

Growth and photosynthetic characteristics in pearl millet under water stress and different potassium supply

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Abstract

Influence of supra-optimal concentrations of K on growth, water relations, and photosynthetic capacity in pearl millet under severe water deficit conditions was assessed in a glasshouse. Nineteen-days-old plants of two lines, ICMV-94133 and WCA-78, of *Pennisetum glaucum* (L.) R.Br. were subjected for 30 d to 235.0, 352.5, and 470.0 mg(K) kg⁻¹(soil) and two water regimes (100 and 30 % field capacity). Increasing K supply did not alleviate the effect of water deficit on the growth of two lines of pearl millet since additional amount of K in the growth medium had no effect on shoot dry mass, relative growth rate, plant leaf area, net assimilation rate, or leaf area ratio, although there was significant effect of drought stress on these variables. Soil moisture had a significant effect on net photosynthetic rate (P_N), transpiration rate, stomatal conductance, and water use efficiency of both pearl millet lines, but there was no significant effect of varying K supply on these variables. In WCA-78 an ameliorative effect of increasing supply of K on P_N was observed under water deficit. Chlorophyll (Chl) *a* and *b* contents increased significantly in both lines with increase in K supply under well watered conditions, but under water deficit they increased only in ICMV-94133. Chl *a/b* ratios were reduced significantly in WCA-78 with increasing K supply under both watering regimes, but by contrast, in ICMV-94133 this variable was decreased only under water stress. Leaf water potential and osmotic potential of both lines decreased significantly with the imposition of drought. Leaf pressure potential in both lines increased with increase in K supply under water stress. Contents of total free amino acids in the leaves of both pearl millet lines increased significantly with increase in K supply under water stress. Potassium supply had no effect on leaf soluble sugars or soluble proteins. Considerable osmotic adjustment occurred in pearl millet plants experiencing water deficit under high K supply.

Additional key words: drought; leaf area; net assimilation rate; net photosynthetic rate; relative growth rate; stomatal conductance; supra-optimal nutrition; transpiration rate; water potential; water use efficiency.

Introduction

The growth of most crops is significantly inhibited by potassium deficiency since potassium is vital for many physiological phenomena, the most prominent of which are osmoregulation, respiration, photosynthesis, protein synthesis, and stomatal movement.

The lower tolerance of K-deficient plants to drought can be primarily attributed to the role of K in stomatal regulation and in osmotic adjustment. An increase in the external K concentration considerably stimulated CO₂ fixation in isolated intact spinach chloroplasts (Pflüger and Cassier 1977). In wheat, K supply supported maximal photosynthesis under well-watered conditions, but

not under water deficit (Sen Gupta *et al.* 1989). However, in the same study the inhibition of photosynthesis in drought-stressed plants was much less severe when they were supplied with 6 mM K. This concentration of K is considered adequate for normal growth of many crop species (Epstein 1972, Sen Gupta *et al.* 1989). However, the hypothesis of the present study was that supra-optimal K concentrations (9 and 12 mM) can alleviate the inhibitory effects of drought on growth, photosynthesis, and other related attributes in pearl millet (*Pennisetum glaucum*), a potential forage and grain crop of drylands (Ashraf *et al.* 2001).

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Materials and methods

Seeds of two lines (ICMV-94133 and WCA-78) of pearl millet [*P. glaucum* (L.) R.Br.] were obtained from the Maize and Millet Research Station, Yousafwala, District Sahiwal, Pakistan. All seed samples were surface sterilised in 5 % sodium hypochlorite solution for 10 min before sowing. The experiment was carried out in a naturally-lit glasshouse at the Nuclear Institute for Agriculture and Biology, Faisalabad, Pakistan (latitude 31°30'N, longitude 73°10'E, and altitude 213 m), where the average PAR measured at noon ranged from 929 to 1 760 $\mu\text{mol m}^{-2} \text{s}^{-1}$, day/night relative humidity was 28/54 %, and temperature was 44/31 °C. In June 1999, 15 seeds of each line were sown randomly about 5 mm deep in plastic pots (25×25.5 cm) which contained 8.0 kg sandy loam soil (pH = 7.76, electrical conductivity = 2.73 dS m^{-1}). After the emergence of seedlings the plants were thinned to nine in each pot. All the pots were irrigated for 34 d with water after which time K treatments began. The treatments with K_2SO_4 were 235.0, 352.5, or 470.0 mg kg^{-1} (dry soil) in half-strength Hoagland's nutrient solution without K. At the same time drought was imposed by maintaining the soil moisture at 30 % field capacity, whereas the well-watered pots were maintained at full field capacity. The moisture content was monitored daily by weighing the pots. The experiment was arranged in a completely randomised design with three replicates. Plants were harvested 15 and 30 d after the start of treatments. Just before the second harvest the following physiological parameters were measured.

