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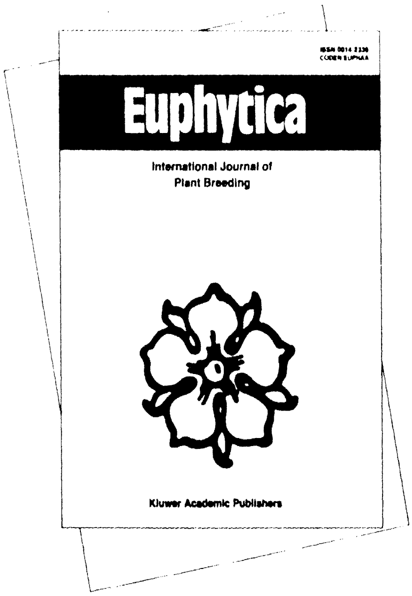

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Effect of water availability pattern on yield of pearl millet in semi-arid tropical environments *

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Summary

Throughout much of the semi-arid tropics, fluctuations in grain yield can largely be attributed to differences in timing and intensity of drought stress. Since seasonal rainfall in these environments is often poorly related to grain yield, the aim of this paper was to establish a relationship between water availability and grain yield for pearl millet (*Pennisetum glaucum* (L.) R. Br.), grown across 24 semi-arid tropical environments in India. We used a simple soil water budget to calculate a water satisfaction index (WSI) throughout the season. The cumulative WSI at maturity explained 76% of the variance in grain yield. This was three times as much as explained by actual rainfall, because WSI accounted for differences in water losses and pan evaporation. A classification of environments into four groups of water availability patterns explained 75% of the environmental sum of squares for grain yield. For a subset of 13 environments, environmental differences in grain number could also be explained by water availability patterns, whereas differences in grain mass were related to both water availability and temperature. Our results indicate that cumulative WSI, which is an integrated measure of plant-available water, can provide an adequate estimation of the environmental potential for yield in environments where grain yield is mainly limited by variable availability of water.

Introduction

Breeding crop varieties for variable moisture environments has traditionally been a difficult area in plant breeding. This difficulty largely results from the very high degree in temporal and spatial variability in available moisture that characterizes these environments (Bidinger et al., 1982; Van Oosterom et al., 1993). If moisture patterns are unpredictable, a breeder is effectively selecting for a broad spectrum of different environments, which require contrasting plant types (Ceccarelli et al., 1991). To enhance the efficiency of breeding for variable moisture environments, these environments need to be characterized in terms of the frequencies of occurrence of certain patterns of water availability and of their effects on the genotype-by-environment (GE) interaction.

A first step in an environmental characterization that is relevant for grain yield is the establishment of a relationship between grain yield and simple environmental parameters. For dry Mediterranean environments, rainfall and temperature have been shown to explain a major proportion of the yield variance across environments for legumes (Erskine & El Ashkar, 1993) and cereals (Blum & Pnuel, 1990; Van Oosterom et al., 1993). In semi-arid tropical environments, however, actual rainfall is often poorly related with grain yield (Frère & Popov, 1979), and other environmental parameters have been proposed to account for differences in grain yield. Muchow et al. (1996) reported that relative transpiration, the ratio of actual to potential transpiration derived from a sorghum growth simulation model, was very effective in identifying groups of seasons with different patterns and frequencies of occurrence of water availability. A simpler water satisfaction index (WSI) has been successfully used to

* ICRISAT Journal Article 1637

Table 1. Mean time from emergence to flowering (fl. in thermal units) and average grain yield (g/m^2) across groups of environments with different patterns of drought occurrence for each entry

