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Flowering response of pearl millet to water stress during panicle development*

BY V. MAHALAKSHMI AND F. R. BIDINGER
International Crops Research Institute for the Semi-Arid Tropics, ICRISAT Patancheru P.O., Andhra Pradesh 502 324, India

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SUMMARY

In pearl millet, severe water deficit during the period of panicle development delays flowering. The flowering response of both main shoot and tillers to water stress during panicle development was investigated using four hybrids. Panicle initiation of all tillers occurred in the three early genotypes despite water stress. In the late genotype, however, panicle initiation of tillers occurred only after the release of stress. The delay in flowering due to water stress was more pronounced in the tillers than in the main shoot. However, the proportion of tillers producing an inflorescence was increased by water stress. Grain yield losses on the main shoot by water stress were compensated by an increase in tiller grain yields. Delay in flowering and buffering by tillers provide an important adaptive mechanism to overcome a period of drought stress prior to flowering.

INTRODUCTION

Pearl millet (*Pennisetum americanum* (L.) Leeke) is grown almost entirely as a rainfed crop in light, shallow soil regions of Asia and Africa with mean annual rainfall ranging from 200 to 800 mm and high mean air temperatures. Variability of rainfall is the major environmental factor limiting its productivity. Rachie & Majumdar (1980) suggested that this crop may be adapted to these environments due to a combination of short growth duration and heat tolerance.

Floral apex differentiation (panicle initiation : PI) in millet occurs at an early stage (Maiti & Bidinger, 1981). Consequently, water stress early in the life cycle of the plant may not only effect vegetative growth, but also reproductive growth and development. Lahiri & Kumar (1966) reported a maximum delay in ear and anther-emergence when plants were subjected to water stress at 6 wk after sowing and an intermediate effect when stress was applied 4–5 wk after sowing. Bidinger, Mahalakshmi, Talukdar & Alagarswamy (1981) reported delayed flowering in millet subjected to water stress during panicle development. Information is lacking on genotypic variation in floral initiation and development, and the change in relative productivity of tillers and main shoot following an episode of water stress at an early stage. This investigation was conducted to examine the nature and pattern of delay in flowering in the main shoot and tillers in pearl millet.

MATERIALS AND METHODS

The experiment was conducted on shallow Alfisols (average soil depth 60 cm) at the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) Center, Patancheru, A. P., India, during January-May 1982. This is normally a rain-free period with high mean

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air temperatures and evaporation rates, and low relative humidities (Table 1) imposing a high atmospheric demand on the crop. Therefore the crop was irrigated and water stress treatment was imposed by withholding irrigation. The available water-holding capacity of the soil was approximately 60 mm. The unirrigated crop was subjected to severe water stress conditions.

Table 1. *Total monthly rainfall and evaporation and mean monthly maximum and minimum temperatures and relative humidity during the crop season (Jan.-May 1982).*

	Jan.	Feb.	Mar.	Apr.	May
Total rainfall (mm)	0	0	0	33·7	38·4
Total open pan evaporation (mm)	169	200	285	306	331
Mean maximum temp. °C	28·5	32	35	37	37
Mean minimum temp. °C	15·6	18·4	21	22	24
Relative humidity at 1417 IST (%)	39	32	27	26	29

The experimental design was a split-plot with two irrigation treatments as the main plots, and four genotypes in the sub-plots. The treatments were replicated three times. The two irrigation treatments were an irrigated control (irrigated to field capacity by surface flooding at 10, 23, 36, 48, 58, 67, 76, 83, 90 days after emergence) and a water stress treatment during panicle development (G.S. 2) where water stress was imposed between 20 and 48 days after emergence. The latter treatment was regularly irrigated to field capacity thereafter until maturity. As flowering and subsequently maturity were delayed by this treatment, irrigation was continued for a longer period than in the control plots.

Three ICRISAT early maturing millet hybrids *viz*., ICH 220, ICH 226, ICH 385 (approximately 75 days) and one late maturing hybrid, ICH 162 (85 days) were grown in the sub-plots consisting of eight rows each of 4 m long. Seeds were machine-sown on ridges 75 cm apart on 19 January. The field was irrigated to field capacity by flooding the furrows between ridges and the crop emerged on 25 January. Ridges were over-sown and plants were thinned 10 days after emergence to 10 cm apart. Nitrogen and phosphate (P_2O_5) each at the rate of 40 kg/ha as ammonium phosphate was banded into the ridges prior to planting. 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 incidence of diseases or pests.