Leaf water potential and its components: A fully expanded youngest leaf (third from the top) was excised from each plant at 08.00 and the leaf water potential was measured with a Scholander type pressure chamber (Arimad-2, ELE International, Tokyo, Japan). A proportion of the leaf used for water potential determination was frozen for two weeks, thawed, and the frozen sap was extracted by crushing the material with a metal rod. After centrifugation (8 000×g) for 4 min, the sap was used directly for osmotic potential determination in a freezing point depression osmometer (*Osmollette-S 4002*, Precision System, Natick, USA). Leaf pressure potential was calculated as the difference between leaf osmotic potential and water potential.

Chlorophyll content was determined by the method of Witham *et al.* (1971). Fresh leaves (1 g) were triturated in 80 % acetone. The absorbance of the extracts was measured at 645, 652, and 663 nm using a spectrophotometer *U-2000* (Hitachi Instruments, Tokyo, Japan).

Soluble proteins and free amino acids: Total soluble proteins were determined as described by Lowry *et al.* (1951). Fresh leaf material (0.2 g) was homogenised in 4 cm^3 of sodium phosphate buffer (pH 7.0) and centri-

fuged. The extracts were treated with appropriate reagents and the absorbances were read at 620 nm. Total free amino acids were determined following Hamilton and Van Slyke (1943). Sample extract (1 cm^3) was treated with 1 cm^3 of 10 % pyridine and 1 cm^3 of 2 % ninhydrin solution. Absorbances were read at 570 nm.

Total soluble sugars were determined following Yemm and Willis (1954). 0.1 g of well ground dry material was homogenised in hot 80 % ethanol and centrifuged at 2 900×g. The residue was retained which was repeatedly washed with 80 % ethanol to remove all the traces of soluble sugars. The filtrate obtained was reacted with anthrone reagent. Absorbance was read at 625 nm.

Gas exchange characteristics: Instantaneous measurements of net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were made on fully expanded youngest leaf of each plant (third leaf from top) using an open system portable infrared gas analyser *LCA-4* (Analytical Development Co., Hoddesdon, England). Measurements were performed from 09.00 to 11.00 (flow of air per unit leaf area 404.8 $\text{mmol m}^{-2} \text{s}^{-1}$, atmospheric pressure 99.2 kPa, water vapour pressure into chamber ranged from 1.12 to 1.22 kPa, PAR at leaf surface up to 1 063 $\mu\text{mol m}^{-2} \text{s}^{-1}$, temperature of leaf up to 34.9 °C, ambient temperature ranged from 32.3 to 37.9 °C, ambient CO_2 concentration 354 $\mu\text{mol mol}^{-1}$). Stomatal conductance of the same leaves was measured with an automatic porometer (*MK3*, Delta-T Devices, Burwell, Cambridge, England).

After all these measurements, the plants were harvested. Plant roots were removed carefully from the soil and then were washed for 2-3 min in distilled water. Fresh masses of shoots and roots of all the plant samples were recorded. Samples were then dried at 65 °C for one week and dry masses recorded.

The following growth attributes were calculated using the formulae listed below:

Leaf area ratio (LAR) = leaf area per plant/dry mass of shoot [$\text{cm}^2 \text{kg}^{-1}$]

Relative growth rate (RGR) = $(1/M) \times (dM/dt)$ [$\text{kg kg}^{-1} \text{d}^{-1}$]
where M = dry mass of shoot, dM = difference in dry masses of shoots at two time intervals (15 and 30 d), and dt = difference in time [d].

Net assimilation rate (NAR) = $(M_2 - M_1) (\log_e L_2 - \log_e L_1) / (t_2 - t_1) (L_2 - L_1)$

where M_2 and M_1 are dry masses, and L_2 and L_1 are leaf areas of shoots at times t_1 and t_2 (15 and 30 d, respectively).