	Time to fl.	Drought environment			
		No drought	Post fl. Moderate	Post fl. Severe	Pre fl. Severe
Hybrids					
HHB 67	664 a	332 abc	199 a	159 a	50 c
RHB 27	668 a	304 cde	193 abc	144 ab	48 c
HHB 68	712 b	328 abc	197 ab	121 abc	60 bc
RHB 23	760 c	301 cde	170 bcde	89 cde	59 bc
RHB 28	775 d	307 bcde	150 ef	106 bcd	46 c
HHB 60	795 e	344 ab	190 abc	92 cde	93 ab
ICMH 84122	864 g	349 a	184 abcd	84 cde	114 a
Mean hybrids	748	324	183	114	67
Varieties					
CZDT 46	762 cd	250 f	141 f	76 de	52 c
ICMV 88904	772 cd	323 abcd	178 abcd	75 de	53 c
ICMV 87125	840 f	320 abcd	166 cdef	86 cde	68 bc
IHPV 85/1	848 f	306 bcde	159 def	59 e	74 bc
WCC 75	865 gh	294 cde	146 ef	63 e	75 bc
PSB 1	870 gh	270 cf	144 cf	75 de	68 bc
ICMV 82113	879 h	288 def	149 ef	82 cde	75 bc
Mean varieties	834	293	155	74	67

Means followed by the same letter are not significantly ($P < 0.05$) different based on Tukey's test for pairwise comparisons.

describe annual variation in grain yield of maize (*Zea mays* L.) at Lome, Togo (Frère & Popov, 1979) and of groundnut (*Arachis hypogea* L.) at Bambey, Senegal (Frère & Popov, 1979) and in India's Rajkot district (Srivastava et al., 1989). If environmental parameters are to be used by breeders for characterizing variable stress environments and identifying suitable selection sites, it is important that these parameters account for most of the variation in both environmental mean yields and the GE interaction.

In this paper, we have used daily observations on rainfall and pan evaporation to derive water availability patterns for pearl millet in 24 environments in the arid and semi-arid tropics of India. The aim of this study was to (1) establish a relationship between water availability and grain yield, and (2) examine the extent that water availability pattern and temperature can account for environmental differences in grain yield, number, and mass. In a subsequent paper (Van Oosterom et al., 1996b) we analyse the effects of water availability pattern and temperature on the genotype-by-environment interaction for grain yield.

Materials and methods

Plant material

The experiment included 16 pearl millet genotypes (*Pennisetum glaucum* (L.) R. Br.), of which 14 were common in all experiments. These 14 genotypes consisted of seven hybrids and seven open-pollinated varieties, all bred in India by various institutions or universities. The hybrids on average flowered earlier than the varieties and had higher yields, especially under post-flowering drought stress (Table 1).

Table 2. Latitude, seasonal rainfall, cumulative soil water satisfaction index (WSI) at flowering (Fl) and 25 days after flowering (= maturity, Mat), mean maximum temperature during grain filling (° C), mean grain yield, grain mass, and grain number for 14 pearl millet genotypes, grown across 24 semi-arid environments in India. Environments are grouped according to the occurrence of drought and temperature stress (see text) and ranked within groups for grain yield

