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GENOTYPIC AND ENVIRONMENTAL VARIATION IN NODAL ROOT GROWTH OF POST-RAINY SEASON (*RABI*) SORGHUM

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SUMMARY

Rapid initiation and growth of nodal roots (NR) are critical for the establishment of post-rainy season (*rabi*) sorghums grown in drying soil. The growth of NR was studied in sorghum in the field when sown at different depths in order to vary the crown depth, when different levels of irrigation water were applied to create different moisture contents in the topsoil, and in a number of cultivars to assess genotypic variability. Variation in sowing depth did not result in differences in NR growth, partly because of the capacity of sorghum to vary the mesocotyl length, which brought the crown to approximately the same depth. Different soil moisture levels in the field affected the elongation rate of NR, but not their initiation. Genotypic variation existed in the thermal time required for NR initiation and rate of elongation. The variation in NR growth was independent of the variation in shoot growth. The genotypic variability in NR growth offers an opportunity for combining root-related traits with useful agronomic characters.

Desarrollo de raíces con nudos en el sorgo de post-estación de lluvias.

RESUMEN

La rápida iniciación y desarrollo de raíces con nudos resulta crítico para el establecimiento de los sorgos de post-estación de lluvias (rabi) cultivados en tierra en vías de secarse. El desarrollo de raíces con nudos fue estudiado con sorgo en campo sembrándolo a distintas profundidades para variar la profundidad de corona, o bien con diferentes niveles de irrigación para dar lugar a un diferente contenido de humedad en la capa de tierra superior, y en una serie de variedades de cultivo para evaluar la variabilidad genotípica. La variación en la profundidad de cultivo no produjo como resultado diferencias en el desarrollo de raíces con nudos, en parte debido a la capacidad del sorgo para variar la longitud de mesocotilo, lo cual llevó a la raíz aproximadamente hasta la misma profundidad. La diferencia en los niveles de humedad de la tierra en el campo afectaron la intensidad de elongación de las raíces con nudos, pero no su iniciación. Existió variación genotípica en cuanto al tiempo térmico requerido para la iniciación de raíces con nudos y la intensidad de elongación. La variación en el desarrollo de raíces con nudos resultó independiente de la variación en el desarrollo de brotes. La variabilidad genotípica en cuanto al desarrollo de raíces con nudos brinda la oportunidad de combinar peculiaridades relativas a las raíces con útiles caracteres agrícolas.

INTRODUCTION

Approximately 40% (6 million ha) of the total sorghum crop area in India is grown during the post-rainy (*rabi*) season in drying soil, where rapid seedling

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establishment is important for good crop stands and high and stable yields (Seetharama *et al.*, 1990). Early vigour is critical if the crop is to use the nutrients from the rapidly drying upper soil layers, and to reduce evaporation from these layers. Seedling establishment and early crop vigour in the *rabi* environment depend largely on the rapid initiation and extension of the crown or nodal roots (NR), as the single seminal (primary) root of sorghum usually lasts only for 10–30 days after sowing (Freeman, 1970). The seminal root can remain active when NR initiation is delayed, but it cannot absorb adequate nutrients and water to sustain plant growth (Bur *et al.*, 1977).

Typically, the first NR is initiated when the first internode reaches its maximum length (about 3–4 days after seedling emergence, Mirhadi and Kobayashi, 1980). When the top 0.3 m soil layer is wet (70% field capacity), NR initiation and establishment proceed at the maximum potential rate (Blum and Ritchie, 1984) but the development of a secondary root system can be prevented or delayed if moisture is deficient at the crown depth (Cornish *et al.*, 1984). Thus sowing depth may also affect NR establishment, especially in drying soil where the seedling crowns of shallow-sown seeds will be located in a dry soil layer (Kanitkar *et al.*, 1968).

Genotypic differences in sorghum rooting pattern have been reported in several studies (Jordan and Miller, 1980; Jordan and Sullivan, 1982; O'Toole and Bland, 1987). However, many of these reports are based on hydroponic or pot studies, where conditions differ considerably from those in the field, especially in the post-rainy season. We tested the hypothesis that the initiation of NR was most affected by the moisture status of the soil around the crown by sowing at different depths and by applying different quantities of irrigation water to the soil surface at sowing. We also examined whether genotypes differ in the time of NR initiation and growth, as this has practical implications for the ICRISAT sorghum improvement programme.

