Effect of drought stress during grain filling in near-isogenic tall and dwarf hybrids of pearl millet (*Pennisetum glaucum*)

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SUMMARY

The susceptibility to drought stress during flowering and grain filling of dwarf hybrids of pearl millet carrying the dwarfing gene d_2 was investigated in 1987 at Patancheru, India, under field conditions during the dry season and, in the rainy season, under a rain shelter, using four pairs of near-isogenic tall and dwarf hybrids. Drought stress during grain filling reduced the number of grains per unit area and individual grain mass. Grain yields of the dwarf hybrids were lower than those of the corresponding tall hybrids in the unstressed control and under drought stress and were associated with a lower individual grain mass in the dwarf lines. In the dwarf hybrids, harvest index was similar to or better than that of the tall versions but a reduced biomass resulted in lower grain yields. Dwarf hybrids were not more adversely affected by water stress, however, than their tall counterparts, indicating that susceptibility to drought stress would not be likely to limit acceptance of new dwarf varieties.

INTRODUCTION

Much of the progress in breeding, and the increases in world-wide grain production, of wheat and rice in the last several decades can be attributed to the introduction and utilization of dwarfing genes. Commercial success of dwarf varieties has largely been in irrigated areas or regions of high rainfall; often their yield advantage is not maintained in drier, rainfed regions (Laing & Fischer 1977; McNeal *et al.* 1972; Gale & Youssefian 1985). In wheat, yield advantage in dwarf varieties was primarily due to an increase in harvest index without any loss in total biomass (Austin *et al.* 1980) and protection from lodging.

Dwarfing genes in pearl millet (*Pennisetum glaucum* (L.) R.Br.) were first reported by Burton & Fortson (1966) and subsequently by Appa Rao *et al.* (1986). Dwarfing genes have been used in an attempt to improve harvest index (Etasse 1972) and to produce varieties more responsive to higher inputs (Jaquinot 1972) but dwarf varieties have never been grown by farmers on any significant scale. Comparisons of dwarf and tall versions of a number of composites (K. N. Rai, unpublished) or landrace varieties (Lambert 1983) indicated the dwarfs yielded as well as or slightly better than the tall versions. Dwarf composites, however, produced significantly lower grain yields than the corresponding tall versions when exposed to water deficits during grain filling (International Crops Research Institute for the Semi-Arid Tropics 1986). Recent studies on tall and dwarf near-isogenic hybrids (isohybrids) of pearl millet indicated that dwarfs were generally lower yielding than their corresponding tall hybrids under favourable agronomic conditions, with an improved harvest index but reduced biomass (Bidinger & Raju 1990).

As pearl millet is almost entirely grown under rainfed conditions in regions of low and erratic rainfall, the success of dwarf varieties or hybrids depends on their ability to yield as well as or more than the tall varieties and to maintain their performance under drought conditions. As this crop is grown by subsistence farmers, the protection from lodging the dwarf varieties might provide under conditions of high fertilizer and moisture may not be of any advantage. This study compared the performance of tall and dwarf near-isogenic hybrids of pearl millet under drought stress during grain filling. Near-isogenic hybrid pairs were used to minimize, as far as possible, the confounding effects of other genes.

MATERIALS AND METHODS

The experiments were conducted in the 1987 dry season (January–May) and in the rain shelter (RS) during the 1987 rainy season at the International

