Thermotolerance of pearl millet and maize at early growth stages: growth and nutrient relations

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Abstract

Thermotolerance of pearl millet (*Pennisetum glaucum* cv. ICMV-94133) and maize (*Zea mays* cv. Golden) was assessed at germination and vegetative stage. Final percentage of germinated seeds and rate of germination (number of days to 50 % germination) decreased due to high temperature (45 °C) similarly in the both species. In contrast, at the vegetative stage, high temperature (38/27 °C) caused a significant reduction in shoot dry mass of maize, whereas this attribute remained almost unchanged in pearl millet. Relative growth rate and net assimilation rate (NAR) increased significantly in pearl millet due to high temperature, but in contrast, in maize NAR was slightly reduced. Concentrations of N, P, and K in the shoots of both species increased at high temperature, but N accumulation was more pronounced in pearl millet than in maize. High temperature caused a marked increase in both shoot and root Ca^{2+} concentration in maize, but it did not affect that of pearl millet. S concentration in the shoots of maize decreased significantly due to high temperature, whereas that in pearl millet remained unaffected. Shoot Na^+ concentration of both species was not significantly affected by high temperature. High temperature caused a significant increase in uptake of N, P, and K^+ in pearl millet, but the uptake of Ca^{2+}, Mg^{2+}, Na^+ and S remained unaffected in this species. In contrast, in maize, a significant increase in uptake of K^+ and Ca^{2+}, and a decrease in uptake of N, S, Mg^{2+}, and Na^+ were found at high temperature. Overall, maize showed lower tolerance to high temperature compared with pearl millet.

Additional key words: germination, high temperature, inorganic nutrients, vegetative stage.

Introduction

Heat stress or high temperature, is prominent among the cardinal ecological factors that determine crop growth and productivity in some regions (Al-Khatib and Paulsen 1999, Smith *et al.* 1999, Huang and Gao 2000, Swanton *et al.* 2000). Extreme temperatures can also limit plant survival and reproduction. In most of the field crops, temperature above 40 °C causes heat injury, severely limits photosynthesis and alters protein metabolism by causing protein breakdown, protein denaturation, enzyme inactivation and other effects (Nakamoto and Hiyama 1999).

Pearl millet needs high temperature in order to achieve rapid growth, especially in the final stages of plant development. Optimum temperature for its development fluctuates between 33 and 34 °C. Final emergence, rate of emergence and seedling growth increased with temperature up to 33 °C. Growth has been found to be slowest at 19.5 °C and fastest at 31.0 °C (Maiti and Wesche-Ebeling 1997). In contrast, maize shows peak germination at 20 - 30 °C, whereas its optimal growth occurs at 18 - 21 °C (Hughes 1979). Temperature of 40 °C or greater has a detrimental effect on maize germination and emergence (Sutcliffe 1977). Therefore, pearl millet is more tolerant to high temperature than maize.

Increasing temperature increases root growth allowing plant roots to explore a larger volume of soil. This increases the absorption of phosphorus (Föhse *et al.* 1988). High temperature also increases the rate of physiological processes involved in plant growth, which determine nutrient absorption (Tollenaar 1989). In a study with maize roots, Bravo and Uribe (1981) examined that uptake of both potassium and phosphorus increased significantly with increase in temperature and the maximum uptake of potassium was observed at 32 °C and that of phosphorus at 38 °C. In contrast, Muldoon

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Abbreviations: LAR - leaf area ratio; NAR - net assimilation rate; RGR - relative growth rate; RIL - relative increase in leaf area.
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et al. (1984), while examining the growth and mineral composition of maize at different temperatures during vegetative stage, found that plant height, dry biomass, leaf area, and number of leaves per plant increased consistently with increasing temperature up to 32/28 °C (day/night). However, leaf N decreased sharply, S concentration decreased slightly, whereas Na^+ concentration was not affected by the increase in temperature. Pattern of diurnal uptake of nitrate in maize seedlings was assessed at varying day/night temperatures of 30/20, 30/30, and 35/35 °C (Polisetty and Hageman 1989). They recorded highest nitrate uptake and dry matter accumulation at 30/30 °C.