MATERIALS AND METHODS

This paper reports on four experiments: Experiment 1 to study the effect of depth of sowing on NR growth; Experiment 2 to study the effect of surface soil moisture on NR growth; and Experiments 3a and 3b, to study genotypic variation in the growth of NR. Experiments 1 and 2 were conducted in 1987; Experiment 3 was conducted in 1988 (3a) and repeated in 1989 with fewer cultivars (3b).

The experiments were grown in a Vertisol field (Typic Pellustert, Kasireddipalli series) at ICRISAT Center, Patancheru, India (18°N, 78°E) during the *rabi* seasons (mid August–December). The soil was medium-deep (1.5 m) with approximately 160 mm of plant available water.

Seeds were sown 50 mm deep (except in Experiment 1, where sowing depth itself was a treatment) using a precision planter (John Deere 7100) on ridges spaced 0.75 m apart. The plots were 2.0 m long on each ridge with a 0.5 m path between adjacent rows. The seedlings were thinned to an average spacing of 50

mm on the ridge. Plant protection measures were taken as required to ensure sufficient seedling population in all experiments.

In Experiment 1, there were three sowing depth treatments (50, 80, and 100 mm), four genotypes and three replications. Plots were arranged in a split-plot design with the depth as the main plot and the 28 plots of four genotypes × seven sampling dates as sub-plots. In Experiment 2, there were four replications, two on either side of a line-source irrigation line (Hanks *et al.*, 1976); three moisture levels (M1, wet; M2; and M3, dry) established on ridges at 2.25, 5.25 and 8.25 m, respectively, from the line-source (Soman, 1990). Eight plots of two genotypes × four sampling dates were arranged randomly within each irrigation level. In Experiments 3a and b, plots of genotype × five sampling dates combinations were arranged in randomized block design with three replications.

Seed material

Experiment 1 contained four genotypes of sorghum (*Sorghum bicolor* (L.) Moench): M 35-1, a popular *rabi* cultivar, E 36-1, an elite germplasm line, SPV 86, a released *rabi* cultivar, and Nagawhite, a line with good seedling vigour. In Experiment 2 only two genotypes, M 35-1 and E 36-1, were studied. Nineteen genotypes were studied in Experiment 3a. These were selected from multilocation *rabi* sorghum trials conducted by ICRISAT in collaboration with the All India Sorghum Improvement Project (AICSIP, 1986). They included six advanced breeding lines (A 4128, A 2719, A 4111, A 4121, A 4123 and A 145), a rainy-season hybrid (CSH 6), three shoot fly (*Atherigona soccata*) resistant sources with good grain yield (PS 30831, P 33200, and P 31920), and five landraces cultivated during the *rabi* season (Lakadi, Sel 3 TL, Sel 3 DE, Jeur 2 DE and Jeur 2 7C), as well as M 35-1, E 36-1, SPV 86 and Nagawhite. Experiment 3b used seven genotypes chosen from Experiment 3a (Sel 3 TL, Jeur 2 DE, Lakadi, A 4128, M35-1, A 145 and Nagawhite). Seeds of all genotypes were produced in the 1986 *rabi* season and were kept in a cold store at 4°C.

Crop-growth environment

Experiments 1, 3a and 3b were sown into a naturally receding soil moisture profile while in Experiment 2 line-source irrigation was applied on the day of sowing.

Soil moisture was sampled gravimetrically at three depths (0–50, 0–100, 100–200 mm) every day in all experiments. In Experiments 1 and 2 one sample per treatment (sowing depth or soil moisture) per replicate, and in Experiment 3a and 3b two samples per replication were taken. Soil temperatures were measured at sowing depth by two thermocouples per treatment connected to a Campbell Scientific 21X datalogger.

In Experiment 3b, the thermal time required for NR initiation was measured by installing thermistors in replicates one and two, each adjacent to the seedlings at crown depth and connected to microvolt integrators (DELTA-T Instruments),

which measured accumulated day-degrees above a 10°C base temperature (Angus *et al.*, 1981).

