Indian J. Plant Physiol., Vol. 16, No. 3&4, (N.S.) pp. 276-284 (July-Dec., 2011)

EFFECT OF TERMINAL WATER STRESS ON GROWTH, PLANT WATER STATUS AND YIELD OF PEARL MILLET GENOTYPES

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Received on 6th January, 2011; Revised and accepted on 14th October, 2011

SUMMARY

Two landrace based population (Western Rajasthan and Barmer Populations), three composites derived from non-land races (Pusa-266, ICTP-8203 and HHVBC) and one variety CZP-9802 of pearl millet (*Pennisetum glaucum* (L.) R. Br.) were subjected to water stress at the reproductive growth stage (50 days after sowing) by withholding irrigation till permanent wilting point in a pot trial. Water deprivation decreased plant water potential and relative water content (RWC) that led to a significant decline in the rate of net photosynthesis (P_N), chlorophyll content, stomatal conductance, chlorophyll fluorescence parameters (Fv/Fm and Fm), nitrate reductase (NR) activity and grain yield. Among various genotypes, Pusa-266 and CZP-9802 showed lower reduction in RWC, P_N, chlorophyll content, Fv/Fm ratio, NR activity and yield under water stress as compared with genotypes ICTP-8203, Barmer Population and Western Rajasthan Population. Thus, a combination of above physiological parameters, which had high correlation with yield as well as moderate to high heritability, can effectively be used to screen genotypes with higher tolerance to terminal drought in pearl millet.

***Keywords*: Chlorophyll fluorescence, correlation, heritability, photosynthesis, water status, yield**

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R.Br.) is grown extensively under rainfed conditions in drought-prone arid and semi-arid regions of North-west and Southern India where annual rainfall ranges between 200-800 mm. Short and erratic rainy seasons, high mean temperature, high potential evapo-transpiration rates and shallow sandy soils with poor water-holding capacity characterize these regions. These factors either alone or in combination result in water stress at one or more stages of plant growth causing yield reduction. Yield losses are highest when water stress coincides with the sensitive stage of crop growth (Hanson and Nelson 1981). Flowering and grain filling stages in pearl millet are most crucial (Mahalakshmi *et al.* 1988 , Om-Prakash *et al.* 2008). Yield reduction occured primarily due to a significant decrease in grain mass caused by reduction in current assimilate supply (Bieler *et al.* 1993). Hence, developing crop cultivars with adequate drought tolerance is an important target for pearl millet improvement under arid areas. Therefore, much research must be concentrated on the identification of parameters associated with drought tolerance in pearl millet (Yadav and Bhatnagar 2001). Stomatal closure and a consequent reduction in photosynthetic activity under drought as well as constitutive water conserving mechanisms have been well documented in pearl millet particularly at low water potentials (Hanson *et al.* 1984, Kholova *et al.* 2010). Likewise, significant genotypic

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differences in nitrate reductase activity and net photosynthetic rates have been observed in diverse pearl millet genotypes under rainfed conditions (Kathju *et al.* 2001).

In recent years, chlorophyll fluorescence has been identified as an important tool in stress physiology research particularly for drought and temperature tolerance (Sayeed 2003). Hybrid Pennisetum (*Pennisetum purpureum*) recorded a progressive decrease in maximum fluorescence (Fm), variable fluorescence (Fv) and their ratio (Fv/Fm) when water level reduced from field capacity to 80, 50 and 35 per cent and high positive correlation was found between the fluorescence parameters and water level (Madkadze and Madkadze 1996). Chlorophyll fluorescence parameters namely Fv/Fm and Fm have also been suggested for screening of genotypes for drought resistance in pearl millet (Madkadge and Madkadge 1996) and wheat (Sayar *et al.* 2008). Though different physiological parameters at different growth stages have been earlier studied with a view to identify traits conferring drought tolerance, their heritability estimates need to be examined as already reported for seedling traits (Arulselvi and Selvi 2009). Thus, the present investigation was undertaken to study the genotypic variations in pearl millet under terminal water stress in relation to water status, chlorophyll fluorescence, net photosynthetic rate and nitrate reductase (NR) activity and to explore the possibility of using them for assessment of drought tolerance in important crops of arid regions.

