weight and transpiration is the water use ratio (WUR). During this period, water was used most efficiently in the wide spacing where the WUR was significantly greater ($P < 0.10$) than that in either of the denser populations.

In Fig. 3b comparable values of WUR were obtained from estimates of soil water loss between 23 and 52 DAS using the neutron probe. Loss of water before 23 DAS must have included a significant component of evaporation from the soil surface and was therefore excluded from the calculation. The WUR's obtained from estimates of transpiration and from direct measurements of changes in soil water content were 2.0 ± 0.43 and 2.13 ± 0.64 mg dry weight per gram of water for the narrow spacing and 2.58 ± 0.14 and 2.67 ± 0.14 mg g^{-1} for the medium spacing. Figures for the wide spacing were less consistent at 3.0 ± 0.05 and 4.7 ± 0.47 mg g^{-1}. The latter (neutron probe) figure is significantly larger ($P < 0.05$) than corresponding values for the denser populations.

Radiation

Measurements of light interception were available on only two blocks and are not comparable with values in Fig. 2. In these blocks, plants in the narrow

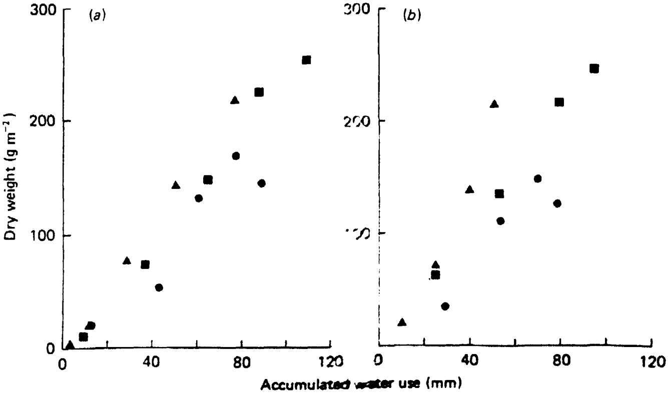

Fig. 3. Relation of accumulated dry weight to accumulated water use (a) from estimates using a porometer and (b) using a neutron probe, for millet at three spacings: ● narrow, ■ medium and ▲ wide.

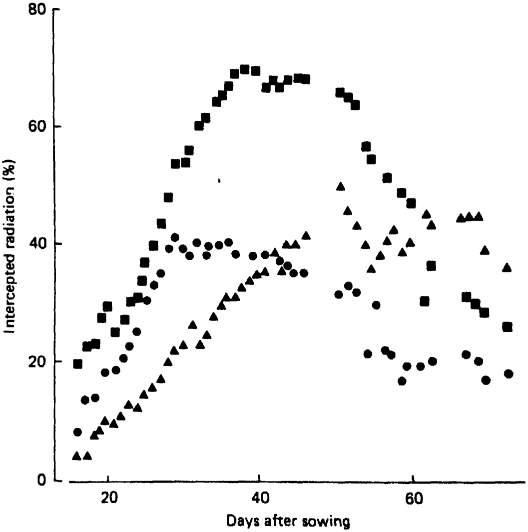

Fig. 4. Percentage of radiation intercepted by millet at three spacings: ● narrow, ■ medium and ▲ wide.

spacing were smaller than average and in the medium spacing they were somewhat larger. In the narrow spacing, interception reached a maximum of 40% at 29 DAS and gradually declined thereafter (Fig. 4). In the medium spacing, a maximum interception, between 65 and 70%, was evident between 35 and 53 DAS. In the wide spacing, interception increased linearly from 17 DAS to a maximum of 50% at 51 DAS. In all treatments fractional interception appeared to fluctuate from day to day during the later stages of growth, because of changes in the orientation of some plants caused by wind damage, and of errors due to accumulation of debris on the tubes during the extremely dusty period. Total daily irradiance ranged from 12 to 21 MJ m^{-2} during the growing season (October 18 to January 12). Figures for intercepted radiation are shown in Table 2.