In view of all these reports it is evident that uptake of different nutrients is affected differently even at the same high temperature regime. In addition, little information is available about the pattern of nutrient uptake and utilization efficiency in species or cultivars differing in thermotolerance. In the present study, we have examined the nutrient relations of maize (relatively sensitive to high temperature) with those of pearl millet, known for its high thermotolerance. We hypothesized that crops differing in thermotolerance have different pattern of nutrient uptake and accumulation under high temperature during active periods of growth. Thus, the principal objective to undertake the present study was to draw relationships between pattern of uptake and accumulation of major nutrients in pearl millet and maize, and their differential thermotolerance to elucidate the mechanism of nutrient acquisition and utilization under high temperature during the early vegetative growth stage. In addition, thermotolerance of the two species was examined during the germination stage since this stage is considered as the most sensitive (Ashraf *et al.* 1994).

Materials and methods

The seed of pearl millet [*Pennisetum glaucum* (L.) R. Br.] cv. ICMV-94133 was obtained from the Department of Botany, University of Agriculture, Faisalabad, whereas that of cv. Golden of maize (*Zea mays* L.) from the Nuclear Institute for Agriculture and Biology, Faisalabad.

Germination experiment: For the determination of final germination percentage and rate of germination, the experiment was conducted in Petri plates in temperature controlled growth chambers. The Petri plates were arranged in a completely randomized design with six replicates. Prior to the sowing of seeds, the Petri plates were lined with filter paper, and moistened with 5 cm^3 of distilled water. For high temperature treatment, the Petri plates were transferred to growth chamber set at 45 °C. The control Petri plates were kept at room temperature (25 °C) in a growth chamber. The number of seeds germinated was recorded daily up to day 8 of sowing. A seed was considered germinated when both radicle and coleoptile had emerged. Final percent germination was calculated from the number of seeds germinated on day 8 of sowing. Rate of germination was calculated as number of days to 50 % germination.

Glasshouse experiment: A glasshouse experiment was conducted during August to November 2000. The soil used in the experiment had the following physico-chemical characteristics: Electric conductivity (ECe) of the soil saturation extract 1.34 mS cm^{-1}, pH of soil saturation extract 7.18, textural class sandy loam, saturation percentage 32.80, extractable nutrients [mg kg^{-1}(dry soil)]: K^+ 101.05, Ca^{2+} 52.78, Mg^{2+} 49.00, N 107.00, P 24.00, S 19.48. The chemical analysis of the soil was carried out according to the methods described by US Salinity Laboratory Staff (1954). Twenty seeds of each crop were sown in each pot (29 cm length and 27 cm diameter) containing 8 kg of soil. The pots were arranged in a completely randomized design with 6 replicates. Thinning was done 10 days after germination to keep 10 seedlings in each pot. High temperature treatment was applied by placing 2-weeks-old plants inside a partially closed glasshouse. The control plants experienced ambient conditions. The temperatures of both these conditions were recorded regularly and mean day/night air temperature was found to be 38/27 °C for heat stress and 31/27 °C for control treatment. The high temperature 38 °C used in this study was so that maize plants could grow and produced some biomass. A temperature higher than this, could have killed all the maize plants. The average relative humidity was 55 % and photoperiod 11 - 12 h. The pots were arranged in a completely randomized design with two treatments and six replicates. Normal irrigation water was used for watering the plants throughout the experiment.

Two plants were harvested from each pot 21 and 42 d after treatment. Plants were uprooted carefully and washed with distilled water. Data for the following parameters were recorded: fresh and dry masses of shoot per plant, leaf area per plant, leaf area ratio, relative increase in leaf area, relative growth rate, net assimilation rate.