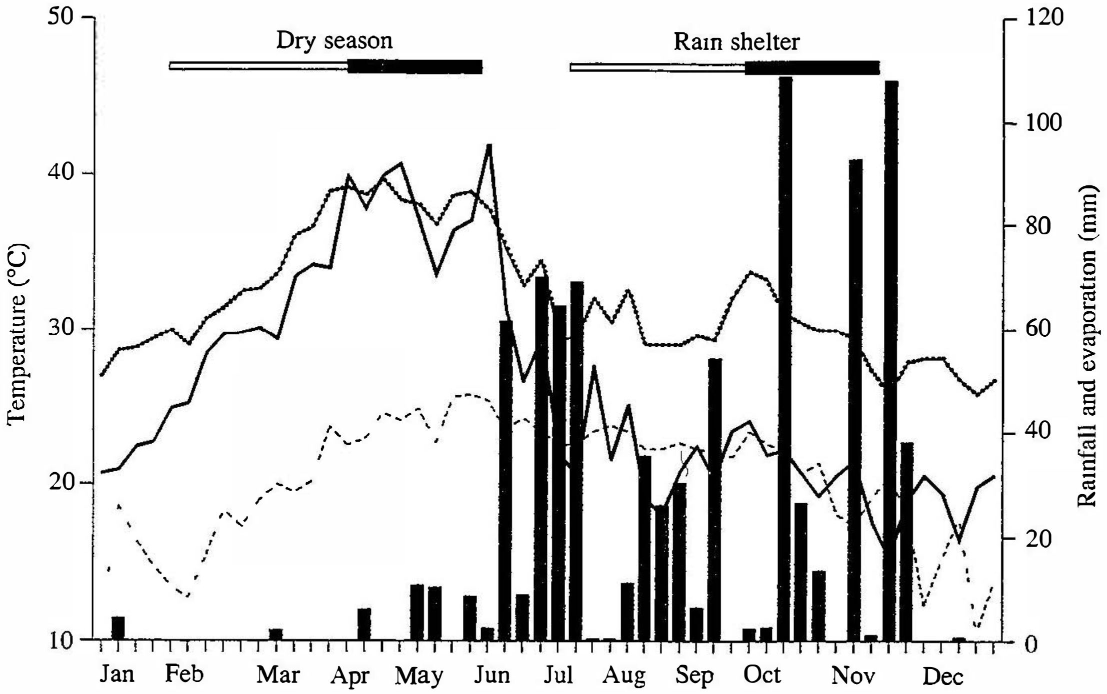

Fig 1 Total weekly rainfall (bars), evaporation (——) and mean weekly minimum (-----) and maximum (—•—) temperatures at Patancheru, India, during 1987 The cropping seasons in the irrigated dry season and rain-sheltered rainy season experiments are indicated by the horizontal bar, the drought-stress periods are indicated by the solid portion of the bar

Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru (17° 30′ N and 78° 16′ E), India The soil was an Alfisol (Udic Rhodustalf) with *c* 60 mm of plant-available moisture Since the dry season is almost rain free, with high atmospheric evaporative demand (Fig 1) the crop was irrigated as necessary except for the treatment period, when irrigation was withheld in the drought stress treatment plots In the rainy season experiment, the crop (both treatments) was sheltered from the rain during the treatment period (boot stage to maturity), and the control treatment was irrigated approximately weekly

Both the experiments were conducted as split-plot designs with four replications The main plot consisted of two moisture treatments: a drought stress treatment during grain filling and an unstressed control The subplots consisted of the two height classes (tall and dwarf) The hybrids of the eight isogenic pairs of each height class were randomly assigned within the subplots as sub-subplots

In the dry season, the crop was irrigated using sprinklers until the earliest genotype reached the boot stage From then on, the unstressed control was irrigated at weekly intervals by flooding the furrow between the ridges to field capacity In the drought stress treatment, each individual genotype received its last irrigation by flooding at the boot leaf stage This ensured a similar physiological stage at treatment for all genotypes, removing differences due to drought escape

In the rainy season experiment, the crop was planted in the rain shelter and irrigated by sprinklers after sowing Since rainfall was adequate (Fig 1), the crop was not irrigated until the implementation of the water-deficit treatment. Both the moisture treatments were sheltered from rain immediately after the earliest genotype reached the boot stage. The control treatment was irrigated (50 mm) at weekly intervals using a drip irrigation system (application rate of 2 litres/h) placed on each ridge The drought stress treatment was similarly irrigated up to the boot leaf stage for each hybrid as in the dry season experiment

