J. agric. Sci., Camb. (1986), **106**, 113–119
With 1 *text-figure*
Printed in Great Britain

Water deficit during panicle development in pearl millet: yield compensation by tillers

By V. MAHALAKSHMI and F. R. BIDINGER
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru P.O., 502324 *A.P., India*

(*Revised MS. received* 9 *July* 1985)

SUMMARY

Water deficit during the panicle development stage reduced the grain yield of the main shoot panicle of pearl millet but this loss was compensated by increased grain yield of the tillers. The potential extent of compensation in grain yield components by tillers was investigated by removing the main shoot at panicle initiation (PI) and flowering stages respectively, for both irrigated and water-stressed plants. Grain yield loss by removal of the main shoot of plants at PI was fully compensated by tiller grain yield in both the irrigated and water-stressed plants. The compensation was, however, only partial when the main shoot was removed at flowering. The compensation for the grain yield loss in the main shoot due to either water stress or removal was through an increase in number of grains on the tillers. This increase was due to an increase in the number of productive tillers in the case of water stress and to both an increase in the number of productive tillers and an increase in the number of grains per panicle in the case of main shoot removal. This compensatory mechanism by tillers plays an important role in overcoming the effects of pre-flowering water stress damage to the main shoot.

INTRODUCTION

Pearl millet [*Pennisetum americanum* (L.) Leeke], a high-tillering, short-duration annual cereal, is grown mainly as a rainfed crop in the regions of South Asia and Africa where mean annual rainfall ranges from 200 to 800 mm. The crop is often subjected to intermittent water deficit due to low and erratic rainfall in these regions.

Since water stress is frequently a short-term or intermittent problem, it would be advantageous to have as much plasticity in development and in yield structures as possible (Turner, 1982). Most cereals produce more tillers than those which actually produce panicles and more florets than those that are actually pollinated and fertilized (Hanson & Nelson, 1981). In pearl millet, for example, only 25% of the tillers produce panicles under optimum conditions (Raymond, 1968; Egharevba, 1977). These extra tillers offer potential for compensation for yield losses due to damage of the main shoot or primary tillers.

Several reports indicate that water deficit during early crop growth has no adverse effect on grain yield in pearl millet (Lahiri & Kharabanda, 1965; Lahiri & Kumar, 1966; Mahalakshmi & Bidinger, 1985). Water deficit during early crop growth stages delays flowering and increases the proportion of tillers producing panicles (Lahiri & Kumar, 1966; Bidinger *et al.* 1982; Mahalakshmi & Bidinger, 1985). Grain yield loss on the main shoot due to water deficit can be compensated for by an increase in the grain yield of tillers (Mahalakshmi & Bidinger, 1985). The present investigation was conducted to determine the extent and nature of this compensation by tillers in pearl millet.

MATERIALS AND METHODS

The experiment was conducted during the 1982 and 1983 dry seasons (January–May) on shallow alfisols (average available water 60 mm) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Centre, Patancheru, India. Weather conditions during the cropping seasons, and the irrigation treatment period are given in Fig. 1. The high mean temperatures, evaporation and low relative humidities imposed a high atmospheric demand on the crops. The crops were irrigated and the water deficit treatment imposed by withholding irrigation.