Environment	Latitude	Seasonal rainfall[a] Actual mm	Seasonal rainfall[a] Effective %[b]	WSI Fl	WSI Mat	Max. Temp. ° C	Grain Yield g/m²	Grain Mass mg	Grain Number /m²
Group 1: non drought stress									
Low temperatures									
Patancheru 89	17°45′	660.6	41.9	100	100	28.7	427	8.82	49342
Durgapura 88	26°90′	458.7	71.6	100	100	32.4	324	-	
Patancheru 88	17°45′	620.1	46.2	100	100	29.2	313	7.97	39791
Anantapur 88 early sowing	14°66′	631.0	42.1	100	100	30.7	273	8.42	33285
Jamnagar 88	22°45′	631.3	51.3	100	89	32.3	267	-	
High temperatures									
Hisar 88 irrigated	29°15′	392.0	73.2	100	99	35.2	354	7.44	48347
Patancheru dry season 89 control	17°45′	719.1	59.8	99	99	36.9	319	7.93	41726
Bawal 88	28°12′	292.8	98.5	100	83	35.9	318		
Patancheru dry season 90 control	17°45′	443.0	86.5	97	87	35.9	283	7.47	38825
Hisar 88	29°15′	342.0	76.6	100	90	35.7	241	7.95	31013
Group 2: Moderate post-flowering drought stress									
Low temperatures									
Jamnagar 89	22°45′	265.5	91.3	95	70	32.3	291	-	-
Anantapur 88 late sowing	14°66′	556.5	31.1	99	62	33.2	192	8.30	23589
Anantapur 89 late sowing	14°66′	234.8	81.9	88	62	33.7	183	6.66	27972
Patancheru 89 stress[c]	17°45′	457.8	26.8	97	60	28.7	168	7.42	22968
High temperatures									
Fatehpur 88	27°17′	304.5	66.8	96	60	34.8	212	-	-
Patancheru dry season 89 stress[d]	17°45′	473.7	52.3	99	60	36.1	170	5.69	30444
Patancheru dry season 90 stress[d]	17°45′	263.0	86.3	98	54	35.9	148	5.27	28402
Durgapura 89	26°90′	420.6	51.7	97	63	35.6	82	-	-
Jobner 88	27°27′	215.3	82.1	100	71	35.5	63	-	-
Group 3: severe post-flowering drought stress									
High temperatures									
Mandor 89	26°30′	251.9	67.8	87	50	36.7	124	-	-
Mandor 88	26°30′	139.1	100.0	92	40	38.0	91	-	-
Jodhpur 88	26°30′	194.7	81.2	97	46	38.0	63	-	-
Group 4: severe pre-flowering drought stress									
Low temperatures									
Anantapur 89 early sowing	14°66′	683.9	39.8	57	44	32.5	81	7.06	11578
High temperatures									
Fatehpur 89	27°17′	110.2	100.0	61	32	34.9	47	-	-

[a] Rainfall plus irrigation. [b] Percentage of actual rainfall. [c] Protected from rainfall after average flowering through a rain-out shelter. [d] Irrigated until average flowering date only.

Environments

The experiment was grown during the rainy seasons of 1988 and 1989, and the dry seasons of 1989 and 1990, in 24 environments (site × year × moisture regime) on experimental farms in north and south India (Table 2). Most experiments conducted during the rainy season were rainfed. At Hisar 1988, however, an irrigation of ca 50 mm was applied around sowing to one of the two experiments. At Patancheru (ICRISAT Center), one experiment in the 1989 rainy season was subjected to drought stress after the flag leaf stage, by protecting the crop from rainfall with a rain-out shelter. During the dry season, two experiments were conducted at Patancheru each season: one control experiment, which was irrigated at regular intervals from sowing until maturity, and one stressed experiment, where irrigation was withheld after flowering. Rainfall during the growing season, including irrigation, ranged from 110 mm at Fatehpur in 1989 to 719 mm at Patancheru in 1989 (Table 2).

The lay-out of the experiment was a randomized complete block design with either three or four replications. Plots consisted of four rows of 5 m length and the row-spacing ranged from ca 50 to 75 cm. Nitrogen (split application) and phosphorus (before sowing) were applied at most locations; the rates varied according to the environment.

Weather data to describe the environments came from meteorological stations, located close to the experiments. For each environment, daily minimum and maximum temperature, rainfall, and class A pan evaporation were available. For Durgapura, data on pan evaporation were not available and data from Fatehpur, the nearest station, were used.

Grain yield was recorded from an area ranging from 3.6 to 15 m^2. For a subset of 13 environments, involving the experiments conducted at Anantapur, Hisar, and Patancheru, grain mass was also measured. Grain number/m^2 was derived from grain yield and grain mass.