Eight pairs of tall and dwarf near-isogenic hybrids were made by crossing four pairs of tall and dwarf near-isogenic inbred lines (isolines), derived by selfing progenies segregating for the d_2 dwarfing gene, from the BC_3F_1 to BC_3F_7 generations of Early composite (ECLI), Medium composite (MCLI) and Nigerian composite (NCLI), on to two dissimilar dwarf male-sterile lines (see Bidinger & Raju 1990 for description of the isolines) As d_2 is recessive, the dwarf isolines produced dwarf hybrids, homozygous at the d_2 locus, and their tall counterparts produced tall hybrids, heterozygous at the d_2 locus Hybrids rather than the inbred lines themselves were used to overcome the effects of inbreeding depression in the test material

Seeds were machine sown in rows on ridges 60 cm apart Each sub-subplot unit consisted of four rows (dry season) or two rows (RS), 4 0 m long. Rows were thinned to 15 cm between plants when the crop was 10 days old Prior to planting, 40 kg N/ha and 18 kg P/ha as diammonium phosphate was banded into ridges. An additional 40 kg N/ha as urea was side dressed at 15 days after sowing.

Days to flowering were recorded when stigmas had emerged on the main shoot panicles of 50% of the plants in a plot. Average crop height at maturity was measured in all plots in the RS. At maturity, panicles from the central two rows of 3 m in the dry season, and the two rows of 3 m ($3{\cdot}6\ m^2$) in the RS were harvested and dried at 60 °C; grain yield and its components were determined from plot harvest.

Data from the two experiments were tested for homogeneity of error variance by a simple F test (Snedecor & Cochran 1967) before pooling, and were analysed by analysis of variance to test the significance of interactions of season (S) × moisture (M) treatment, S × height (H), and S × H × M.

RESULTS AND DISCUSSION

Effects

In both experiments drought stress reduced grain yields (Table 1). Grain yield was reduced more in the dry season experiment (36%) than in the RS (23%), as higher mean air temperatures and evaporation rates during the dry season (Fig. 1) resulted in a more severe water deficit in this experiment. Both number of grains per unit area and individual grain mass were reduced by drought stress in the two experiments, but the reduction in individual grain mass was only 16 and 10% in the dry season and RS, respectively, compared with a reduction of 24 and 13% in number of grains. A similar yield component response to severe water stress during flowering and grain filling in pearl millet has been reported previously, despite the fact that individual grain mass is derived entirely after flowering (Mahalakshmi *et al.* 1988). The decline in number of grains was probably the result of the allocation of available carbohydrate to fill the remaining grains and to maintain a minimum grain mass which ensures future propagation and survival.

Biomass was reduced in both experiments, but harvest index (HI) was reduced only in the dry season. Similar results have been reported in sorghum; except under severe drought stress, when biomass was reduced to *c.* 50% of that of the unstressed control, harvest index was not affected by water deficit (Garrity *et al.* 1982; Wright *et al.* 1983).

Effect of plant height

The difference in total plant height in RS between the tall and dwarf hybrids was 58 cm. There was no difference between the two groups in the time to flowering in the two experiments (Table 1). Mean grain mass was lower in the dwarfs than in the tall hybrids in both experiments. This was offset by more grains in the dwarfs in the dry season, resulting in no significant differences in grain yield in the two classes in this season. In the RS experiment, however, numbers of grains did not differ between the dwarf and tall hybrids, resulting in a lower yield in the dwarf hybrids, because of their lower grain mass.

In a number of comparisons of near-isogenic lines/varieties of wheat, the dwarf isolines/varieties were reported as outyielding the tall isolines (Allen *et al.* 1986; Brandle & Knott 1986; Gale & Youssefian 1985; Udden & Marshall 1989). Dwarf isolines of wheat generally have more grains than tall versions, which is often partially, but not totally, offset by a lower grain mass (Gale & Youssefian 1985; Brandle & Knott 1986). Reports of similar studies in sorghum, however, indicate that dwarf lines often yield less than tall lines, because they do not produce more grains to compensate for their lower mass (Casady 1965; Campbell *et al.* 1975).