In each year the experimental design was a split-

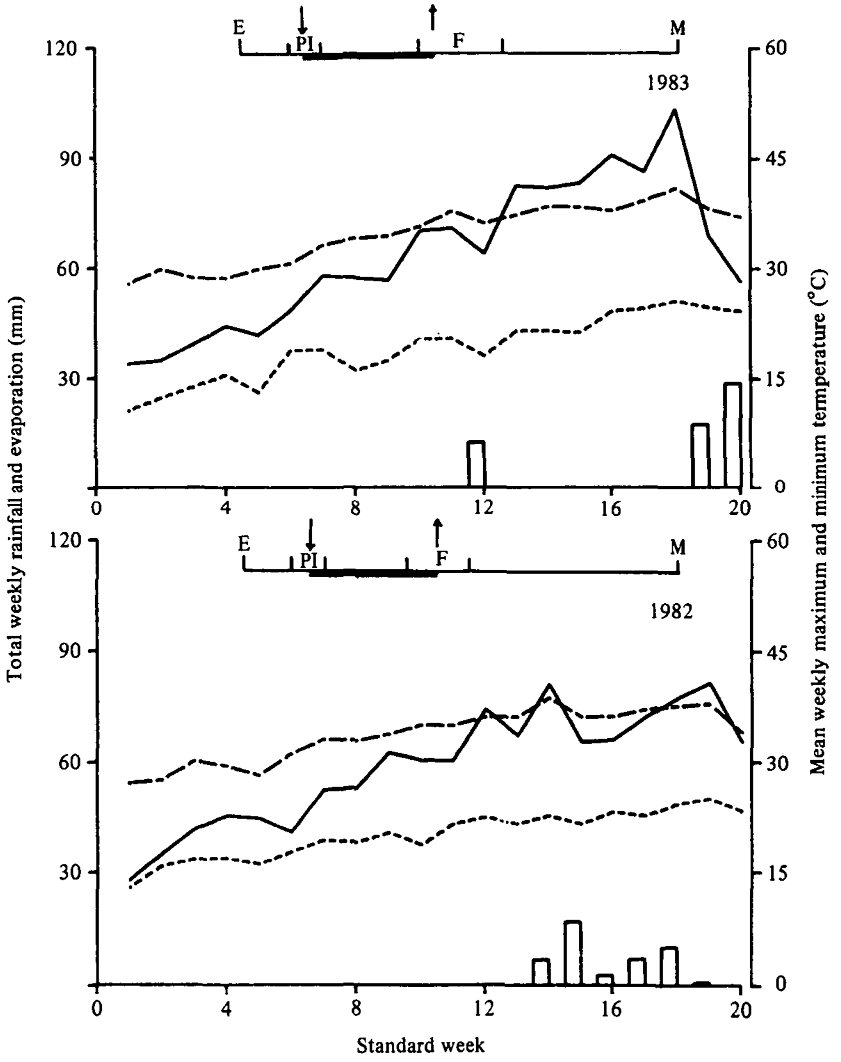

Fig. 1. Total weekly rainfall (□) and evaporation (—) and mean weekly maximum (– – –) and minimum (······) temperatures during 1982 and 1983 cropping season. Arrows indicate beginning (↓) and end (↑) of stress period. E, PI, F, and M are emergence, panicle initiation, flowering and maturity of the crop respectively.

plot with two irrigation treatments as the main plots; four genotypes and three main shoot treatments (see below) were arranged in a factorial design in the subplots. The treatments were replicated three times. The two irrigation (I) treatments in both years were an irrigated control (I–C) (irrigated throughout to field capacity by flooding the furrows between the ridges at approximately 10-day intervals) and a water stress (I–S) treatment which was imposed between 20 and 48 days after emergence (approximately from panicle initiation to flowering in the main shoot). The water stress treatment was regularly irrigated to field capacity from emergence to 20 days and between 48 days and physiological maturity. In 1983, the initial irrigations (emergence to 20 days) were given by overhead sprinklers to reduce leaching of fertilizer nitrogen. As flowering and subsequent maturity were delayed by this treatment, irrigation was continued for a longer period than in the control plots.

In 1982, three main shoot (MS) treatments were used: (1) control (MS–C), where the main shoot was intact, (2) main shoot removal (MS–MR) at panicle initiation (PI) and (3) main shoot removal at flowering stage (F). In 1983, there were only two

Table 1. *Mean number of days to flowering and number of panicles/plant for the four hybrids in* 1982 *and* 1983

1982			1983		
Genotype	Number of days to flowering	Number of panicles/plant	Genotype	Number of days to flowering	Number of particles/plant
ICH 226	43	2·14	ICH 226	47	1·94
ICH 220	46	1·69	ICH 220	49	2·13
ICH 385	45	1·62	ICH 425	65	1·26
ICH 162	56	1·32	ICH 162	61	1·60

main shoot treatments, comprising a control and main shoot removal at PI.