Five plants from each plot were dissected and examined under a stereo-binocular microscope at regular intervals to determine the number of days to PI of the main shoot and tillers. When apices of at least three plants had differentiated into a dome-like structure (Maiti & Bidinger, 1981) that day was designated as the day of initiation. Individual inflorescences on plants in the inner two rows of each plot were tagged to determine the frequency and pattern of flowering in the main shoot and tillers. The frequency distributions of both main shoot and tillers of each genotype in the two treatments were compared by Kolmogorov-Smirnov test (Conover, 1971). The central four rows were harvested at crop maturity for determining yield and yield components. The data were analysed using analysis of variance.

The time to panicle initiation of the main shoot and tillers was unaffected by water stress in the three early maturing hybrids *viz*., ICH 220, ICH 226 and ICH 385 (Table 2). In the late hybrid ICH 162, however, tillers initiated panicles in the stress treatment only after the release of water stress. Flowering of the main shoot and tillers was delayed by stress in all four hybrids. Even though all tillers on a plant underwent floral differentiation only a few of them produced a mature inflorescence. Water stress reduced the total number of tillers/plant, but the number of panicles/plant was increased (Table 3). In water stressed plants the

Table 2. *Days to floral initiation (PI) and flowering (F) of the main shoot and tillers (T1, T2, . . . etc. = Tiller 1, Tiller 2 . . . etc.) in the four hybrids in the two treatments*

Genotype	Treatment	Main shoot		T1		T2		T3		T4	
		PI	F	PI	F	PI	F	PI	F	PI	F
ICH 220	Irrigated	18	49	26	54	27	54	28	55	32	63
	Stress	18	58	25	69	26	71	28	78	28	72
ICH 226	Irrigated	17	44	23	47	25	49	26	50	28	NF
	Stress	17	49	24	67	26	70	27	73	29	76
ICH 385	Irrigated	17	47	26	50	27	50	29	51	34	NF
	Stress	17	56	26	68	27	76	29	72	30	70
ICH 162	Irrigated	25	58	36	58	38	NF	40	NF	41	NF
	Stress	28	70	53	76	55	74	56	NF	57	NF

NF = Not flowered; SE < 1·0

proportion of all tillers producing inflorescences was higher than in irrigated controls in all four hybrids.

The extent of delay in flowering of a main shoot or tiller inflorescence was related to the time of its floral differentiation (Fig. 1*a*). Later initiated apices were delayed more than the earlier ones. Days to PI and duration of panicle development (days from PI to flowering) were differently related in the two treatments (Fig. 1*b*). In the irrigated treatment there was no effect of time of PI on panicle development duration. In the water stress treatment however, the later initiated apices took longer to develop.

The flowering pattern of main shoots and of tillers of irrigated plants followed a normal distribution with a modal class around the mean visual estimate of flowering day, in all the hybrids (Fig. 2). Flowering of tillers in the stress treatment, however, was delayed and the pattern tended to be skewed towards later flowering. In the late hybrid ICH 162, flowering was delayed in both the main shoot and tillers by stress and both distributions were skewed.

With irrigation the contribution to total grain yield by the main shoot was more than that of the tillers in all hybrids (Table 4). In the high-tillering hybrids (ICH 220, ICH 226 and ICH 385) the tillers contributed about 25–35% of the total grain yield in the irrigated treatment. In the low tillering ICH 162 however, the tiller grain yields accounted for only it 10% of the total in the irrigated treatment. Main shoot grain yields were reduced in

Table 3. *Total number of tillers/plant (including main shoot), panicles/plant and % of plants bearing inflorescence on subsequent tillers (T1, T2, . . . etc. = Tiller 1, Tiller 2, . . . etc.)*

Genotype	Treatment	Tillers/ plant	Panicles/ plant	% of tillers producing an inflorescence			
				T1	T2	T3	T4
ICH 220	Irrigated	4·82	1·53	31	14	6	2
	Stress	4·40	1·96	52	31	12	1
ICH 226	Irrigated	4·42	1·53	31	16	6	0
	Stress	4·31	1·93	50	28	10	1
ICH 385	Irrigated	4·56	1·42	29	11	2	0
	Stress	4·29	1·95	55	30	7	3
ICH 162	Irrigated	5·84	1·05	4	1	0	0
	Stress	5·20	1·30	25	5	0	0
S.E. for Genotype		0·15	0·12				
S.E. for Treatment		0·08	0·11				

Table 4. *Mean grain yield and yield components in the four hybrids in the two treatments*