Determination of mineral composition: The dried ground shoot and root material (0.1 g) was digested in sulfuric acid + hydrogen peroxide mixture according to the method of Wolf (1982). The volume of extracts was made 50 cm^3 with distilled water, filtered and used for the determination of mineral nutrients. Na, K and Ca were determined by flame photometer (*Jenway PFP7, Gransmore Green*, Dunmow, UK). Phosphorus was determined using a spectrophotometer (*Hitachi-220*, Tokyo, Japan) following Jackson (1962). Total nitrogen was estimated by the Kjeldhal apparatus (Bremner 1965). Sulfur was determined following the protocol of US Salinity Laboratory Staff (1954) on the basis that SO_4^{2-} is precipitated in dilute HCl with $BaCl_2$ under controlled conditions to form $BaSO_4$ crystals of uniform size. Suspension was measured at 420 nm and SO_4^{2-} concentration was obtained from standard curve. Mg^{2+} was determined on an atomic absorption spectrophotometer (*Analyst-100*, *Perkin Elmer*, Beaconsfield, Germany).

Statistical analysis of data: Analysis of variance following Steel and Torrie (1980) was used. The mean values were compared with the Least Significant Difference (LSD) test following Snedecor and Cochran (1980).

Results

Final percentage of germinated seeds and rate of germination (days to 50 % germination) of pearl millet and maize decreased at high temperature (Table 1). However, species did not differ significantly in either of these two variables.

Table 1. Germination percentage and rate of germination (days to 50 % germination) of pearl millet and maize when seeds were subjected for 8 d to 25 (control) or 45 °C (heat stress). Means ± SE, *n* = 6; S - species, T - treatments, NS - non-significant.

	Species	25 °C	45 °C
Germination percentage	pearl millet	75.78 ± 3.39	44.28 ± 3.56
	maize	67.18 ± 4.10	55.26 ± 6.39
		(S × T) = NS	
Rate of germination	pearl millet	2.08 ± 0.14	3.65 ± 0.38
	maize	2.34 ± 0.18	3.04 ± 0.55
		(S × T) = NS	

At the vegetative stage, shoot dry mass of maize decreased significantly at high temperature, whereas shoot length increased. In contrast, both the attributes remained almost unchanged in pearl millet at high temperature (Table 2). Shoot fresh mass also remained unaffected in both species at high temperature. Relative growth rate (RGR) and net assimilation rate (NAR) increased significantly in pearl millet at high temperature, but in contrast, in maize NAR was slightly reduced at high temperature (Table 2). Although relative increase in leaf area (RIL) increased in both species due to high temperature, it was more pronounced in pearl millet. Leaf area ratio (LAR) increased in maize at high temperature, whereas that of pearl millet remained unaffected (Table 2).

N concentration in the shoots and roots of both pearl millet and maize increased significantly due to high temperature, but this increase was more pronounced in the shoots of pearl millet than that in maize (Table 3). P concentration in the shoots and roots of pearl millet increased significantly due to high temperature, but in contrast, in maize shoot P increased and root P decreased considerably at high temperature (Table 3). Shoot K^+ proportionately increased in both species at high temperature, but high temperature did not cause a significant effect on root K^+ of both species (Table 3). High temperature caused a marked increase in both shoot and root Ca^{2+} of maize, but did not affect that of pearl millet (Table 3). High temperature did not cause a significant effect on Mg^{2+} concentration in shoots and roots of both species, and the species also did not differ significantly for this variable (Table 3). S concentration in the shoots of maize decreased significantly at high temperature, whereas that in the roots increased. However, high temperature did not cause any significant effect on S concentration of both shoots and roots of pearl millet (Table 3). Shoot Na^+ concentration of both the species was not significantly affected by high temperature, however, high temperature caused a significant effect on root Na^+. Species did not differ significantly with respect to shoot Na^+ (Table 3), but a significant increase in root Na^+ was found in both species. Pearl millet accumulated considerably higher Na^+ in the roots than maize under both temperature regimes (Table 3).