MATERIALS AND METHODS

The present investigation was conducted in the net house with six genotypes of pearl millet including two landrace based population (Western Rajasthan population and Barmer population) and one variety CZP-9802 and three composites derived from non-land races (Pusa-266, ICTP-8203 and HHVBC) selected on the basis of their differential ability to yield under arid conditions. The genotypes were selected to cover the entire range of phenotype traits in good genetic background. Western Rajasthan population, Barmer population and CZP 9802 were early to medium maturing, high tillering and small panicles. On the other hand HHVBC represented type with extremely low tillering, very thick panicles and bold seed. ICTP 8203 and Pusa 266 were moderate in tillering with thick and medium-long panicles.

Two sets of pots for each genotype were maintained throughout the experimentation. Each set had 8 glazed pots. Under each set two plants of each genotype were raised in each glazed pot containing 40 kg loamy sand soil (Typic camborthids) having 7.1% clay, 5.6% silt, 63.1% fine sand and 24.1% coarse sand. The soil contained 0.28% organic carbon, 0.023% total nitrogen, 80 kg ha^{-1} available N, 12 kg ha^{-1} available P and 120 kg ha^{-1} available K. All pots were given a basal dose of 40 kg N ha^{-1} (through urea) and 40 kg P_2O_5 ha^{-1} (through single super phosphate) at the time of sowing. Soil moisture in the pots was maintained closer to field capacity (10% w/w) by regular watering until 40 days after sowing, when 50% flowering was observed in most of the genotypes. At this stage one set of pots under each genotype was subjected to water stress by withholding of water (for six days) till 50 per cent plants of each genotypes wilted. The other set of irrigated plants under each genotype served as control. Just prior to rewatering at this stage, observations were recorded, in quadraplicate on plant water potential (Ø plant) wherein plants were uprooted, obliquely cut at soil line and inserted in pressure chamber (PMS Instrument Co., USA). Thereafter, N_2 gas free of water vapor was passed under pressure till the appearance of xylem sap from the cut end. Relative water content (RWC) of leaves of each genotype was estimated according to the standard procedure and calculated using the formula: RWC (%) = (fresh weight – dry weight)/(saturated weight – dry weight)×100 (Slatyer and Mcllroy 1961). Ø plant and RWC were again measured 2 days after re-watering in both control and water stressed plants.

The rate of net photosynthesis was measured in two uppermost fully expanded leaves of intact plants using a LICOR-6200 portable photosynthetic system that simultaneously recorded observations on stomatal conductance. These measurements were made on 4 plants in each genotype between 10.30 to 12.00 hours in both control and drought stressed plants just prior to rewatering and 2 days later. At the same time chlorophyll fluorescence parameters namely Fv/Fm and Fm were measured in two uppermost fully expanded leaves of control and drought stressed plants in each genotype using Chlorophyll Fluorescence Meter (OS- 30P make).

The two uppermost fully expanded leaves from 4 pots (replicates) in each treatment were analyzed for the estimation of total chlorophyll (Arnon 1949) and *in vivo* estimation of NR activity in leaf discs using KNO_3 as substrate (Jaworski 1971). Both these estimations were made just prior to termination of water stress and 2 days after rewatering. Data on grain yield and dry matter of above ground biomass were recorded at harvest from 8 pots in each treatment. Data were subjected to analysis of variance adopting two factorial completely randomized designs where genotypes and water stress were the two variables. Data on grain yield under control and stress was also used to calculate the drought susceptibility index (DSI) of the genotypes following Fisher and Maurer (1978). Correlation of physiological traits with grain yield and their broad sense heritability was also worked out using standard procedures (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

Water stress significantly reduced grain and dry matter yield in all the pearl millet genotypes (Table 1). The magnitude of reduction varied considerably under different genotypes. The reduction in grain yield was more than 50 per cent in Barmer and Western Rajasthan population and 44.1% in the composite cv. ICTP-8203. On the contrary, composite Pusa-266 with only 13.2% and var. CZP-9802 with 26.2% reduction in grain yield under terminal drought. Thus, the latter two genotypes showed better drought tolerance than other genotypes in relation to grain yield (Table 1). Such genotypic variations are also well documented in pearl millet under field drought conditions (Kathju *et al.* 2001, Yadav 2010). Bieler *et al.* (1993) observed that pearl millet lines with longer grain filling periods under well-watered conditions had larger reductions in the duration of grain filling period and in final grain mass under drought. The higher reduction in grain yield of landrace-based population in the present study may also be possibly due to their longer grain filling periods. The data on dry matter production further revealed that the adverse effects of drought were more pronounced in long duration land races viz. Western Rajasthan and Barmer populations (30-31% reduction) as compared to composites Pusa-266, ICTP-9802 and HHVBC (11-15% reduction). However, in general the reductions were lesser in magnitude on DMP than grain yield because stress was imposed at the flowering stage when the vegetative growth phase was almost over. Results demonstrated that there are differences among genotypes for their ability to produce grain and stover which could be exploited in breeding program.