Crop water satisfaction index

The amount of water available to the crop was calculated using a soil water budget described by Frère & Popov (1979). In this budget, daily rainfall and stored soil water from previous days represent available water for crop growth, whereas pan evaporation multiplied by a crop coefficient represents the water needs of the crop. Crop coefficients were adapted from those reported by Dancette (1983) for pearl millet in a Sudanian-Sahelian environment. The coefficient was set to 0.3 early in the season, gradually increased to 1.0 around flowering, and declined to 0.6 at maturity. The time from sowing to flowering varied with environment; therefore, adjustments for the values of the crop coefficient were made early in the season, since most of the variation in crop duration can be attributed to variation in the vegetative phase (Craufurd & Bidinger, 1988). The balance between water supply and requirement was calculated for successive 5-day periods.

The water budget calculates a water satisfaction index (WSI) that has a value of 100 at sowing and remains so until a deficit occurs, i.e. when available water drops below the amount of water required by the crop. This deficit, expressed as a percentage of the seasonal water requirement, is then subtracted from 100. Each successive deficit, expressed in the same way, is subtracted from the value of WSI at that particular moment in the season. In case of heavy rainfall, the budget assumes that the soil will recharge to its maximum water holding capacity; the remainder of the rainfall is lost as run-off or deep drainage. The soil water holding capacity was estimated from the soil type and depth, and was set to values ranging from 50 mm for shallow sandy soils to 150 mm for deeper alluvial soils. The changes in WSI before and after flowering are thus estimates of the magnitude of the pre- and post-flowering drought stress.

Calculations for the water balance started five days before sowing, reflecting the practice that pearl millet is sown directly after the first rains of the season. Because the rainy season is preceded by a long, hot, and dry summer, the effect of stored soil water on water availability is limited and was hence ignored. The calculations for the water balance continued until about four weeks after the average flowering date, which moment represents crop maturity (Craufurd & Bidinger, 1988).

Effects of environmental parameters on grain yield

To assess which environmental parameters determined grain yield, rainfall-related data were derived from actual rainfall by adjustments for run-off, crop coefficients, and pan evaporation.

Table 3. Percentage of variance (R^2, adjusted for degrees of freedom) in grain yield of pearl millet across 24 semi-arid environments in India, accounted for by actual, corrected, and effective rainfall, their ratios with cumulative pan evaporation, and cumulative water satisfaction index (WSI) at 25 days after flowering

	Rainfall	Rainfall evap. ratio[a]	Cum. WSI at 25 DAF
Seasonal rainfall	Adjusted R^2 (grain yield)		
Actual	0.242	0.287	
Corrected[b]	0.456	0.674	0.689
Effective[c]	0.478	0.734	0.756

[a] Seasonal rainfall divided by cumulative seasonal pan evaporation; ratio's > 1 were set to 1. See text.
[b] Seasonal rainfall minus run-off, estimated from the water budget and assuming a fixed crop coefficient of one throughout the season.
[c] Seasonal rainfall minus run-off, estimated from the water budget and assuming a seasonal change in the crop coefficient.

Effective rainfall was defined as the actual seasonal rainfall minus water losses due to run-off and deep drainage. Water losses were estimated from the water budget described above. Since the crop coefficients used in that budget affect water requirements and hence run-off and deep drainage, we also defined corrected rainfall, calculated similarly as effective rainfall, but assuming a fixed crop coefficient of one throughout the season. This represents a situation where water requirements permanently equal pan evaporation.

To adjust for environmental differences in evaporative demands, the values for actual, corrected, and effective rainfall were expressed as a fraction of the seasonal pan evaporation. Fractions exceeding one were set to one, indicating that in those environments rainfall was sufficient to account for the evaporative demands.

Classification of environments

Environments were grouped for water availability pattern using the average linkage method. This method defines the distance between two clusters as the average distance between pairs of observations, one in each cluster (SAS, 1985). An analysis of variance for grain yield, number, and mass was performed to calculate the percentage of the environmental sum of squares accounted for by the clustering.

Results

Effects of environmental parameters on grain yield

Actual seasonal rainfall explained only 24.2% of the variance in grain yield (Table 3), because of a wide range in rainfall in both high- and low-yielding environments (Fig. 1a). If actual rainfall was adjusted for pan evaporation, the fit improved only marginally (adj. R^2 = 0.287, Table 3). Since the estimated water losses were significantly correlated with total rainfall (r = 0.91), but not with mean grain yield (r = 0.27), this poor relationship between rainfall and grain yield may have been due to a discrepancy between actual and effective rainfall.