Plant measurements

At each sampling, whole plots were dug and soil around the seedlings was removed manually. The soil attached to the roots was then washed carefully up to the tip of NR. The recovery of the root system was good until 18 days after sowing (DAS). Measurements were taken on 10 seedlings per plot at each sampling. Roots (seminal and NR) and shoots of the seedlings were separated. The number and length of NR, and the length of the seminal root were recorded. The laterals on NR were not measured separately as they were just forming by 18 DAS and were too short and thin to measure. The length of the root was measured by a root-length meter based on the line-intercept method. Leaf area was recorded and the oven-dry mass of roots, shoots and leaves determined.

Additionally, in Experiments 1 and 2 the lengths of the mesocotyls were measured on 10 seedlings at four DAS, to assess the crown depth, before separating them into roots and shoots.

In Experiment 3b observations on NR initiation of all genotypes were made daily on randomly selected seedlings in each plot by removing the soil around the crown; NR initiation was defined as the time when seedlings had at least one NR 1.0 mm long.

RESULTS AND DISCUSSION

In general the weather conditions during the experiments were typical of the *rabi* season at this location. The daily mean maximum air temperatures were 27.6°C (Experiments 1 and 2), 27.9°C (Experiment 3a), and 29.9°C (Experiment 3b). The daily mean minima were 15.3, 13.4 and 17.3°C, respectively, for these experiments. Except for 1 mm 12 DAS in Experiment 2, there was no significant rainfall during the growth period of any of these experiments.

Effect of sowing depth (Experiment 1)

The mesocotyl lengths increased with the depth of sowing in all genotypes (Table 1). There were significant effects of both the depth of sowing and genotype on mesocotyl lengths measured four DAS but no significant interaction. The difference in mean mesocotyl length between the 50 mm and 80 mm sowing depths was large (26 mm), but the mean mesocotyl length at the 100 mm sowing depth did not significantly differ from that at the 80 mm sowing depth. Nagawhite had the longest mesocotyl, probably because of its good seedling vigour.

The varietal difference found in mesocotyl length caused a concomitant genotypic variation in crown depth (Table 1). The general plasticity in the response of mesocotyl length to sowing depth reduced the variation in crown depth in all genotypes despite the differences in sowing depths. While this can be a positive adaptive mechanism, aiding seedling emergence even when the seeds are

Table 1. *Mesocotyl length and estimated crown depth (mm) of sorghum genotypes measured four DAS at three sowing depths (mm) (Experiment 1)*

	Mesocotyl length				Estimated crown depth			
	Sowing depth				Sowing depth			
	50	80	100	Mean	50	80	100	Mean
Genotype								
E 36-1	18	45	55	39	32	35	45	37
M 35-1	17	38	41	32	33	43	59	45
SPV 86	11	42	42	32	39	38	58	45
Nagawhite	20	47	59	42	30	33	41	39
Mean	17	43	49		31	37	51	
SE		±2.6				±2.8		

placed deep, it minimizes the possibility of the crown being located in a moister soil layer. We know of no references in the literature to direct measurements and changes in mesocotyl length in sorghum due to variation in depth of sowing. However, Wanjari and Bhoyar (1980) observed an increase in seedling emergence as a result of genotypic variation in mesocotyl length when genotypes were sown at the same depth. This was confirmed by Maiti and Gutierrez (1986) who found that sorghum genotypes with long mesocotyls emerged when sown at 150 mm depth while those with short mesocotyls failed to do so. Farmers sowing late in the *rabi* season benefit from this characteristic by sowing their sorghum in deeper but moist soil layers.

Radicle length of four-day old seedlings varied with sowing depth in all genotypes ($P < 0.05$) while the genotypic differences were not significant (Table 2). The shallow-sown seeds produced longer radicles than those sown deep. When sown deep (80 and 100 mm), the mesocotyl (shoot axis) extended at the cost of radicle growth (root axis). There were no genotype × depth interactions; all the genotypes produced longer radicles when sown at 50 mm depth.