Genotype	Treatment	Main	Tiller	Main	Tiller	Main	Tiller
		Grain yield/m^2 (g)		No of grains/m^2 (x 10^4)		1000 grain weight (g)	
ICH 220	Irrigated	179	84	2·7	1·6	6·6	5·3
	Stress	136	173	2·0	3·1	7·0	5·6
ICH 226	Irrigated	196	99	2·8	2·0	7·0	5·0
	Stress	99	127	1·7	2·4	6·0	5·4
ICH 385	Irrigated	177	55	3·1	1·3	5·6	4·3
	Stress	114	133	2·1	2·7	5·4	5·0
ICH 162	Irrigated	253	19	4·0	0·4	6·4	5·6
	Stress	224	59	2·9	1·1	7·8	5·9
SE for Genotype		13·9	11·9	0·19	0·25	0·31	0·14
SE for Treatment		7·3	12·9	0·22	0·20	0·30	0·15

the stress treatment mainly due to a reduction in grain numbers. The grain yield of tillers increased due to water stress, as did tiller grain numbers. The 1000 grain weights of both the main shoot and tiller grains were not affected by stress except in ICH 162. In all hybrids the individual grain weight of tillers was less than that of the main shoot.

Water stress during panicle development of millet delayed flowering and increased the numbers of productive tillers on the plant. This confirms our earlier observation (Bidinger *et al.*, 1981). Lahiri & Kumar (1966) also reported delayed flowering when pearl millet plants were droughted at an early stage (4–6 wk old). Angus & Moncur (1977) found that in wheat mild water stress hastened anthesis while severe stress delayed it. They further noted that this effect was more pronounced in tillers than in the main shoot. In sorghum Whiteman & Wilson (1965) found delayed emergence of panicles due to water stress and the period of delay was closely related to the corresponding periods of water stress. In maize, landrace 'Michoacan 21', plants remained without flowering during water stress but recovered and flowered on rewatering (Palacios de la Rosa, 1959).

There was no relationship between the time to PI and days for panicle development in irrigated controls (Fig. 1*b*). Stern & Kirby (1979) reported that in wheat the period from terminal spikelet initiation to ear emergence was similar in all sowing treatments and cultivars though the time for spikelet initiation was reduced in later sowing due to photoperiod effects.

The results from this study indicated that in pearl millet the rate of panicle development was slowed by water deficit. Nicholls & May (1963) reported that in barley the rate of primordia production of the apex was reduced by a soil water deficit, but alleviation of stress caused an accelerated rate of primordium formation so that final grain number was the same as that of the control. In water stress treatment for every additional day for panicle initiation there was a delay of about 1 day (Fig. 1*a*; $b=0 \cdot 97$) in flowering under stress when compared to the irrigated controls or an additional day for the panicle development (Fig. 1*b*; $b=0 \cdot 85$). This was due to the progressive increase in the intensity of stress with time rather than to any specific ontogenetic differences. Angus & Moncur (1977) also found a similar delay in flowering in wheat plants for every day the plants were subjected to water stress. In ICH 162, however, the panicle initiation of tillers was also affected by water stress. As this was a late maturing hybrid the stress was more severe when the tillers were undergoing differentiation, suggesting that severe stress at the time of PI suspends PI. This, however, needs further investigation.

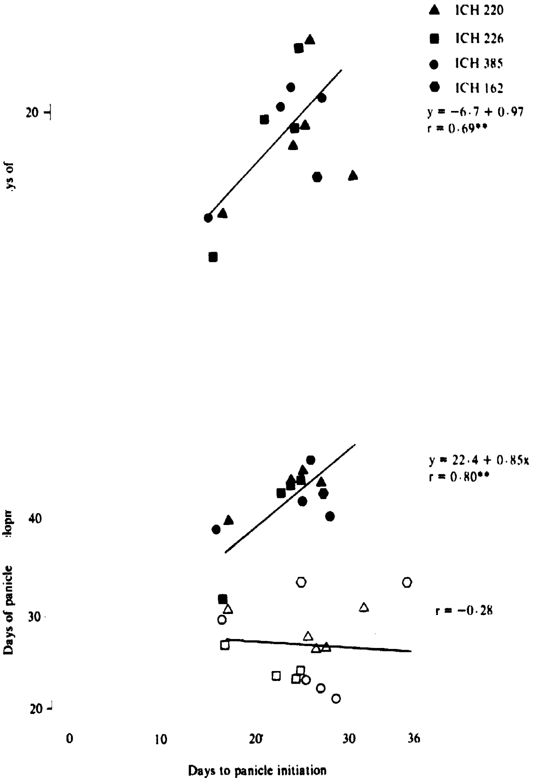

Fig. 1. Relationship between days to panicle initiation (both main shoot and tillers included) and (a) days of delay in flowering under stress and (b) days of panicle development in irrigated (open symbols) and stresed (closed symbols) treatment in the three early hybrids.