In 1982, three early flowering and one late flowering hybrids, and two early flowering and two late flowering hybrids in 1983 (Table 1) were grown in the subplots consisting of eight rows each 4 m long. Seeds were machine-sown on ridges 75 cm apart, rows were sown more thickly than required plant density and plants were thinned 10 days after emergence to 10 cm apart. Prior to sowing, nitrogen and phosphate (P_2O_5) fertilizer each at the rate of 40 kg/ha as ammonium phosphate was placed in the ridges. Additional nitrogen at the rate of 40 kg/ha was side dressed when the crop was 15 days old. The plots were kept free from weeds and there was no noticeable incidence of diseases or pests.

In the 1982 experiments, the central four rows were harvested at crop maturity and the main shoot panicles and tiller panicles were separated for determining grain yield and its components.

Compensation in the main shoot treatment and irrigation were determined as given below:

$$\begin{aligned}\text{Comp}\cdot_{\text{MS}} &= \text{GY-MS}_{\text{MS-C}} \\ &\quad -(\text{GY-T}_{\text{MS-MR}}-\text{GY-T}_{\text{MS-C}}), \\ \text{Comp}\cdot_{\text{I}} &= (\text{GY-T}_{\text{I-S}}-\text{GY-T}_{\text{I-C}}) \\ &\quad -(\text{GY-MS}_{\text{I-C}}-\text{GY-MS}_{\text{I-S}}),\end{aligned}$$

where $\text{Comp}\cdot_{\text{MS}}$ and $\text{Comp}\cdot_{\text{I}}$ are the compensation in main shoot and irrigation treatments respectively. GY-MS and GY-T are grain yield of main shoot and tillers respectively and the subscript MS- and I- are the main shoot and irrigation treatments respectively.

In 1983, owing to soil crusting at seedling emergence the plant stands were not uniform; since tillering is influenced by plant density, 15 well-bordered plants were selected from each plot, and separated into individual tillers (T_i). The yield and yield components on an individual tiller basis were determined and reported as yield and yield components per plant.

RESULTS AND DISCUSSION

Grain yield

Water stress during panicle development affected the growth and development of the main shoot in both years, resulting in a decrease in its grain yield which was compensated by extra grain yield of the tillers (Tables 2 and 4). In ICH 220 in 1982, the compensation by tillers (+89 g/m^2) greatly exceeded the loss in the main shoot (−43 g/m^2) resulting in significantly higher grain yields under water stress conditions (Table 2). Lahiri (1978) also observed that water stress at an early stage of development in pearl millet caused an increase in grain yield in some genotypes and the extent of grain yield loss was minimal in others. ICH 385 and ICH 162 showed no significant reduction in grain yields in the stress treatment but in ICH 226, grain yield loss of the main shoot (−97 g/m^2) was only partially compensated for by the tillers (+28 g/m^2), resulting in reduced grain yields under water stress. In 1983, yield reductions in the main shoot were less in the water stress treatment than in 1982 (Table 4), since the plants flowered later relative to the termination of the stress (Fig. 1). Water stress again induced a small increase in tiller grain yields, resulting in full yield compensation (102–112%) in all genotypes.

In both years the reduction in main shoot grain yields was correlated with the time to flowering ($r = -0{\cdot}96$) but the change in total yield was not related to phenology, although differences among genotypes in compensation (except for ICH 226 in 1982) were small. The net yield reduction in the water stress treatment in ICH 226 in 1982 probably occurred because it flowered before the termination of the stress (Table 1), for flowering and early grain filling are very sensitive to water stress in pearl millet (Seetharama *et al.* 1982).

Reduction in grain yield due to the removal of the main shoot at PI under irrigation in 1982 was fully compensated in three of the four genotypes (82–100%) (Table 2). In ICH 162, however, the

Table 2. *Mean grain yield (g/m^2) in the four hybrids in the two irrigation treatments and the three main shoot treatments in* 1982

		Main shoot treatment*				
		Control			MR-PI	MR-F
Treatment	Genotype	Main	Tiller	Total	Tiller	Tiller
Irrigated	ICH 226	196	99	295	260	192
Stressed		99	127	226	227	202
Irrigated	ICH 220	179	84	263	263	204
Stressed		136	173	309	266	257
Irrigated	ICH 385	177	55	232	220	160
Stressed		114	133	247	250	270
Irrigated	ICH 162	253	19	272	196	149
Stressed		224	59	283	295	158
s.e. 1	—	—	15·4[a]	—	13·0[b]	—
s.e. 2	—	—	13·1[a]	—	10·9[b]	—
Irrigated	Mean	201	64	266	235	176
Stressed	Mean	143	123	266	260	222
s.e. 3	—	—	7·8[a]	—	6·8[b]	—
s.e. 4	—	—	6·7[a]	—	5·8[b]	—