Table 1. Drought susceptibility index (DSI), grain yield and shoot dry matter of pearl millet genotypes subjected to water stress at flowering stage

Genotypes	DSI	Grain yield (g plant^{-1}) Control		Grain yield (g plant^{-1}) Water stress	Dry weight shoot (g plant^{-1}) Control		Dry weight shoot (g plant^{-1}) Water stress
West. Raj. Pop.	1.340	11.85		5.84	43.78		30.09
Barmer Pop.	1.353	8.47		4.13	39.08		27.39
CZP-9802	0.693	9.46		6.98	39.62		30.72
Pusa-266	0.348	8.96		7.78	32.26		28.40
ICTP-8203	1.166	10.08		5.63	41.03		34.86
HHVBC	1.001	7.94		4.93	42.08		37.14
Mean	-	9.46		5.88	39.64		31.43
LSD (p=0.05)		G	D	G x D	G	D	G x D
		0.82	0.47	1.16	2.28	1.31	3.22

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Exposure to water stress at the flowering stage significantly decreased plant water potential and relative water content in all the genotypes (Table 2). $Ø_{plant}$ ranged from –1.01 to –1.15 MPa in well-watered control plants and from –2.05 in cv. Western Rajasthan Population to –2.35 MPa in cv. ICTP-8203 under water stress. The reduction in water potential was associated with a significant decrease in RWC in all the genotypes but showed variation from 47.1% (cv. HHVBC) to 56.8% (cv. CZP-9802) showing genotypic variations in response to water stress. Genotype CZP-9802 with 31.2% and Barmer Population with 34.3% exhibited relatively less per cent reduction in RWC than Western Rajasthan populations (44.5%) and ICTP-8203 (43.2%). The RWC was completely normalized after 2 days of rewatering whereas $Ø_{plant}$ could not recover fully and values were lower than control plants in all the genotypes. Pusa – 266 and CZP – 9802 recorded maximum recovery upon re-watering in terms of $Ø_{plant}$. Water stress is known to decrease leaf water potential and RWC in different crops (Hsiao 1973) including pearl millet (Subramanian and Maheswari 1989). Genotypic differences have also been reported in response to terminal water stress (Afria and Shrikant 2004) as well as under rainfed conditions (Kathju *et al.* 2001).

A drastic reduction (more than 60 per cent) in net photosynthetic rate (P_N) and more than 80% reduction in leaf stomatal conductance (gs) observed under water deprivation in all the genotypes (Fig. 1 and Table 3), is a well known response to drought in higher plants (Hsiao 1973). However, highest reduction in ICTP-8203 (77.3%) followed by Barmer Population (74.5%) and HHVBC (73.4%) reflected significant genotypic variation in pearl millet. In contrast CZP-9802 and Pusa-266 showed comparatively less reduction in P_N (63-67%) as compared to respective controls. Furthermore, on re-watering the extent of recovery was also better in these two genotypes as compared to ICTP-8203 and HHVBC. Photosynthetic rate was higher in Pusa-266, CZP-9802 and ICTP-8203 compared to remaining genotypes. Western Rajasthan and Barmer populations that had lower photosynthetic rate under non stressed condition. ICTP – 8203, however, recorded maximum reduction upon stress besides least recovery upon re-watering.

Water stress induced decline in P_N was accompanied with a significant and drastic reduction in stomatal conductance. Similar effects of water stress had been reported in other crops like clusterbean (Kuhad and Sheoran 1986) and moth bean (Garg *et al.* 2004).