Table 2. *Radicle length (mm) of sorghum genotypes measured four DAS at three sowing depths (mm) (Experiment 1)*

	Sowing depth			
	50	80	100	Mean
Genotype				
E 36-1	84	55	61	67
M 35-1	99	61	52	71
SPV 86	83	59	65	69
Nagawhite	84	61	67	71
Mean	88	59	61	
SE		±3.7		

The total seedling dry mass, leaf area, and shoot and root dry masses differed among the genotypes up to 15 DAS ($P < 0.01$). However, sowing depth did not affect any of these variables. Similarly, the root:shoot ratio was affected only by genotype, and not by depth of sowing. There were no genotype × depth interactions in any of these growth components.

Sowing depth did not affect NR number and growth, partly because the variable length of the mesocotyl located the crown close to the soil surface at all sowing depths. Thus the possible manipulation of the depth of the crown by increasing sowing depth was defeated by the sorghum plant's capacity to vary mesocotyl length.

Effect of soil moisture (Experiment 2)

The two genotypes used in Experiment 2 differed in mesocotyl length, resulting in a difference in mean crown depth between E 36-1 (25 mm) and M 35-1 (36 mm) when sown at the 50 mm depth. However, in Experiment 1 the crown depths of these two genotypes at the same sowing depth (50 mm) did not differ. This discrepancy was mainly due to the relatively longer mesocotyl of E 36-1 in Experiment 2. Nevertheless, it should be noted that these two genotypes had a significantly different crown depth at the two deeper sowing depths (Table 1). The surface soil moisture levels differed significantly between treatments (Fig. 1). The moisture treatment did not affect the number or mass of NR per seedling when measured at 14 DAS, but by 18 DAS, NR length and mass of both genotypes were significantly greater in the wetter treatments. The length and dry mass of NR in M1 was less than in M2, probably because of excess wetting in M1. However, there were no significant effects of moisture level on NR number, indicating that moisture affects the extension growth of NR but has little or no

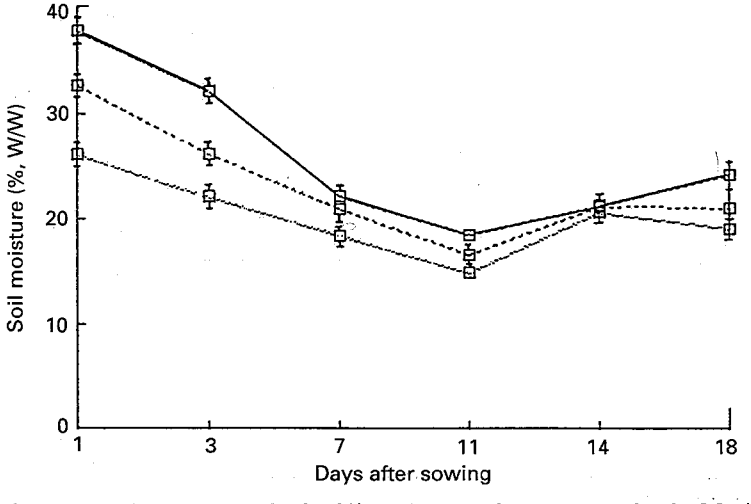

Fig. 1. The change in soil moisture in the 0–100 mm layer at three irrigation levels, M1 (———) wet, M2 (– – – –), and M3 (.....) dry, Experiment 2.

Table 3. *Number, length (mm) and dry mass (mg) of NR and total roots per seedling 18 DAS for two genotypes at three levels of irrigation (Experiment 2)*

Genotype	Irrigation level		
	M1 (wet)	M2	M3 (dry)
	NR number		
E 36-1	2.8	2.7	3.5
M 35-1	3.0	3.0	2.1
SE		±0.75	
	NR length		
E 36-1	255	262	20
M 35-1	269	301	97
SE		±54.8	
	NR dry mass		
E 36-1	6.67	9.43	2.30
M35-1	7.23	7.40	2.65
SE		±1.33	
	Total root dry mass		
E 36-1	11.03	12.70	7.59
M 35-1	11.73	11.23	6.49
SE		±1.31	

effect on NR initiation (Table 3). This finding differs from those of Blum and Arkin (1984) and Blum and Ritchie (1984), whose pot studies showed that drying of the topsoil around the crown inhibited formation of crown roots. The soil drying that occurred in our studies may not have been extensive enough to inhibit NR initiation, in contrast to the drying of soil in the pots. Unrealistically rapid soil drying can be a problem in pot studies, especially those involving moisture stress treatments. In the present study, the soil in the field dried slowly until 11 DAS (Fig. 1), and did not restrict extension growth of NR (Table 3) or inhibit NR initiation.