Statistical analysis of data: Analysis of variance for all the parameters was computed using a *COSTAT* computer package (*CoHort Software*, Berkeley, USA). The least significant differences between the mean values were calculated following Snedecor and Cochran (1980).

Results

Increased K supply to 19 d-old plants of two lines of pearl millet for a period of 30 d had no significant effect on shoot fresh and dry matters, leaf area per plant, LAR,

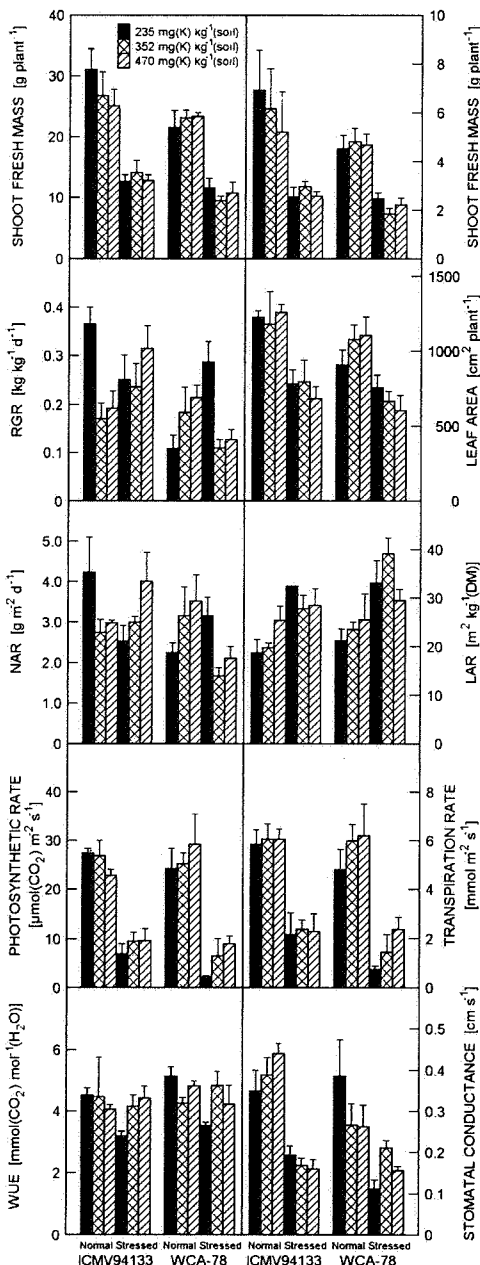


Fig. 1. Growth attributes and gas exchange characteristics of two lines of pearl millet when 19-d-old plants were subjected for 30 d to different K supply [235.0, 352.5, or 470.0 mg kg⁻¹(soil)] under well watered or drought conditions (soil moisture 100 or 30 % of full capacity). Normal = well-watered; stressed = drought stressed.

RGR, or NAR, although water deficit significantly decreased the earlier three growth variables (Fig. 1). However, lines differed significantly for all these variables except NAR ($p < 0.01$). Interactions of different factors were non-significant reflecting that lines had similar response to varying K supply or watering regimes.

Water deficit caused a significant decline ($p < 0.001$) in P_N , g_s , and E of both pearl millet lines (Fig. 1), but in contrast, there was no significant effect of varying soil K levels on these variables. Comparison of the lines shows that there was an increasing trend in P_N and E in WCA-78 with increase in K supply under both well watered and water deficit conditions, but in contrast, such pattern was not found in ICMV-94133 (Fig. 1). Values of g_s in ICMV-94133 increased and in WCA-78 decreased with increasing supply of K under well-watered conditions (Fig. 1), but there was a slight decrease in this variable in the former line under water deficit. However, patterns of increase or decrease in WUE at watering regimes or external K levels were not consistent in both lines (Fig. 1).

Both lines of pearl millet differed significantly only in Chl *a* content (Table 1). Chl *a* and Chl *b* contents increased significantly in both lines with increase in K supply under well-watered conditions, but under water deficit they increased only in ICMV-94133. Chl *a/b* ratio was reduced significantly in WCA-78 with increasing supply of K under both watering regimes, but by contrast, in ICMV-94133 this variable was decreased only under water deficit (Table 1).

