

Effect of Water Deficit on Yield and Protein Content in Pearl Millet Grains

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Seventy-two pearl millet genotypes were water stressed at panicle development and grain filling stages. Neither grain yields, yield components, protein percent nor total protein per unit area were affected by water deficit during panicle development but protein content per grain was increased. When plants were water stressed during grain filling, grain yield, grains per unit area and 1000 grain weight were reduced, but grain protein percentage increased. Total protein per unit area was reduced primarily due to lower grain yield. The protein content per grain was unaffected by stress, suggesting that the apparent increase in protein percentage is due to reduced carbohydrate accumulation under stress.

Keywords: Water deficit; pearl millet; grain yield; grain protein.

1. Introduction

Pearl millet (*Pennisetum americanum* (L.) Leeke), is the sixth most important cereal in the world and the main source of calories and protein for many people. The crop is grown exclusively under natural rainfall, without irrigation in the semi-arid tropical regions of South Asia and Africa where the mean annual rainfall ranges from 200–800 mm. Interseasonal and intraseasonal variation in the amount and distribution of rainfall is the major factor limiting its productivity.

Quantitatively, the most important component of grain dry matter other than starch is protein. Pearl millet grain is equal or superior in protein content to wheat, rice, maize, and sorghum grains.¹ Two of the most important factors influencing the protein content of cereals are soil moisture and nitrogen availability.²⁻⁴ A frequently observed effect of water deficit during the reproductive stages on grain quality in cereals is an increase in protein content.⁵ The present investigation was designed to evaluate the effect of drought at two growth stages on grain yield and protein content.

2. Experimental

2.1. Growing season

Experiments were conducted on shallow Alfisols (depth 60 cm) during the 1981 dry season at the International Crops Research Institute for the Semi-arid Tropics (ICRISAT) Center, Patancheru, AP, India. This is almost a rain-free period (total rainfall from January to May being 9.7 cm) with high mean maximum (34°C) and minimum (19.8°C) air temperatures and low relative humidities and therefore large evaporation rates (9.7 mm day⁻¹). The average total available water holding capacity of the soil was 60 mm. The crop was irrigated and the water deficit was imposed by withholding irrigation at the desired periods.

2.2. Experimental treatments and cultural practices

The study consisted of three experiments of 24 pearl millet genotypes each; pearl millet hybrid trial 1980 (PMHT 1980); pearl millet synthetic trial 1980 (PMST 1980), and pearl millet variety trial 1980 (PMVT 1980). The experimental designs were a split plot with the three irrigation treatments as the main-plots and the genotypes in the sub-plot. The treatments were replicated four times. The three irrigation treatments were an irrigated control (irrigated approximately at weekly intervals to field capacity by surface flooding of furrows between ridges), a midseason stress where water deficit was imposed during panicle development stage (growth stage two, GS2) and a terminal stress where water deficit was imposed during grain filling stage (growth stage three, GS3). The sub-plot unit consisted of four ridges each 4 m long and 75 cm apart. Seeds were machine sown on ridges. Plots were oversown and plants were thinned to 10 cm spacing between 10 and 15 days after emergence. Nitrogen and phosphate (P_2O_5) at the rate of 40 kg ha^{-1} each were applied as ammonium phosphate as basal dose before planting and an additional $40 \text{ kg ha}^{-1} \text{ N}$ as urea was side dressed 15 days after crop emergence. Plots were kept free from weeds and there was no incidence of diseases or pests. The central two rows of 3 m (4.5 m^2) were harvested at maturity, and yield and yield components determined.

2.3. Protein analysis

Whole grain samples from all plots were ground to a fine powder in a Udy Cyclone Mill using a 0.4 mm screen. The nitrogen content of the finely ground material was determined by a rapid procedure using a Technicon Auto Analyser⁶ and crude protein was calculated as $\text{N} \times 6.25$.

3. Results

3.1. Effect of water deficit on grain yield and protein

In the irrigated control, hybrids flowering earlier produced a greater number of panicles per plant than the synthetics and varieties. The hybrids also had a higher potential grain yield than the open pollinated varieties or synthetics. Mean protein % levels did not differ among the trials although there were significant genotypic differences within the trials in irrigated controls (Table 1).