* See Materials and Methods for definition of treatments.
s.e. 1 for comparing G × M means at the same level of I.
s.e. 2 for comparing I means at the same or different levels of G × M.
s.e. 3 for comparing M means at the the same level of I.
s.e. 4 for comparing I means at the same level of M.
[a] Total grain yield (g/m^2); [b] tiller grain yield (g/m^2).

compensation was only partial (70%) because it produced one very large inflorescence and few, if any, tiller inflorescences (Table 1). Removal of the main shoot in this genotype caused a loss of 93% of the grain yield per plant. Removal of the main shoot at PI in the water stressed treatment in 1982 resulted in complete compensation (101–105%) by tillers in three of the four genotypes. In ICH 220, however, the compensation was only partial.

Removal of the main shoot at PI in both irrigation treatments in 1983 stimulated greater increases in the grain yield of tillers than in 1982, resulting in significant increases in grain yield in both irrigated and stressed treatments (Table 4).

Removal of the main shoot at flowering in 1982 was only partially compensated in both the irrigated (47–62%) and water stressed (44–76%) treatments (Table 2). The competition to the tillers by the presence of the main shoot during the panicle development stage reduced the potential of the tillers to compensate. Lahiri & Kumar (1966) observed a similar ability to compensate for loss due to water stress in pearl millet which decreased as the plants aged.

Number of productive tillers

In both years, water deficit during panicle development induced additional tillers to bear an inflorescence in all the genotypes (Tables 3 and 4). Main shoot removal at both PI and flowering also induced additional tillers to produce an inflorescence; this effect was greater when compared with the water stress treatment in which the main shoot was intact (Tables 3 and 4). The water deficit and the main shoot removal treatments generally had additive effects on the number of productive tillers.

The increase in the number of productive tillers in 1983 in the case of stress was due to small increases over all tiller positions, which resulted in a significant increase in the total number of productive tillers (Table 4). However, in the main shoot removal treatment, increases were large at the T_1 and T_2 positions and at the T_3 and T_4–T_5 positions the increases were generally similar to those in the control. Wilson & Whiteman (1965) reported that with short drought exposures in sorghum, apex removal led to an increased number of tillers. Longer exposures to drought caused death of the main shoot apex, which also increased the number of tillers.

Mechanisms of compensation

Water stress over the period it was imposed had no effect on 1000-grain weight in either year since the stress was relieved at the time of flowering. The compensation for the losses in grain yield suffered by the main shoot under water stress or for its

Table 3. *Number of panicles/plant and number of grains in the two irrigation treatments and the three main shoot treatments in* 1982

	Main shoot treatment*				
	Control				
Treatment	Main	Tiller	Total	MR-PI Tiller	MR-F Tiller
			Number of panicles/plant		
Irrigated	1·00	0·69	1·69	2·23	2·20
Stressed	1·00	1·27	2·27	2·80	2·52
S.E. 1	—	—	0·091	—	—
S.E. 2	—	—	0·085	—	—
			Number of grains ('000/m^2)		
Irrigated	31·7	13·0	44·7	44·6	33·5
Stressed	21·6	22·9	44·5	44·1	36·2
S.E. 1	—	1·63[a]	—	1·41[b]	—
S.E. 2	—	1·41[a]	—	1·37[b]	—

* See Materials and Methods for definition of treatments.
S.E. 1 for comparing M means at the same level of I.
S.E. 2 for comparing I means at the same level of M.
[a] Number of grains/m^2; [b] number of grains on tillers/m^2.