Table 2. Influence of water stress at flowering stage on plant water potential ($ø_{plant}$) and relative water content (RWC) of pearl millet genotypes

Genotypes	$ø_{plant}$ (-MPa)				RWC (%)			
	Stressed		Rewatered		Stressed		Rewatered	
	C	D	C	D	C	D	C	D
West. Raj. Pop.	1.01	2.05	1.15	1.75	86.7	48.1	84.4	85.2
Barmer Pop.	1.05	2.25	1.05	1.65	80.5	52.9	82.7	83.6
CZP-9802	1.08	2.20	1.10	1.35	82.5	56.8	85.2	86.7
Pusa-266	1.05	2.25	1.20	1.30	88.2	52.8	88.9	88.7
ICTP-8203	1.15	2.35	1.10	1.60	81.1	50.7	85.2	86.0
HHVBC	1.05	2.20	1.15	1.45	82.9	47.1	85.7	86.5
Mean	1.06	2.22	1.13	1.52	83.8	51.4	86.7	86.0
LSD (p=0.05)	G 0.09, D 0.05	G x D 0.13	G 0.13, D 0.09	G x D 0.22	G 2.7, D 1.6	G x D 3.8	G 2.2, D NS	G x D NS

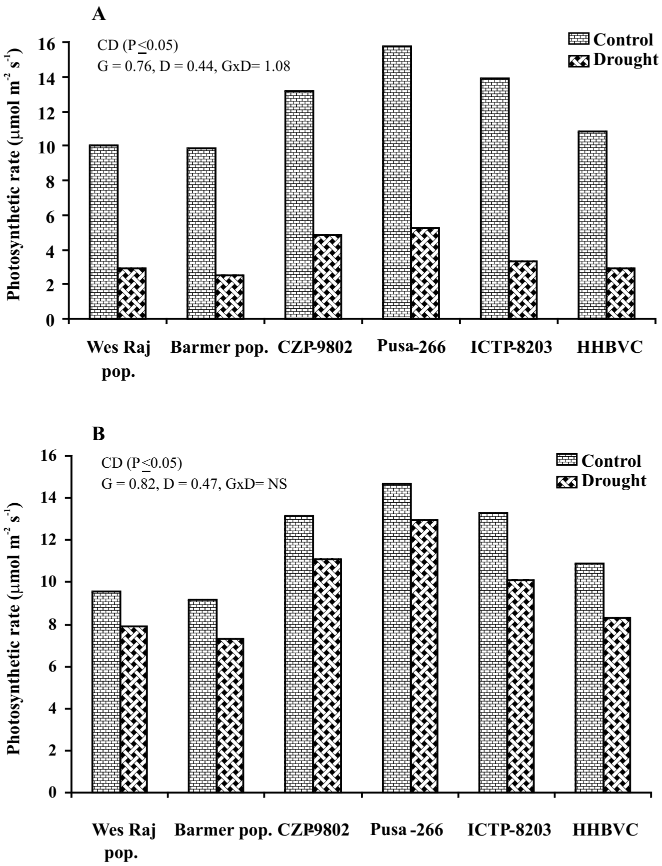

Fig. 1. Influence of water stress (A) and re-watering (B) at flowering stage on net photosynthetic rate of pearl millet genotypes under control and drought conditions.

Decreased photosynthesis under water stress has been attributed mainly to decreased leaf 'gs' due to reduced leaf turgor because of lowered RWC and plant water potential (Hsiao 1973). The maintenance of higher P_N and 'gs 'by certain genotypes in the present study (viz. Pusa-266 and CZP-9802) may be due to their high plant water status and capacity to recover upon re-watering. On the contrary, stomatal conductance in stressed plants was 40 to 50 per cent lower than the control plants in genotypes Western Rajasthan Population, HHVBC and ICTP-9802, even two days after re-watering. Though genotype Barmer Population recorded recovery comparable to Pusa – 266 and CZP – 9802 in terms of 'gs' it had lower P_N as such which along with stomatal conductance registered drastic reduction upon stress.

Water stress also caused a significant reduction in total chlorophyll content in all the genotypes (Table 3). The reduction was highest in Barmer population (43.0%), followed by 30.8% in Western Rajasthan population and 28.5% in ICTP-8203. On the contrary genotypes Pusa-266 and CZP-9802 experienced less decrease in chlorophyll content as compared to control plants. The recovery was above 90 per cent on rewatering of stressed plants in all genotypes except Barmer population where its chlorophyll content remained 26.3% lower than in the control plants. Such genotypic variation has earlier been reported in clusterbean (Garg *et al.* 1998) as well

Table 3. Influence of water stress at flowering stage on chlorophyll content and stomatal conductance of pearl millet genotypes