Adjustment for water losses considerably improved the relationship between rainfall and grain yield (Table 3). Effective rainfall was slightly more efficient than corrected rainfall. Adjustment for pan evaporation yielded another substantial improvement, increasing the adjusted R^2 to 0.734 in the case of effective rainfall (Table 3). Actual seasonal rainfall, water losses (and therefore soil water holding capacity), and pan evaporation together thus explained a major part of the variance in environmental mean grain yield.

The cumulative WSI at 25 DAF was for both corrected and effective rainfall slightly more efficient in explaining yield differences than the correction for pan evaporation (Table 3). The cumulative WSI at 25 DAF, as calculated by the soil water budget (Frère & Popov, 1979), explained 75.6% of the variance in grain yield between environments.

The upper limit for grain yield at a certain WSI was a linear function of WSI (Fig. 1b). The dry environments had, with a few exceptions, grain yields that were close to this upper limit. Most non drought-stressed environments, by contrast, yielded considerably below this limit. The upper limit, based on six environments (Fig. 1b), was: GRAIN YIELD = 428.2 - 5.393 × ΔWSI–PRE - 5.734 × ΔWSI–POST where ΔWSI–PRE and ΔWSI–POST represent the changes in WSI before and after flowering, respectively. The reductions in grain yield due to pre- and post-flowering drought were in both cases significant at $P < 0.001$ but were not significantly different from each other. We obtained similar results if the complete set of 24 environments was used, indicating that the six environments were a representative sub-sample. The results indicate that a water deficit of 10% of the seasonal water requirements of the crop causes a yield decrease > 0.5 ton/ha.

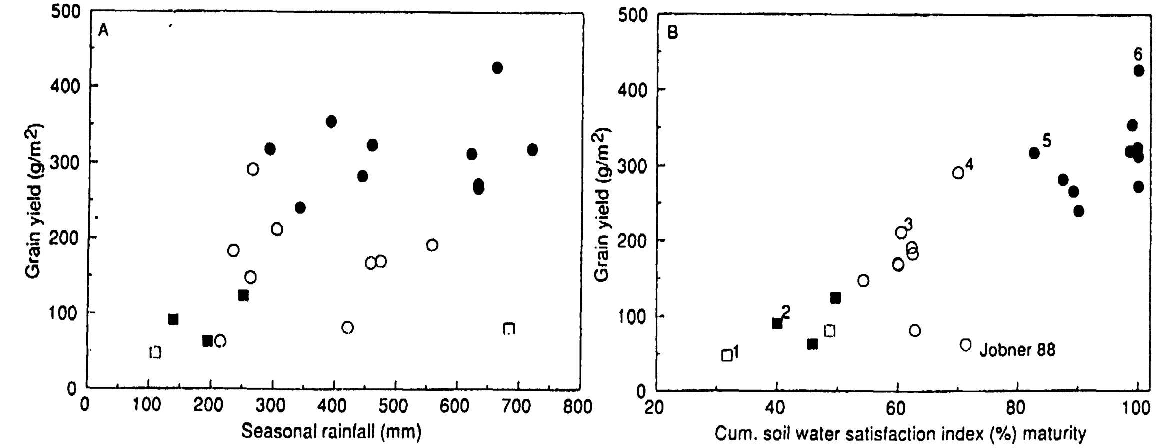

Fig. 1. Relation between (A) seasonal rainfall and grain yield and (B) cumulative soil water satisfaction index (WSI) at 25 days after flowering and grain yield for environments without drought stress (●), environments with moderate post-flowering drought stress (○), environments with severe post-flowering drought stress (■), and environments with pre-flowering drought stress (□). Numbers in Fig. 1B refer to the six environments used for calculating upper limits for grain yield (see text).