**Significant at 1% level of probability.

ns = significant.

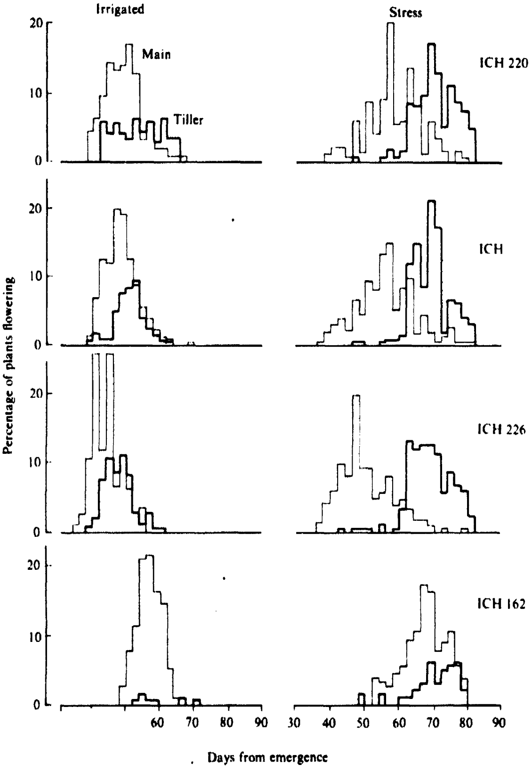

Fig. 2. Histogram showing flowering percentage of main shoot and tillers of plants in the four hybrids in the two treatments. Kolmogorov – Smirnov (Two tail) test for comparison of the frequency distribution of the tillers in the two treatments in the four hybrids were all significant ($P < 0.05$). Frequency distribution of ICH 162 main shoot in the treatment was also significant.

In spite of undergoing panicle differentiation not all tillers developed to produce an inflorescence. Water stress during G.S. 2 promoted a greater proportion of tillers into developing an inflorescence. High tillering crops such as wheat, rice and barley produce many more tillers than are capable of yielding grains. A beneficial role for tillers in adverse environmental conditions has nevertheless been suggested for wheat and rice (Yoshida, 1972). Damptey & Aspinall (1976) found that an episode of water stress during early tassel development promoted the development of lower axillary inflorescences in sweet corn. Damptey, Coombe & Aspinall (1978*a*, 1978*b*) further demonstrated that the water stress effects on sweet corn could be induced either by tassel removal or by external application of abscisic acid (ABA). Accumulation of ABA under water stress has been reported in pearl millet (Henson, Mahalakshmi, Bidinger & Alagarswamy, 1981). The possible role of the accumulated ABA in promoting the development of additional tillers also needs further investigation.

Water stress reduced the grain yield of main shoot by reducing the grain number component. he reduction in grain number could be due to a reduction in the number of florets being formed or fewer florets being fertile or a combination of the two in the stressed treatment. Grain yield losses on the main shoot of millet due to water stress were compensated by an increase in tiller grain yields. This was reflected as increased numbers of productive tillers per plant and increased tiller grain numbers per unit area. Blum (1973) and Bagga, Ghare & Asana (1973) showed that in sorghum when number of panicles per unit area was reduced by drought stress, the grain weight per panicle was increased due to an increase in the grain number per panicle. In pearl millet, however, total number of panicle per unit area was increased under water stress during G.S. 2 by an increase in productive tillers. The individual grain weight was not affected in the early hybrids though there was an increase in individual grain weight in ICH 162. This was expected since the stress was released at the time of flowering and in cereals primarily only current photosynthates are utilised for grain-filling (Stoy, 1965). Main shoots of ICH 162 flowered after release of water stress and individual grains had less competition for development due to reduction in grain numbers. Reduction in number of grains per panicle either by removal or by unfavourable environment can be compensated for by larger and heavier grains (Hamilton, Balasubramanian, Reddy & Rao, 1982; Eastin, 1981) though the potential for compensation by increasing grain weight is limited (Fisher, 1973).

The ability of the millet crop to delay flowering could play an important role under mporary adverse environmental conditions. Since this crop is grown largely during the rainy season the chances of water stress being alleviated by rains are generally high. The developmental plasticity in tillering could play an important compensatory role in overcoming grain yield losses by the main shoot. The extent of the compensation and the role of environmental factors and hormones in controlling this response deserves further investigation.

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