Table 1. Summary of treatment means of the experiments (averaged over 24 genotypes) for yield and yield components

Treatments	No. of heads/plant	Days to flowering	Grain dry wt g m^{-2}	1000 grain wt. g	No. of grains 10^4 m^{-2}	Protein (%)	Total protein g m^{-2}	Protein/1000 grains mg
<i>PMHT 1980</i>								
Irrigated	2.4	53	251	6.0	42	9.5	24	580
GS2 stress	3.6	61	214	5.9	37	11.6	25	680
GS3 stress	1.4	53	109	4.5	24	14.4	15	630
CD $P=0.05$	0.20	1.3	23.7	0.28	3.3	0.93	1.2	62
<i>PMVT 1980</i>								
Irrigated	1.7	56	217	6.4	34	9.6	21	610
GS2 stress	2.8	64	235	6.6	36	10.4	24	690
GS3 stress	1.3	55	104	5.3	20	12.9	13	670
CD $P=0.05$	0.22	1.5	23.2	0.41	3.8	1.49	2.0	71
<i>PMST 1980</i>								
Irrigated	1.7	56	221	6.5	34	9.7	21	630
GS2 stress	2.9	65	207	6.3	33	12.1	25	760
GS3 stress	1.2	56	97	4.7	20	14.2	13	650
CD $P=0.05$	0.16	0.8	35.0	0.70	5.0	2.05	3.4	36

Flowering was delayed and the number of heads per plant increased when plants were stressed during panicle development. In the hybrids the number of grains and grain yield per unit area were reduced by stress. Grain yield per unit area, number of grains per unit area, and 1000 grain weight were not affected in the open-pollinated varieties. Protein % increased in hybrids and synthetics, and protein content per grain increased in all trials. The total harvested protein increased under stress but this was significant only in the open-pollinated varieties and synthetics.

Water deficit during grain filling did not affect flowering but reduced the number of ears per plant and grain yield per unit area in all trials. Both yield components, number of grains per unit area and 1000 grain weight were reduced by stress during GS3. Protein % was increased by water deficit during grain filling; total protein harvested per unit area was, however, reduced in all trials. Protein content per grain (mg/1000 grains) was not affected by water deficit.

There were significant differences among the genotypes for all the variables. Interactions of genotypes \times stress treatment were, however, not significant for protein % and protein content/grain (unpublished data).

3.2. Relationships among components

The error variances of the trials were homogeneous and therefore the data were combined. Relationships among yield, yield components, and the various expressions of protein were determined for all genotypes in the irrigated control and two water deficit treatments (Table 2).

Table 2. Correlation coefficients (r) between yield, yield components, protein % and protein content in three treatments ($n=72$)

	Number of grains m^{-2}	1000 grain wt	Protein %	Total protein	Protein/ grain
<i>Irrigated control</i>					
Grain yield	0.82**	-0.09	-0.29*	0.77**	-0.15
Number of grains m^{-2}		-0.46**	-0.16	0.69**	-0.47**
1000 grain wt			-0.11	0.03	0.65**
% Protein				0.37**	0.67**
Total protein					0.29*
<i>GS2 stress</i>					
Grain yield	0.79**	-0.06	-0.33**	0.84**	-0.19
Number of grains m^{-2}		-0.53**	-0.13	0.75**	-0.57**
1000 grain wt			-0.21	0.07	0.71**
% protein				-0.22	0.52**
Total protein					0.08
<i>GS3 stress</i>					
Grain yield	0.87**	0.59**	-0.60**	0.87**	0.19
Number of grains m^{-2}		0.16	-0.40**	0.89**	-0.14
1000 grain wt			-0.59**	0.46**	0.69**
% Protein				-0.31**	0.16
Total protein					0.30*

* Significant at 0.05 level of probability.

** Significant at 0.01 level of probability.

Grain yield was very highly correlated with grain number in the three treatments but was related to 1000 grain weight only in the GS3 stress treatment. Although there was a significant, negative relationship between 1000 grain weight and number of grains per unit area in irrigated and GS2 treatments, there was no relationship between them in the GS3 stress treatment (Table 2).

Protein % and grain yield were negatively correlated in the irrigated, and the two stress treatments. The relationship, however, was weaker in the irrigated control and GS2 stress treatments than in the GS3 stress treatment (Table 2).