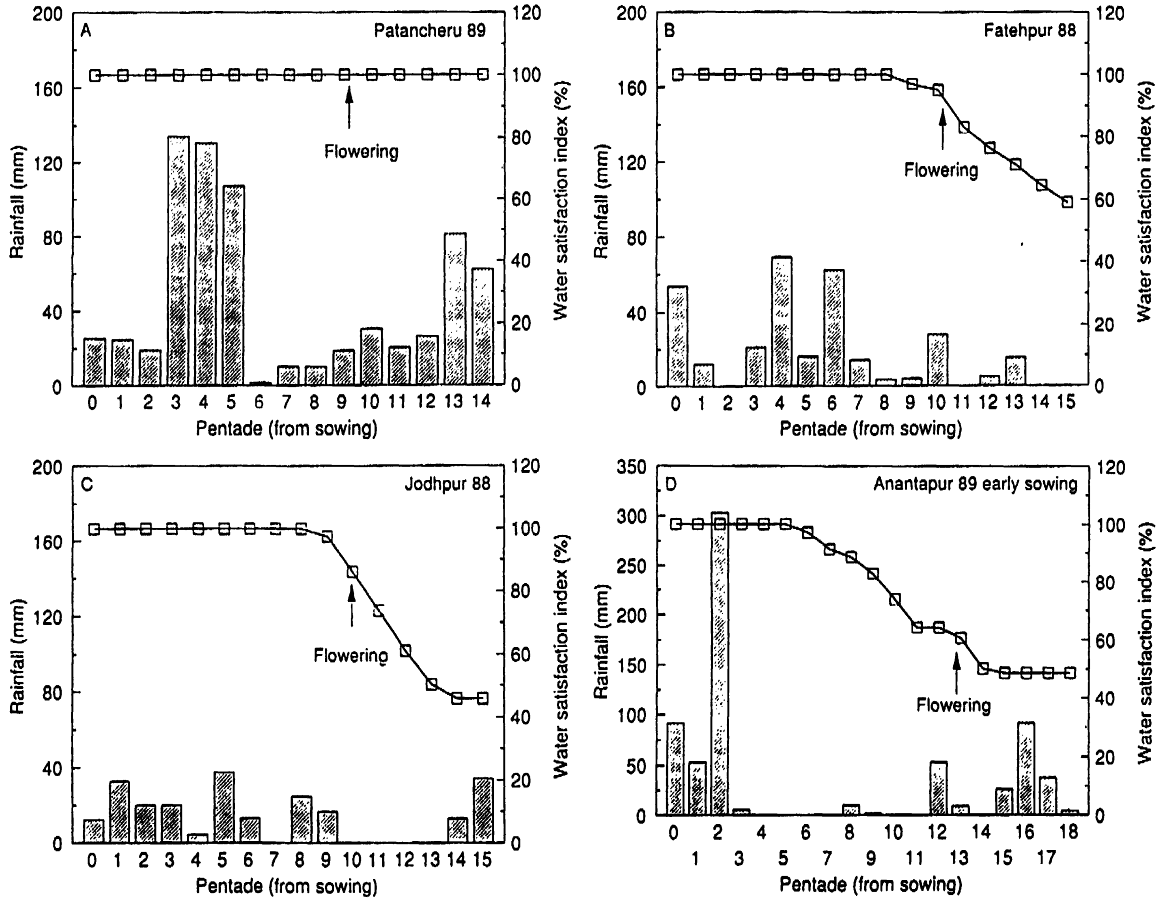

Fig. 2. Rainfall (bars) and cumulative soil water satisfaction index (WSI, □) at four contrasting environments (A) Patancheru 1989, non-stress, (B) Fatehpur 1988, post-flowering drought stress, (C) Jodhpur 1988, severe post-flowering drought stress and (D) Anantapur 1989 early sowing, pre-flowering drought stress. Arrows indicate the average time of flowering.