Genotypes	Total Chlorophyll (mg g^{-1}dw)				Stomatal conductance (cm s^{-1})			
	Stressed		Rewatered		Stressed		Rewatered	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought
West. Raj. Pop.	8.78	6.08	8.85	8.22	0.502	0.067	0.443	0.267
Barmer Pop.	11.35	6.47	11.38	8.39	0.532	0.053	0.425	0.330
CZP-9802	9.71	8.56	9.58	8.75	0.515	0.067	0.437	0.348
Pusa-266	11.91	10.84	11.55	10.71	0.425	0.080	0.440	0.350
ICTP-8203	10.49	7.50	9.55	8.91	0.520	0.041	0.438	0.260
HHVBC	8.79	6.58	8.34	7.35	0.353	0.057	0.340	0.170
Mean	10.17	7.67	9.88	8.72	0.475	0.061	0.421	0.288
LSD (p=0.05)	G 0.56 D 0.32	G x D 0.79	G 0.48 D 0.28	G x D 0.68	G 0.025 D 0.014	G x D 0.035	G 0.039 D 0.022	G x D 0.055

as in pearl millet under water limited field conditions (Kathju *et al.* 2001).

NR, the key enzyme for nitrate reduction in higher plants is known to be highly sensitive to water stress (Vyas *et al.* 1985). In the present study also NR activity was drastically reduced under water deficits and the reduction was as high as 96.1% in cv. HHVBC and more than 90% in remaining genotypes except Pusa-266 (84.7%) and CZP- 9802 (89.3%) as compared to control plants (Fig. 2). However, NR activity was quickly restored to normal on re-watering and after 2 days of re-watering, the enzyme activity was much higher than control plants in all the genotypes. This indicates that nitrogen metabolism in pearl millet plant has a capacity to recover from detrimental effects of water stress after the plants are re-watered. However, genotypic variations appeared in the extent of recovery as observed in the present study. Interestingly among the genotypes studied CZP-9802 and Pusa–266 recorded less reduction in NRA upon stress besides more per cent increase in its activity over control (57.7 to 60.3%) upon re-watering. In contrast the percent recovery was only 13.4 to 31.4% in other genotypes. Significant genotypic differences in NR activity under water stress had been reported earlier in both water stressed and rainfed pearl millet (Garg *et al.* 1981, Kathju *et al.* 2001) and clusterbean (Garg *et al.* 1998).

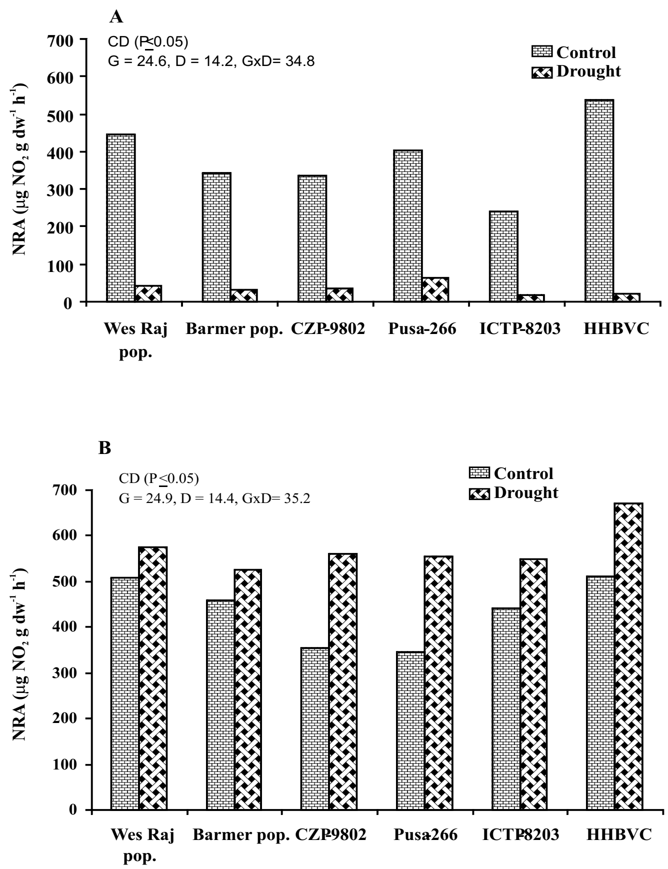

Fig. 1. Influence of water stress (A) and re-watering (B) at flowering stage on net photosynthetic rate of pearl millet genotypes under control and drought conditions.