The dwarf millet isohybrids in this study seemed to fall between the patterns for wheat and sorghum. Grain mass was lower than in the tall hybrids in both seasons and treatments; this was compensated for by a higher number of grains in the dry season, but not in the rainy (RS) season. Comparisons of a larger set of dwarf isohybrids in the rainy season showed consistently lower yields in the dwarf hybrids, for the same reason as reported in the rainy season experiment in this study (Bidinger & Raju 1990). However, Bidinger & Raju found that dwarf hybrids on certain male-sterile lines produced more grain than the tall counterparts and suggested selection of both dwarf pollinators and male-sterile lines to produce superior dwarf hybrids. K. N. Rai (unpublished) also reported a slight reduction in grain size in a set of dwarf composites, compared with their tall parents, but the dwarfs still maintained a slight yield advantage (5%) over the tall versions.

The yield advantage in dwarf wheats was also generally associated with an improvement in HI without a reduction in biomass (Austin *et al.* 1980). In the present study there was either no significant difference in biomass and HI between the dwarf and tall hybrids (in the dry season, when grain yields were similar), or the dwarf hybrids had considerably lower biomass compared with the tall versions, with similar HI (RS, when grain yields were lower in the dwarfs). An earlier study on isohybrids in pearl millet also reported lower biomass in dwarfs compared with their tall counterparts (Bidinger & Raju 1990).

Interactions of height × water deficit

Analysis of main effects and interactions of interest for grain yield and its components is presented in Table 2. Combined analysis of the two seasons' data showed no significant interaction of the moisture treatment with season, indicating no influence of the season on the moisture treatment effects, despite the

Table 1. *Mean grain yield and yield components of four pairs of tall and dwarf near-isogenic hybrids of pearl millet at Patancheru, India, in 1987 in the dry season and in the rainy season under a rain shelter*

	Dry season			Rain shelter		
Height class	Control	Drought stress*	Mean	Control	Drought stress*	Mean
Height (cm)						
Tall	—	—	—	170	169	169
Dwarf	—	—	—	111	111	111
Mean	—	—	—	141	140	
S.E.D. (moisture)	—			4·8		
S.E.D (height)	—			1·6		
Days to flowering						
Tall	50	49	49·5	47	47	47
Dwarf	49	50	49·5	46	47	47
Mean	49	49		46	47	
S.E.D. (moisture)	0·7			0·3		
S.E.D. (height)	0·0			0·6		
Grain yield (g/m²)						
Tall	327	222	275	396	319	358
Dwarf	341	208	274	365	279	323
Mean	334	215		388	299	
S.E.D (moisture)	8·8			15·8		
S.E.D. (height)	11·5			11·7		
Number of grains (× 10³/m²)						
Tall	41·7	33·0	37·4	46·4	42·0	44·1
Dwarf	47·5	35·0	41·2	48·0	40·6	44·3
Mean	44·6	34·0		47·2	41·3	
S.E.D. (moisture)	1·24			1·62		
S.E.D. (height)	1·25			1·66		
Single-grain mass (g/10³)						
Tall	8·0	6·8	7·4	8·6	7·6	8·1
Dwarf	7·3	6·0	6·6	7·7	6·9	7·3
Mean	7·6	6·4		8·1	7·3	
S.E.D. (moisture)	0·24			0·17		
S.E.D. (height)	0·09			0·10		
Biomass (g/m²)						
Tall	886	700	793	1013	817	916
Dwarf	858	650	754	886	700	795
Mean	872	675		951	759	
S.E.D (moisture)	18·8			25·0		
S.E.D (height)	23·4			28·8		
Harvest index (%)						
Tall	37	32	34·5	39	39	39
Dwarf	40	32	36·0	41	39	40
Mean	38	32		40	39	
S.E.D (moisture)	0·65			0·95		
S.E.D (height)	0·78			0·49		

* Last irrigation at boot leaf stage.

differences in environmental conditions, and consequently in the severity of stress, in the two seasons. There also was no effect of season on height class for grain yield, number of grains and individual grain mass.