The differences in soil moisture levels were not large enough to cause any significant differences in seedling dry mass, shoot dry mass or leaf area. However, there was a significant effect of moisture treatment on total root mass. Thus secondary root growth is probably the first component of growth to be affected by depletion of soil moisture.

Effect of genotype (Experiments 3a and 3b)

The thermal time from sowing to the initiation of NR varied from 133 degree days for Sel 3 TL, a *rabi* landrace successful even under very dry conditions, to 183 degree days for A 4128, selected for rainy season conditions (Table 4). The

Table 4. *Thermal time (day degrees above 10°C) required for the first appearance of NR on seedlings of seven sorghum genotypes (Experiment 3b)*

	Thermal time
Sel 3 TL	133
Jeur 2 DE	166
A 4128	183
M 35-1	161
Nagawhite	166
Lakadi	166
A 145	166
Mean	163
SE	±5.3

variation found among this limited number of genotypes indicates that there are good prospects for identifying genotypes with rapid NR initiation. The soil temperatures during the experiment ranged between 29.3 and 32.0°C at the 50 mm depth.

Genotypes showed sufficient variation in NR length per seedling for effective selection (Table 5), but there was no significant variation in NR number, in contrast to the findings of Seetharama *et al.* (1990).

Table 5. *Mean NR number and length (mm) per seedling at 18 DAS, and the mean relative extension rate (mm mm^{-1} d^{-1}) of NR for the first 18 DAS for 19 sorghum genotypes (Experiment 3a)*

	NR number	NR length	Relative extension rate
PS 30831	5.2	137	0.33
Sel 3 DE	5.4	206	—
A 4128	5.5	212	0.20
A 2719	5.0	216	0.53
A 145	5.5	237	0.52
Jeur 2 DE	5.4	238	—
E 36-1	6.9	255	0.50
P 33200	6.5	311	0.47
Nagawhite	6.4	313	0.39
A 4111	7.1	316	0.31
Sel 3 TL	5.9	321	—
SPV 86	5.4	338	0.45
CSH 1	5.8	348	0.27
P 31920	6.2	351	0.43
M 35-1	6.1	367	0.36
A 4121	6.4	382	0.57
A 4123	6.5	485	0.51
Jeur 2 7C	6.7	486	—
Lakadi	7.6	538	—
Mean	6.1	319	0.47
SE	±0.59	±78.3	±0.03

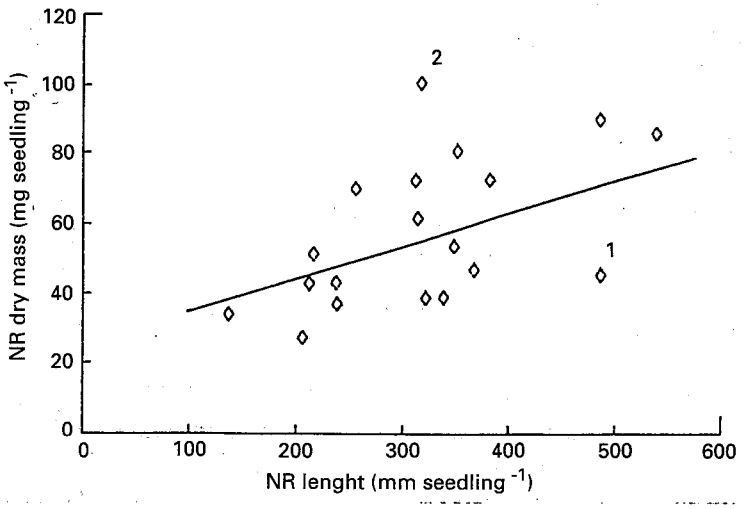

Fig. 2. Relationship between NR dry mass per plant (mg) and NR length per plant (mm) for 19 genotypes (Experiment 3a). The outliers represent genotypes with very thin (1, Jeur 2 7C) or very thick (2, A 4111) nodal roots.