Protein % was positively related to protein content per grain but independent of grain size in the irrigated control and GS2 stress treatments. In the GS3 stress treatment protein % was unrelated to protein content per grain but negatively related to the 1000 grain weight (i.e., there was higher protein % in cultivars with less well filled grains) (Table 2).

Total protein harvested per unit area was significantly correlated with grain yield and number of grains per unit area in all treatments. The relationship of total protein harvested and protein % varied with the treatment; being positive in the irrigated control, unrelated in the GS2 stress, and negative in the GS3 stress. The latter relationship, although apparently contradictory, was a result of a strong negative relationship of protein % and grain yield, which was the major determinant of total protein harvested (Table 2).

4. Discussion

4.1. Yield-protein relationship in the irrigated control

A significant but weak relationship of grain protein % and grain yield has been previously reported for pearl millet.^{7,8} Variation in grain protein % among genotypes was primarily a function of variation in protein content per grain, as differences in grain size were not related to differences in protein %.

Total protein production was related, as expected, to both grain yield and grain protein % but the former component accounted for the majority (65%) of the variation, indicating that increased protein production is most easily achieved by increasing yield. In wheat, total protein production was unrelated to protein %, and depended primarily on total grain yield.⁹ Similar results have been reported for sorghum¹⁰ and for maize.¹¹

4.2. Water stress during panicle development

Water deficit during the panicle development stage did not reduce grain yield since flowering was delayed and number of panicles per plant increased. Similar effects of water deficit during this stage have been reported for pearl millet where the grain yield losses on the main shoot were compensated by an increase in the tiller grain yield.¹² Species which flower over an extended period, usually because of progressive flowering of tillers that develop after the main stem, are less affected by isolated periods of stress.^{13,14}

The significant increase in protein % in two of the three trials in the GS2 stress treatment was probably due to a greater retention of soil N and/or availability of nitrogen during grain filling in this treatment. Nitrogen loss from the root zone may have been reduced during the dry period and/or some mineralisation could have occurred after rewatering. Similar effects of increased soil N on grain protein % have been reported for wheat.³ To what degree the response to GS2 stress of both grain yield and protein % were due to the fact that these trials were conducted in adequately fertilised conditions is not known. In general, however, protein % was related to grain yield (negatively) and the protein content of the grain (positively) in non-stressed control as well as in GS2 stress treatment.

The small increase in total protein yield per unit area in two of the three trials was apparently due to the increase in protein percentage where yield was not significantly reduced (PMVT and PMST). Protein yield was, however, primarily dependent on grain yield, as in the case of the irrigated controls. A stress before grain filling thus seems to have little direct effect on grain protein percentage or protein yield in pearl millet.

4.3. Water deficit during grain filling

Water deficit during grain filling reduced grain yield through a reduction of both grain number per unit area and grain size. The loss of grains was due to both reduction in head numbers as late tillers failed to develop under stress, and to a reduction in mean grain number per head. Both these effects are common in cereals subjected to stress during flowering.^{5,15}

Reduction in grain size probably was due primarily to the reduced availability of current photosynthates for grain filling rather than reduced rate of translocation of carbohydrates to the grain.¹⁶ This frequently results in an earlier termination of grain growth under grain filling stress.⁴ Variation in grain size was a significant factor in grain yield in the GS3 stress, but it was not observed in the other two treatments where the crop was not stressed during grain filling.

Protein % increased significantly in all three trials under GS3 stress, a common finding in cereals.^{4, 17-19} Protein content per grain was increased however, but not significantly in this treatment. This fact, combined with the negative relationship of protein % and 1000 grain weight, makes it clear that the major effect of water deficit on protein % was on carbohydrate accumulation in the grain, rather than nitrogen mobilisation or protein synthesis. Either protein and carbohydrate synthesis are affected differently by water deficit or the duration of the two processes is different. It has been reported that carbohydrates cease to accumulate 28 days after anthesis in water stressed wheat and barley plants, compared to 45 days in irrigated plants.⁴ Protein content per grain in irrigated plants increased up to 35 days and was not affected by stress. There are very few reports of grain protein synthesis under conditions of water deficit and there is no evidence to suggest that stress causes protein to accumulate earlier in grain development. Protein content per grain is subjected to less variation by environmental conditions than grain protein %.⁹

There were significant differences among the genotypes for grain yield, protein percentage and protein content per grain but genotype \times water deficit treatment interactions were not significant. This implies that the extent of water deficit effects was similar in all genotypes. This observation is of particular interest in breeding for quality characters.