The relation between dry matter and accumulated intercepted radiation between 17 and 73 DAS is presented in Fig. 5. The accumulated dry matter is an average for the two blocks in which radiation was measured. Excluding four points to the right of the sloping dotted line, the dry weight increased in proportion to intercepted radiation (solid line). Although a single linear regression has been fitted, there is evidence of curvature in the relation for both the narrow and medium spacings. The two horizontal broken lines indicate the trend of measurements on the narrow spacing at 52, 59 and 73 DAS and on the

Table 2. *Maximum daily and total seasonal interception of radiation by the millet crops*

Spacing	Maximum daily intercepted radiation (MJ m^{-2})	Total intercepted radiation between 16 and 73 DAS (MJ m^{-2})
Narrow	8.4	297
Medium	12.9	508
Wide	9.5	289

medium spacing at 73 DAS. For these dates and spacings, the rate of dry matter accumulation was less than expected on the basis of light interception, presumably as a result of drought.

DISCUSSION

In this experiment, the stands which produced most dry matter per unit field area and most yield were those sown at planting densities of 2.9 and 5.8 plants per m^2, that is in the wide and medium row spacings. In the local farming system, millet is often planted in a 1 x 1 m square arrangement (P. Vossen, personal communication). The main factor compensating for smaller plant populations was the contribution from additional viable tillers, which constituted 70% of total plant weight in the widest spacing compared with only 35% in the narrowest (see Paper I). Consequently, there were 38 panicles per m^2 in the wide spacing compared with only 15 in the narrow. Prolific tillering can be ascribed mainly to the fact that there was very little mutual shading in the lowest and intermediate populations so that relatively large amounts of assimilates were produced per plant.

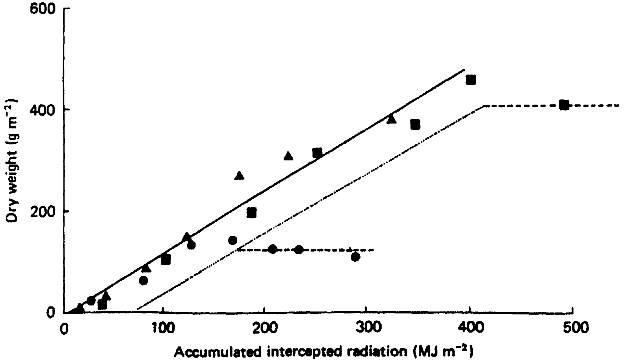

Fig. 5. The relation between dry weight of the millet crop and accumulated intercepted radiation between 17 and 73 DAS, at three spacings: ● narrow, ■ medium and ▲ wide. A regression ($r^2 = 0.96$; slope = 1.34 g MJ^{-1}) is fitted through all points to the left of the sloping dotted line. The horizontal dashed lines represent the medium and narrow spacings when water deficits appear to limit production.

Plants in the two widest spacings grew throughout the season at a rate which was closely related to the amount of radiation intercepted, i.e. at about 1.3 g MJ^{-1}. In the narrowest spacing, the same relation between growth and radiation was maintained until anthesis. Thereafter, there was no net increase of dry weight but there is evidence (see Paper I) that the movement of material stored in the stem allowed the main-stem panicle to reach a maximum weight of 5.3 g compared with 18.3 g in the widest spacing.

The weight of dry matter produced per unit ground area was approximately proportional to the loss of water from each stand. The constant of proportionality was the same in the narrow and medium spacing but was greater in the wide spacing. This difference may be a consequence of greater humidity in the microclimate of the densest stands during early growth or of a higher level of internal CO_2 concentration in stressed leaves during the later stages of growth.

The experiment provided a further demonstration of the principle that the yield of a crop growing on stored water is determined not just by the total amount of water available within the root zone but also by the rate at which it becomes accessible to roots (Passioura, 1974). To achieve maximum yield in millet, and probably in many other cereals, this rate should be such that when roots stop growing after anthesis, water continues to reach them by mass flow down a potential gradient. The availability of water during the period when grains are filling helps to delay leaf senescence so that the duration of this phase is longer than when metabolites are drawn from resources in the stem. It is still far from clear, however, why the ratio of grain weight at harvest to shoot dry weight should be so insensitive to population and environmental differences.

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