Mean relative extension rate of NR, calculated from sequential samples at 12, 14, 16 and 18 DAS, ranged from 0.20 to 0.57 mm mm^{-1} d^{-1} (Table 5). There were, however, no differences in the rate of accumulation of dry mass among genotypes, suggesting that genotypic differences were due to differences in the thickness of NR (Fig. 2). NR dry mass was linearly related to NR length per seedling ($y = 22.1 + 0.11x$, $r = 0.54$, $P < 0.05$). However, there are outliers (Fig. 2), which indicate the presence of thinner (Jeur 2 7C, 10.8 mm mg^{-1}) and thicker (A 4111, 3.1 mm mg^{-1}) roots, i.e. variation in the specific length of NR. This implies genotypic differences in the depth of root penetration into the soil profile and therefore in the volume of soil exploited per unit dry matter invested in the root. Such variation may be useful in the development of breeding lines with more efficient root systems, without a reduction in the size of the shoot system.

Shoot mass per seedling did not differ significantly among genotypes at any sampling in Experiment 3b but root dry mass differed significantly at 18 DAS ($P < 0.05$). The differences in root growth among genotypes were mainly due to the differences in NR growth. Total seedling mass followed the pattern of root mass, and differed significantly among genotypes at 18 DAS. Considering the independent nature of the variation observed in root growth compared with shoot growth in these experiments, it was important to determine whether these parameters were related. The rates of dry mass accumulation by shoots explained only 46% of the variation in NR growth. Similarly, the variation in the rate of leaf expansion accounted for only 40% of the variation in the extension rate of NR. However, seedling growth rate was significantly related to NR dry mass ($r = 0.78$, $P < 0.001$), as expected because most of the variation in seedling mass was due to variation in NR mass. The absolute rates of increase of NR number and length of

Table 6. *Increases in number d^{-1} and length (mm d^{-1}) of NR of four genotypes in the 1988 (Experiment 3a) and 1989 (Experiment 3b)* rabi *seasons (standard errors in parentheses)*

	Number		Length	
	1988	1989	1988	1989
M 35-1	0.7 (0.10)	0.6 (0.07)	52 (12)	37 (7)
Nagawhite	0.6 (0.07)	0.6 (0.08)	43 (4)	35 (13)
A 145	0.7 (0.09)	0.6 (0.20)	36 (7)	29 (8)
A 4128	0.4 (0.02)	0.5 (0.20)	23 (1)	21 (9)
Mean	0.6 (0.07)	0.6 (0.03)	39 (6)	31 (4)

four representative genotypes were consistent between 1988 and 1989 (Table 6). However, seasonal variation in these traits was evident when the 1987 data were also considered (Tables 3 and 5). For M 35-1 and E 36-1, the two genotypes studied in 1987 and 1988 experiments, the NR numbers at 18 DAS in 1987 were almost half of those observed in 1988, though the total NR lengths were similar. The reason for this annual variation in NR number is not known. The difference in moisture content of the soil at crown depth at the time of initiation of NR was only 3% between 1987 (21.2%) and 1988 (24.5%) and this would not be enough to cause variation in NR initiation, as evident from Experiment 2. Further studies are required to understand this type of seasonal variation and to separate the genotypic and environmental components of variation.

The correlation of the rate of seedling growth before NR initiation with the length of NR three days after NR initiation was significant ($r = 0.64$, $P < 0.01$, 1988 data), but explained only 40% of the variation in NR length among the genotypes. Therefore it is necessary to quantify root growth independently of shoot growth in order to select on the basis of root growth characteristics.

This study showed that there was genotypic variation in the time of NR initiation, NR growth rate and NR length but not in NR number. Moreover, the variation in the growth of the root systems, especially that of nodal root growth, was independent of the variation in shoot growth in the genotypes considered.

When sown in drying soil, sorghums with more rapid NR initiation and growth performed better but greater sowing depth did not improve NR growth in the field. Genotypic variation in the time of NR initiation and extension growth may prove useful in selecting for better crop establishment in *rabi* sorghum. Seetharama *et al.* (1990) obtained high broad-sense heritability values for NR length ($h^2 = 0.66$), indicating that genetic advance is possible for this trait. Combining such root-related traits with other useful agronomic characters is necessary for crop improvement.

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