Table 4. *Number of panicles/plant, grain yield/plant and number of grains/panicle for tillers* (T_i) *and total number of panicles/plant, grain yield/plant and number of grains/plant in the two irrigation treatments in the two main shoot treatments in* 1983

Treatment*	Main	T_1	T_2	T_3	T_4–T_5	Total
			Number of panicles/plant			
C-irrigated	1·00	0·46	0·18	0·05	0·04	1·74
C-stressed	1·00	0·62	0·32	0·14	0·08	2·15
MR-irrigated	0·00	1·00	0·86	0·24	0·00	2·09
MR-stressed	0·00	1·00	0·97	0·50	0·15	2·62
S.E. 1	—	0·032	0·051	0·053	—	0·123
S.E. 2	—	0·037	0·054	0·061	—	0·112
			Grain yield (g/plant)			
C-irrigated	15·03	3·33	1·25	0·17	0·31	20·00
C-stressed	13·08	5·11	2·14	0·73	0·37	21·30
MR-irrigated	0·00	17·33	9·74	1·91	0·00	29·00
MR-stressed	0·00	16·26	11·50	1·56	0·00	29·3
S.E. 1	—	0·61	0·75	0·42	—	0·83
S.E. 2	—	1·10	1·10	0·47	—	1·50
			Number of grains/panicle			
C-irrigated	2149	1280	965	217	225	3057
C-stressed	1943	1352	989	601	429	3325
MR-irrigated	0	2701	1728	587	0	4754
MR-stressed	0	2259	1802	1148	165	4806
S.E. 1	—	134	208	179	—	126
S.E. 2	—	187	238	156	—	229

* See Materials and Methods for definition of treatments.
S.E. 1 for comparing M means at the same level of I.
S.E. 2 for comparing I means at the same level of M.

removal was derived from the increase in the number of grains produced by the tillers (Table 3).

The increased number of grains on the tillers could be a result of (1) an increase in the number of productive tillers on the plant, (2) an increase in the number of grains on a tiller panicle or (3) a combination of the two. These effects could not be distinguished in 1982, since tillers were pooled for determining grain yield and yield components. In 1983, a detailed examination of these effects was carried out on an individual tiller basis for both the water stress treatment and that involving removal of the main shoot at PI.

In the water stress treatment the compensation in grain yield was generally due to an increase in the number of tillers producing panicles at all tiller positions (Table 4). These changes were not significant for given tiller positions but they were significant as an aggregate. Changes in number of grains per tiller were small and generally not significant (Table 4). The exception to this pattern was in ICH 162 where compensation was by number grains per tiller rather than number of tillers. Irrespective of the mode of compensation, however, the total number of grains per plant in the stress treatment was similar to that of the irrigated control (Table 4).

Removal of the main shoot at PI in the irrigated treatment increased the number of tillers bearing panicles as well as number of grains per panicle at the T_1–T_3 positions, resulting in a significant increase in the total number of grains per plant (Table 4). In fact, the first tiller produced a similar number of grains to the main shoot of control plants when it was removed at PI. Removal of the main shoot at PI in the water stress treatment also resulted in compensation by both an increased number of tillers and an increased number of grains per tiller (Table 4). The degree of compensation by both mechanisms was generally similar to that in the irrigated main shoot removal treatment, although there was some evidence of genotypic differences in the number of grains per panicle, particularly for T_1.

These two types of responses, increase in number of productive tillers and in the number of grains on each productive tiller, appear to be associated with the two types of control of tiller growth in the presence of the main shoot: dominance and competition for resources. The water stress treatment reduced the dominance of the main shoot and allowed additional tillers to complete their development (Mahalakshmi & Bidinger, 1985). The removal of the main shoot at PI had a similar result, although in both cases the higher order tillers apparently re-established the dominance pattern as there was still a decreasing proportion of later tillers which completed development. Kirby & Jones (1977) reported a similar response to main shoot removal in barley.

The nature of water stress–dominance interaction is not clear, although work on maize suggests that hormones may be involved. Damptey, Coombe & Aspinall (1978*a*, *b*) reported that removal of tassels or exogenous application of abscisic acid (ABA) stimulated additional inflorescence development in maize. They concluded that a water deficit at the critical stage of tassel development can affect the growth and metabolism of the tassel so as to reduce its dominance and allow development of inflorescences at the lower nodes. Henson *et al.* (1981) reported an accumulation of ABA under conditions of water stress in pearl millet. This may be responsible for the break in apical dominance under stress and needs further investigation.

The response to reduced competition (an increase in the number of tiller grains) was evident only in the main shoot removal treatments. When the competition from the main shoot was eliminated entirely, the number of grains on all the subsequent tillers increased significantly. The results in all cases indicate that the first tiller has a potential number of grains equal to that of the main shoot, when the competition from the latter is removed.