Neither of the major interactions of interest in this study, moisture treatment by height class (M × H), and moisture treatment by height class by season (M × H × S), were significant, for either grain yield or its components. Grain yield reduction due to drought stress averaged over the two experiments was higher in the dwarf (31 %) than in the tall hybrids (25 %) but

Table 2 *Combined analysis of variance for dry season and rain shelter experiments with four pairs of tall and dwarf near-isogenic hybrids of pearl millet at Patancheru, India, in 1987. Data are F ratios for moisture (M), season (S), height (H), genotype (G), and their interactions for grain yield and yield components*

		F ratios			
Source	D F	Grain yield	Single-grain mass	Number of grains/m²	Bio-mass
M	1	121 2	55 6	74 2	89 3
M × S	1	2 6	1 3	4 8	0·1
H	1	5 6	107·2	2·7	26 5
H × S	1	3 6	1 6	2 0	5·
M × H	1	0·	0 01	2 7	0 1
M × H × S	1	0 8	0 2	0 5	0 9
G	7	6 9	31 0	8 6	5 9
G × S	7	7 0	45 7	5 5	12 6
G × M	7	1 3	3 3	0 7	0 9
G × H	7	1 9	1 5	0 9	1 7

this difference was not significant. The reduction in grain yield in both height classes was due to a reduction in number of grains/unit area and individual grain mass (Tables 1 and 2). Number of grains/unit area was reduced by 21% by drought stress in the dwarfs compared with a 15% reduction in tall hybrids. Individual grain mass was reduced by *c.* 14% in both hybrid groups. Biomass and harvest index were also reduced in a similar proportion in the two height classes by drought stress.

Comparisons of height classes in wheat generally indicate less advantage to dwarfs under drought stress (Brandle & Knott 1986, Laing & Fischer 1977, Udden & Marshall 1989). Reductions in number of grains and grain mass under stress were generally similar in dwarf and tall isolines in wheat (Brandle & Knott 1986, Udden & Marshall 1989) and sorghum (Campbell *et al* 1975). In a controlled study with near-isogenic dwarf (*Rht2*) and tall lines in wheat, the dwarf lines yielded more than their tall counterparts in fully irrigated conditions and in early and late droughts, although the percentage reduction in the drought treatments was greater in the semidwarf lines than in the tall versions (Innes *et al* 1985). Dwarf millet thus appears to respond to drought stress in a manner similar to that of dwarf wheat and dwarf sorghum, although it resembles sorghum more than wheat in that there is no clearly established superiority of the dwarfs in favourable environments.

Hurd (1974) suggested that poorer root development of semidwarf wheats rendered them more vulnerable to drought stress than tall varieties. Innes *et al* (1985) found that water use was similar in the two height classes of wheat in the early drought treatment but that the tall varieties extracted more water in the late drought treatment. Other studies, however, have reported no differences in rooting pattern or water extraction pattern in semidwarf and tall varieties of wheat (Cholick *et al.* 1977; Pepe & Welsh 1979; Holbrook & Welsh 1980) and barley (Irvine *et al.* 1980). It is possible that the generally lower productivity of dwarf hybrids of pearl millet could be the result of poorer root development, although studies on root development in pearl millet suggest no association with height class (Tongoona *et al.* 1984).

The dwarfs of pearl millet seem to be less productive under all situations. The protection from lodging under high-input conditions which the dwarfs might offer is of minor consequence as the crop is grown by subsistence farmers without any added inputs. The results from this study indicate that dwarf hybrids of pearl millet are not more vulnerable to drought stress during grain filling than their tall isohybrids. Thus the usefulness of dwarfing genes appears to be limited more by overall productivity, rather than by any adverse effect of water deficit.

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