Table 4. Analysis of variance for grain yield, grain mass, and grain number of pearl millet across semi-arid environments in India. The subdivision of the environmental effect is based on cumulative water satisfaction index (WSI) and the subsequent subdivision on WSI and maximum temperatures during grain filling (see Table 2). Values in parentheses give the percentage of the sum of squares of environments, explained by the grouping

Source	Grain yield		Grain mass		Grain number	
	df	Sum of squares	df	Sum of squares	df	Sum of squares (× 10^6)
Genotypes (G)	13	489070	13	6.446	13	12795
Environments (E)	23	12778842	12	6.921	12	70902
G × E	299	1303044	156	3.017	156	13436
Rep (environment)	63	357558	37	0.384	37	1735
Error	815	1348982	478	3.061	478	23094
Division of environments for cumulative WSI						
between clusters	3	9567839 (74.9)	2	2.863 (41.4)	2	53966 (76.1)
within clusters	20	3211003	10	4.058	10	16936
Subsequent subdivision for temperature during grain filling						
between clusters	6	10304294 (80.6)	4	5.831 (84.2)	4	55220 (77.9)
within clusters	17	2474548	8	1.090	8	15682

A WSI of ca 23 at maturity was the threshold below which the crop would not yield any grain.

Classification of environments

Because cumulative WSI at 25 DAF explained a major proportion of the variance in grain yield, environments were grouped based on their water availability patterns throughout the season. To account for differences in season length between environments, the variables used for clustering were the cumulative water sufficiency indices during the last 13 pentades of the growing season (Fig. 2). The clustering divided the environments into four groups (Table 2, Fig. 2). The first group consisted of environments without drought stress, where WSI remained close to 100 throughout the entire crop cycle (Fig. 2a). Environments in the second group were characterized by a high WSI at flowering, but a decrease during grain filling to values between 50 and 70 (Fig. 2b). Pearl millet in these environments thus experienced moderate post-flowering drought stress. The third group contained environments with a similar pattern for WSI as the previous group, but with more severe post-flowering drought stress (Fig. 2c), resulting in a cumulative WSI at maturity between 40 and 50 (Table 2). The last group consisted of two environments in which the most severe drought stress occurred before flowering (Fig. 2d); WSI around flowering was considerably lower than in the other groups.

The above grouping of environments explained 74.9% of the environmental sum of squares (SS) for grain yield (Table 4). For a subset of 13 environments, a comparable fraction (76.1%) was explained for grain number. This was partly the result of the extremely low grain numbers following the pre-flowering drought at Anantapur 1989, which were due to a severe reduction in grain numbers per panicle (data not presented). In addition, environments experiencing post-flowering drought stress consistently had lower grain numbers than those without drought stress (Table 2). For grain mass, however, the grouping of environments by cumulative WSI explained only 41.4% of the SS of environments. But a subdivision of these groups by temperature more than doubled this percentage (Table 4). High maximum temperatures (> 34° C) during grain filling had a negative effect on grain mass. Environmental mean grain yield and grain number thus mainly depended on the occurrence of drought stress, while grain mass was also affected by temperature.

Discussion

Rainfall in the semi-arid tropics often comes in heavy showers, interspersed with dry spells. Consequently, actual rainfall is generally poorly related to grain yield. For groundnut, grown for 32 seasons at Bambey, Senegal, Frère & Popov (1979) found no correlation between total rainfall and grain yield. Our results are consistent with this observation and indicated that yield differences could be explained by cumulative WSI at maturity, but not by the rainfall-evaporation ratio. This superiority of WSI over the rainfall-evaporation ratio confirms results of Muchow et al. (1996) and suggests that water losses (due to run-off or deep drainage) account for the poor relationship between grain yield and rainfall in semi-arid tropical environments.