Pearl millet, thus, has a marked capacity to compensate for the total loss (by removal) of its main shoot or for reduction in its size by water stress during panicle development. In environments where water and nutrients are not limiting, the tillering habit has been considered to be a wasteful process (Donald, 1968). Although the potential sink size in pearl millet is far greater than that realized under favourable conditions, this 'extra' sink capacity represented by the higher order tillers provides the needed flexibility to adjust to adverse environmental conditions in which the primary sinks are adversely affected. Thus, the asynchronous tillering habit of the crop is an important productive mechanism conferring adaptation to low and erratic rainfall.

REFERENCES

BIDINGER, F. R., MAHALAKSHMI, V., TALUKDAR, B. S. & ALAGARSWAMY, G. (1982). Improvement of drought resistance in pearl millet. In *Drought Resistance in Crops with Emphasis on Rice*, pp. 357–375 Los Baños, Philippines: International Rice Research Institute.

DAMPTEY, H. B., COOMBE, B. G. & ASPINALL, D. (1978*a*). Water deficit and inflorescence development in *Zea mays*: the role of the developing tassel. *Annals of Botany* **42**, 849–854.

DAMPTEY, H. B., COOMBE, B. G. & ASPINALL, D. (1978*b*). Apical dominance, water deficit and axillary inflorescence growth in *Zea mays*: the role of abscisic acid. *Annals of Botany* **42**, 1447–1458.

DONALD, C. M. (1968). The breeding of crop ideotypes. *Euphytica* **17**, 385–403.

EGHAREVBA, P. N. (1977). Tiller number and millet grain productivity. *Cereal Research Communications* **5**, 235–247.

HANSON, A. D. & NELSON, C. E. (1981). Water: adaptation of crops to drought-prone environments. In *The Biology of Crop Productivity* (ed. P. S. Carlson), pp. 78–152. New York: Academic Press.

HENSON, I. E., MAHALAKSHMI, V., BIDINGER, F. R. & ALAGARSWAMY, G. (1981). Genotypic variation in pearl millet [*Pennisetum americanum* (L.) Leeke] in the ability to accumulate abscisic acid in response to water stress. *Journal of Experimental Botany* **32**, 1211–1221.

KIRBY, E. J. M. & JONES, H. G. (1977). The relations between the main shoot and tillers in barley plants. *Journal of Agricultural Science, Cambridge* **88**, 381–389.

LAHIRI, A. N. (1978). Plant water relations as a basis for maximizing plant production in the arid areas. *Proceedings of the Indian National Science Academy* B **44**, 344–356.

LAHIRI, A. N. & KHARABANDA, B. C. (1965). Studies of plant–water relationships: effects of moisture deficit at various developmental stages of bullrush millet. *Proceedings of National Institute of Science, India* B **31**, 14–24.

LAHIRI, A. N. & KUMAR, V. (1966). Studies on plant water relationship. Further studies on drought mediated alterations in performance of bulrush millet. *Proceedings of National Institute of Science, India* B **32**, 116–129.

MAHALAKSHMI, V. & BIDINGER, F. R. (1985). Flowering response of pearl millet to water stress during panicle development. *Annals of Applied Biology* (in the Press).

RAYMOND, D. C. (1968). For a better understanding of the growth and development of pennisetum millets. *Agronomie Tropicale* **23**, 844–863.

SEETHARAMA, N., MAHALAKSHMI, V., BIDINGER, F. R. & SARDAR SINGH (1982). Response of sorghum and millet crops to drought stress in semi-arid India. In *International Symposium on Agrometeorology of Sorghum and Millet in Semi-Arid Tropics*, pp. 159–175. Patancheru, India: International Crops Research Institute for the Semi Arid Tropics.

TURNER, N. C. (1982). The role of shoot characteristics in drought resistance of crop plants. In *Drought Resistance in Crops with Emphasis on Rice*, pp. 115–134. Los Baños. Philippines: International Rice Research Institute.

WILSON, G. L. & WHITEMAN, P. C. (1965). The influence of shoot removal on drought survival of sorghum. *University of Queensland Papers* **4**, 223–229.