Discussion

Exposure of seeds of pearl millet and maize to constant heat stress (45 °C) for a period of 8 d proved to be detrimental since rate of germination and final germination percentage of both the species were markedly decreased. In addition, the species response to high temperature at the germination stage was not different from each other. Lack of difference between the species could be due to the high temperature, 45 °C to which they were exposed. In view of some earlier reports the optimum temperature for seed germination of both

Table 2. Different growth attributes of pearl millet and maize at the seedling stage when 14-d-old plants were subjected for 42 d to 31 (control) or 38 °C (heat stress). Means ± SE, n = 6. Means with different letters in each column (a-b) and each row (x-y) differ significantly at the 5 % level (S - species, T - treatments, NS - non-significant).

Attribute	Species	31 °C	38 °C
Shoot fresh mass [g]	pearl millet	16.80 ± 1.37	16.32 ± 0.66
	maize	25.67 ± 1.45	23.95 ± 1.02
		(S × T) = NS	
Shoot dry mass [g]	pearl millet	3.50 ± 0.22 ax	3.35 ± 0.17 ax
	maize	6.13 ± 0.35 bx	4.16 ± 0.32 by
		(S × T) = 0.71	
Shoot length [cm]	pearl millet	49.95 ± 1.70 ax	53.24 ± 1.17 ax
	maize	45.82 ± 1.38 bx	59.82 ± 0.85 by
		(S × T) = 4.00	
Plant leaf area [cm^2]	pearl millet	741.54 ± 56.2	698.46 ± 81.2
	maize	1735.38 ± 134.3	1430.76 ± 106.2
		(S × T) = NS	
LAR [cm^2 g^{-1}]	pearl millet	226.25 ± 19.3	220.00 ± 14.3
	maize	301.25 ± 21.2	348.87 ± 16.2
		(S × T) = NS	
RGR [g g^{-1} d^{-1}]	pearl millet	0.102 ± 0.017	0.196 ± 0.351
	maize	0.150 ± 0.020	0.133 ± 0.029
		(S × T) = NS	
NAR [mg cm^{-2} d^{-1}]	pearl millet	0.199 ± 0.180 ax	0.270 ± 0.024 ay
	maize	0.182 ± 0.151 ax	0.155 ± 0.018 bx
		(S × T) = 0.046	
RIL [cm^2 d^{-1}]	pearl millet	0.024 ± 0.008	0.035 ± 0.009
	maize	0.037 ± 0.004	0.043 ± 0.003
		(S × T) = NS	

species is much lower than that used in the present study (Hughes 1979, Mortlock and Vanderlip 1989). For example, Maiti and Wesche-Ebeling (1997) observed an increase in seed germination of pearl millet from 10 °C to an optimum at 33 - 34 °C and then a decline to zero at 45 - 47 °C.

Heat stress (38 °C) applied at the vegetative stage appeared to be a significant constraint for the vegetative growth of maize since shoot dry mass and NAR of this species were adversely affected due to this temperature. The reduction in growth at high temperature in maize may be due to reduction in photosynthesis (Berry and Björkman 1980). Also in wheat, a species sensitive to high temperature like maize, leaf photosynthesis and Hill reaction declined earlier than other processes such as N assimilation (Al-Khatib and Paulsen 1999). In contrast, in pearl millet biomass production and leaf area remained unaffected under high temperature, but relative growth rate (RGR) and NAR increased considerably. These results are the manifestation of relatively higher thermotolerance of pearl millet compared with maize. In the present study only one cultivar of each species was examined and other cultivars could show different thermotolerance. Thus the conclusions presented here should be interpreted with some caution.

It is known that plants use inorganic minerals for nutrition, but many factors including high temperature influence nutrient uptake in plants (Marschner 1995, Taiz and Zeiger 2002). In the present study, it was found that concentrations of N in the shoots and roots and N uptake in pearl millet increased considerably, whereas in maize, N uptake decreased at high temperature. High accumulation of N in pearl millet is quite parallel to what has earlier been reported in rice that N concentration in leaves increased markedly at high soil temperature (Bhattacharya and De Datta 1971). Thus, high thermotolerance of pearl millet could be related to its high N uptake and accumulation in the tissues (Mengel and Kirkby 1987, Marschner 1995). However, in maize, high temperature significantly caused a reduction in N uptake but the overall N accumulation in leaves was not markedly affected due to high temperature. Also Polisetty and Hageman (1989) found a low N uptake and dry matter accumulation in maize at day/night temperature 35/35 °C.