The photochemical capacity of photosystem II (PS II) is normally measured by means of the ratio of variable (Fv) to maximum (Fm) chlorophyll fluorescence. In the present study observations recorded on Fv/Fm revealed that water stress caused a significant reduction in this ratio (Fv/Fm) in different genotypes (Table 4). The reduction was 29-39 % in HHVBC and Barmer Population and only 3.0 to 3.8% in Pusa-266 and CZP-9802, compared to well watered control plants. The data obtained on maximal fluorescence (Fm) also reflected similar trend (as for Fv/Fm ratio). Genotypic variations in response to water deficit, indicating varying degree of adverse effects of water stress on photosynthetic efficiency. Data clearly indicated that genotypes CZP-9802 and Pusa-266 were able to maintain higher Fv/Fm ratio under water deficits and were therefore capable of higher quantum efficiency. However, upon rewatering, Fv / Fm ratio of stressed plants was comparable to or higher than control plants probably because of enhanced variable fluorescence in all genotypes. Madakadze and Madakadze (1996) also observed decreased Fm and Fv/Fm ratio under decreasing water levels in pearl millet but these decreases were recovered within 24 hours of rewatering to field capacity. This suggested that chlorophyll fluorescence can be used as a non-destructive tool for screening of drought tolerance in hybrid *Pennisetum*. Genetic variability for Fv and Fv/Fm parameter has also been reported in wheat (Sayar *et al.* 2008) and many other crops (Sayeed 2003).

Correlations of physiological traits with grain yield in pearl millet are of great importance for selecting traits under diverse environments. Stomatal conductance by virtue of its effect on movement of carbon dioxide and water vapor across leaf affects transpiration, water balance and photosynthesis throughout the growing

Table 4. Influence of water stress at the flowering stage on variable to maximum fluorescence ratio (Fv/Fm) and maximum fluorescence (Fm) of pearl millet genotypes

Genotypes	Fv/Fm				Fm			
	Stressed		Rewatered		Stressed		Rewatered	
	C	D	C	D	C	D	C	D
West. Raj. Pop.	0.605	0.467	0.604	0.678	138.0	127.5	120.5	155.5
Barmer Pop.	0.669	0.474	0.610	0.710	149.0	126.5	107.2	112.0
CZP-9802	0.669	0.639	0.604	0.606	176.0	173.0	119.0	132.7
Pusa-266	0.654	0.635	0.627	0.610	138.0	129.0	115.7	108.7
ICTP-8203	0.691	0.517	0.586	0.671	166.0	131.5	117.0	143.5
HHVBC	0.666	0.409	0.628	0.550	151.5	132.0	146.2	114.5
Mean	0.658	0.523	0.610	0.610	150.2	135.5	121.0	127.8
LSD (p=0.05)	G D G x D 0.042 0.024 0.060		G D G x D 0.047 NS 0.067		G D G x D 17.6 10.2 24.9		G D G x D 18.8 10.8 26.6	

period. This along with other parameters like NR, chlorophyll content and fluorescence in turn are known to play significant role in yield accumulation. High correlation of chlorophyll fluorescence parameters with grain yield has also been reported in wheat (Sayar *et al*. 2008). Significant correlation of a character coupled with its high heritability indicates good genetic control and stability. Perusal of data revealed significant positive correlation of grain yield with all physiological parameters having significant differences except plant water potential with which it had, as expected logically, a negative correlation (Table 5). These physiological traits also had moderate to high heritability which implied less influence of environmental factors on them. Suggesting that selection for higher values of these parameters will be effective for developing drought tolerant lines in breeding program.

In conclusion the results of the present study revealed that genotypes Pusa-266 and CZP-9802 were more tolerant to terminal drought as compared to ICTP-8203, Barmer and Western Rajasthan populations. They were characterized by high yields under water stress conditions. The tolerant genotypes also invariably reflected more favorable plant water status, higher net photosynthesis and less metabolic derangements in terms of chlorophyll content and fluorescence parameters. So, they may also serve as sources of germplasm for breeding for drought tolerance in pearl millet. Additionally a large number of genotypes of this crop can also be screened for drought tolerance using these physiological parameters.

Table 5. Broad sense heritability and correlation of different physiological traits with grain yield of pearl millet

Parameters	Correlation** Coefficient	Broad sense Heritability
Plant water potential	-0.778	49.3
Relative water content	0.810	61.8
Net photosynthetic rate	0.763	48.7
Chlorophyll	0.631	75.8
Stomatal conductance	0.838	47.4
Variable to maximum fluorescence (Fv/Fm)	0.687	59.3
Maximum fluorescence (Fm)	0.365	45.5
Nitrate reductase activity	0.729	49.9

** Significant at 1 % level except Fm that is at 5 %

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