Cumulative WSI at maturity was a good indicator of grain yield, notwithstanding the simplifications in its calculation. The soil water budget, for example, did not account for (1) run-off that may have occurred during heavy showers, when rainfall exceeds the rate of infiltration, (2) temporal differences in rooting depth and infiltration, (3) the relationship between transpiration and fraction of extractable soil water, and (4) the effects of environmental differences in biomass production on crop coefficients. The use of the crop coefficient, however, had in our study (Table 3) only a limited effect on the results. The advantage of the water budget is its simplicity. Only rainfall, pan evaporation, and an estimate of soil water holding capacity are required as input. The calculations can be done manually (see Frère & Popov, 1979), but are also easily computerized. Previous studies (Frère & Popov, 1979; Srivastava et al., 1989) have shown the usefulness of the water budget for explaining seasonal differences in water availability within locations. Our study shows that it is also useful across a geographically wide range of locations. More sophisticated models may provide more reliable estimates of available soil water (Muchow et al., 1996), but are less likely to be used in plant-breeding programs in developing countries with limited computational resources.

Cumulative WSI at maturity was linearly related to the upper limit for grain yield at that WSI. In drought-stressed environments, grain yield was generally close to this upper limit, suggesting that water availability indeed was the main restriction for higher yields. One exception was Jobner 1988 (Fig. 1), where salinity occurred in addition to drought. In most non drought-stressed environments, however, yields were well below the upper limit, indicating that other factors were restricting (e.g., soil fertility, solar radiation, diseases, lodging). The linear relationship between WSI and the upper limit for grain yield at that WSI is in accordance with the linear relation between seasonal rainfall and yield of cereals in areas where run-off is a minor component of the water balance (Blum & Pnuel, 1990; Van Oosterom et al., 1993). In semi-arid regions where grain yield is mainly limited by a variable availability of water, cumulative WSI, which is an integrated measure of plant-available water, can provide a good indication of the environmental yield potential.

Rainfall late in the season had a significant effect on grain yield. This is in contrast with results for arid Mediterranean environments in Western Australia (Karimi & Siddique, 1991) and West Asia (Erskine & El Ashkar, 1993; Van Oosterom et al., 1993), where grain yields mainly depend on rainfall early in the season and subsequent storage in the soil profile. The importance in our experiments of late rains was associated with the relatively low water holding capacity of the soils, which reduces the possibilities of buffering drought spells. The environments in which much pearl millet is grown are characterized by low, erratic rainfall, high evaporative demands, and shallow, sandy soils (Bidinger et al., 1982). A relative water deficit of 10% reduced in our study the yield with $>$ 0.5 ton/ha, or 13% of the maximum yield. These numbers are in accordance with those reported by Mahalakshmi et al. (1988) for pearl millet grown in a line source sprinkler experiment. Adaptation of the crop phenology to available water patterns is in these environments therefore important to maximize grain yields.

Drought stress affected grain yield through differential effects on the yield components. Grain number was especially affected by pre-flowering drought (Anantapur 1989 early sowing) through a reduction in grain number per panicle. Reduced grain numbers can result from a negative effect of drought on assimilate availability and crop growth rate during panicle initiation (Hawkins & Cooper, 1981; Brown et al., 1987; Craufurd & Peacock, 1993). However, the reduction was partly compensated by enhanced tillering when the stress was relieved, confirming results of Mahalakshmi & Bidinger (1986). The reduction in grain number following post-flowering drought stress was in accordance with results of Bidinger et al. (1987) for pearl millet. Grain mass was most affected by drought and high temperature during grain filling. Maximum temperatures during this period were within the range where higher temperatures reduced the kernel size of sorghum (*Sorghum bicolor* (L.) Moench) (Chowdhury

& Wardlaw, 1978). The overall effect of temperature on grain yield was limited (Table 4), presumably due to the stronger effect of water availability. The analyses show that stress occurrence has different effects on yield components, and that hence contrasting plant types might be required for different environments.

Cumulative WSI at maturity was strongly associated with grain yield and can therefore be useful in characterizing drought occurrence in environments where rainfall is poorly associated with grain yield. For breeders, such a characterization is of interest because it enables a quantification of the importance of stress occurrence on the GE interaction for grain yield. This will be the subject of a second paper in this series (Van Oosterom et al., 1996b).

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