Although leaf K^+ content and K^+ uptake increased significantly in both the species, the extent of these two K^+ attributes was markedly higher in pearl millet than that in maize. Almost similar results were earlier reported by Place *et al.* (1971) working with rice. Since K^+ plays important role in water balance, stomatal regulation, and many others, the higher accumulation and uptake of K^+ in pearl millet may also have contributed to higher growth of pearl millet than that of maize at high temperature.

Muldoon *et al*. (1984) found that S concentration in maize decreased slightly at high temperature, whereas Na^+ concentration was not affected . Similar results were recorded in the present study, although root Na^+ in maize increased significantly at high temperature.

In conclusion, maize exhibited lower tolerance to high temperature compared with pearl millet on the basis of growth performance. The low thermotolerance of maize was found to be associated with low uptake and accumulation of N, P, and K^+ in plant tissues at high temperature.

Table 3. Nutrient concentration [mg g^{-1} (d.m.)] in shoots and roots of pearl millet and maize at the vegetative stage when 14-d-old plants were subjected for 42 d to 31 (control) or 38 °C (heat stress). Means ± SE, *n* = 6. Means with different letters in each column (a-b) and each row (x-y) differ significantly at the 5 % level (S - species, T - treatments, NS - non-significant).

Nutrient	Species	Shoot 31 °C	Shoot 38 °C	Root 31 °C	Root 38 °C
N	pearl millet	8.87 ± 0.54 ax	14.70 ± 0.33 ay	6.53 ± 0.27	8.28 ± 0.38
	maize	12.10 ± 0.45 bx	13.30 ± 0.37 by	6.76 ± 0.31	9.56 ± 0.42
		(S × T) = 1.14			
P	pearl millet	2.50 ± 0.14	4.39 ± 0.29	1.92 ± 0.09 ax	3.91 ± 0.27 ay
	maize	3.74 ± 0.19	5.11 ± 0.29	10.54 ± 0.49 bx	5.63 ± 0.27 by
		(S × T) = NS			
K^+	pearl millet	18.50 ± 1.72	27.05 ± 1.42	9.55 ± 0.91	9.55 ± 0.37
	maize	12.66 ± 1.39	22.08 ± 1.08	8.71 ± 0.65	7.03 ± 0.47
		(S × T) = NS			
Ca^{2+}	pearl millet	2.82 ± 0.21 ax	2.93 ± 0.33 ax	0.88 ± 0.07 ax	1.03 ± 0.03 ax
	maize	1.35 ± 0.09 bx	2.90 ± 1.17 ay	1.02 ± 0.15 ax	1.73 ± 0.17 by
		(S × T) = 0.59			
Mg^{2+}	pearl millet	9.15 ± 1.03	7.70 ± 0.90	9.41 ± 0.88	11.39 ± 0.98
	maize	6.15 ± 0.53	6.73 ± 1.00	8.35 ± 0.90	9.43 ± 1.08
		(S × T) = NS			
S	pearl millet	5.95 ± 0.29 ax	5.49 ± 0.35 ax	5.65 ± 0.25 ax	5.20 ± 0.36 ax
	maize	7.40 ± 0.35 bx	4.75 ± 0.29 ay	4.72 ± 0.26 bx	6.29 ± 0.24 by
		(S × T) = 0.87			
Na^+	pearl millet	2.43 ± 0.43	2.49 ± 0.10	6.37 ± 0.31	8.29 ± 0.75
	maize	2.79 ± 0.19	2.70 ± 0.28	17.18 ± 1.53	21.45 ± 1.14
		(S × T) = NS			

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