The availability of protein to people depending upon pearl millet as the major protein source in years with drought during grain filling will thus depend largely on grain supplies. With restricted supplies, energy deficiency will be a greater problem than protein deficiency. With adequate food supply, protein intake would increase.

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References

- Burton, G. W.; Wallace, A. T.; Rachie, K. O. Chemical composition and nutritive value of pearl millet [*Pennisetum typhoides* (Burm.) Stapf and E. C. Hubbard] grain. *Crop Sci.* 1972, **12**, 187-188.
- Dunetz, S. Effect of soil type soil moisture and nitrogen fertilizer on the growth of spring wheat. *Can. J. Soil Sci.* 1961, **4**, 44-51.
- Terman, G. L.; Ramig, R. E.; Dreier, A. P.; Olson, R. A. Yield-protein relationship in wheat grain, as affected by nitrogen and water. *Agron J.* 1969, **61**, 755-758.
- Brooks, A.; Jenner, C. F.; Aspinall, D. Effects of water deficit on endosperm starch granules and on grain physiology of wheat and barley. *Aust. J. Plant Physiol.* 1982, **9**, 423-436.
- Salter, P. J.; Goode, J. E. Crop responses to water at different stages of growth. Commonwealth Bureau of Horticulture and Plantation Crops, *Research Review No. 2*, 1967, 247 pp.
- Singh, U.; Jambunathan, R. Evaluation of rapid methods for the estimation of protein in chickpea (*Cicer arietinum*). *J. Sci. Food Agric.* 1980, **31**, 247-254.
- Deosthale, Y. G.; Rao, R. J.; Nagarajan, V.; Pant, K. C. Varietal differences in protein and amino acids of grain bajra (*Pennisetum typhoides*). *Indian J. Nutr. Diet.* 1971, **87**, 303-308.
- Kumar, K. A.; Gupta, S. C.; Andrews, D. J. Relationship between nutritional quality and grain yield in pearl millet. *Crop Sci.* 1983, **23**, 232-235.
- Loffer, C. M.; Bausch, R. H. Selection for grain protein, grain yield and nitrogen partitioning efficiency in hard red spring wheat. *Crop Sci.* 1982, **22**, 591-595.
- Crook, W. J.; Cassady, A. J. Heritability and interrelationships of grain protein content and other agronomic traits in sorghum. *Crop Sci.* 1974, **14**, 622-624.
- Dudley, J. E.; Lambert, R. J.; Alexander, D. E. Variability and relationships among characters in *Zea mays* L. synthetics with improved protein quality. *Crop Sci.* 1971, **11**, 512-514.
- Mahalakshmi, V.; Bidinger, F. R. Flowering response of pearl millet to water stress during panicle development. *Annals Appl. Biol.* 1985, **106**, 571-578.
- Aspinall, D.; Nicholls, P. B.; May, L. H. The effects of soil moisture stress on the growth of barley. 1. Vegetative development and grain yield. *Aust. J. Agric. Res.* 1964, **15**, 729-745.

14. Turner, N.C. The role of shoot characteristic in drought resistance of crop plants. In *Drought Resistance in Crops with Emphasis on Rice*. Los Banos, Philippines: IRRI, 1982, pp. 115-134.
15. Denmead, O. T.; Shaw, R. H. The effect of soil moisture stress at different stages of growth on the development and yield of corn. *Agron. J.* 1960, **52**, 385-390.
16. Wardlaw, I.F. The control and pattern of movements of carbohydrates in plants. *Bot. Rev.* 1966, **34**, 101-108.
17. Hutcheon, W. L.; Paul, E. A. Control of the protein content of Thatcher wheat by nitrogen fertilization and moisture stress. *Can. J. Soil Sci.* 1966, **46**, 101-108.
18. Gomez, K. A.; De Datta, S. K. Influence of environment on protein content of rice. *Agron J.* 1975, **67**, 565-568.
19. Day, W.; Legg, B. J.; French, B. K.; Johnston, A. E.; Lawlor, D. W.; Jeffers, W. D. A drought experiment using mobile shelters: the effect of drought on barley yield, water use and nutrient uptake. *J. Agric. Sci. Camb.* 1978, **91**, 599-623.