Leaf water potential and osmotic potential of both lines decreased significantly with the imposition of drought (Table 1). However, in ICMV-94133 there was a significant decrease in leaf water potential with increase in K supply under well-watered conditions, whereas in WCA-78 no such decrease was found under either watering treatment. Leaf osmotic potential decreased significantly with increasing supply of K under water deficit, but under well-watered conditions such decrease was observed only in ICMV-94133. Pressure potential in both lines increased with increase in soil K level under both watering regimes (Table 1).

Watering regimes had significant effect on contents of soluble sugars, soluble proteins, and total free amino acids in the leaves of both lines of pearl millet, but external K levels had significant effect only on free amino acids (Table 2). Contents of leaf soluble proteins and total free amino acids increased in ICMV-94133 with increasing supply of K under well-watered conditions, but in contrast, in WCA-78 such increase in these variables was found under both watering treatments.

Table 1. Chlorophyll (Chl) contents and water relation parameters of two lines of pearl millet when 19 d-old plants were subjected for 30 d to varying K supply [235.0, 352.5, or 470.0 mg kg⁻¹(soil)] under well-watered or drought conditions.

Parameter	Line	Well-watered			Drought-stressed		
		235.0	352.5	470.0	235.0	352.5	470.0
Chl <i>a</i> [g kg ⁻¹ (FM)]	ICMV94133	0.120±0.020	0.220±0.006	0.290±0.006	0.210±0.048	0.250±0.043	0.310±0.003
	WCA-78	0.150±0.029	0.300±0.006	0.300±0.006	0.280±0.012	0.280±0.026	0.270±0.003
Chl <i>b</i> [g kg ⁻¹ (FM)]	ICMV94133	0.050±0.013	0.090±0.003	0.150±0.014	0.110±0.040	0.170±0.064	0.240±0.009
	WCA-78	0.060±0.007	0.160±0.015	0.200±0.058	0.200±0.080	0.200±0.058	0.180±0.020
Chl <i>a b</i>	ICMV94133	2.33±0.167	2.65±0.167	2.01±0.168	2.11±0.242	1.83±0.404	1.29±0.035
	WCA-78	2.69±0.352	1.92±0.156	1.68±0.358	2.35±0.058	1.52±0.392	1.53±0.040
Water potential [-MPa]	ICMV94133	0.98±0.03	1.12±0.09	1.30±0.08	1.98±0.12	2.02±0.08	1.96±0.11
	WCA-78	1.12±0.04	1.14±0.04	1.19±0.02	1.95±0.03	1.92±0.01	1.87±0.04
Osmotic potential [-MPa]	ICMV94133	1.07±0.03	1.24±0.06	1.51±0.04	2.19±0.21	2.25±0.13	2.25±0.10
	WCA-78	1.35±0.07	1.24±0.04	1.28±0.04	2.10±0.18	2.19±0.13	2.25±0.05
Pressure potential [MPa]	ICMV94133	0.090±0.015	0.125±0.068	0.210±0.068	0.288±0.031	0.306±0.014	0.300±0.078
	WCA-78	0.230±0.090	0.100±0.040	0.260±0.130	0.328±0.044	0.367±0.075	0.388±0.075

Table 2. Contents of soluble sugars, soluble proteins, and total free amino acids in the leaves of two lines of pearl millet when 19 d-old plants were subjected for 30 d to varying K supply [235.0, 352.5, or 470.0 mg kg⁻¹(soil)] under well-watered or drought conditions.

Parameter	Line	Well-watered			Drought-stressed		
		235.0	352.5	470.0	235.0	352.5	470.0
Soluble sugars [g kg ⁻¹ (DM)]	ICMV94133	4.19±0.81	5.80±1.03	7.25±1.86	3.02±0.70	7.06±0.38	3.45±0.74
	WCA-78	7.14±1.24	5.09±0.72	8.04±1.52	2.56±0.52	2.04±0.14	2.55±0.27
Soluble proteins [g kg ⁻¹ (FM)]	ICMV94133	0.79±0.17	1.63±0.46	3.26±0.14	1.57±0.14	0.92±0.13	1.02±0.13
	WCA-78	1.37±0.47	2.58±0.42	1.82±0.19	1.32±0.24	1.75±0.41	1.49±0.39
Free amino acids [g kg ⁻¹ (FM)]	ICMV94133	0.281±0.052	0.226±0.029	0.391±0.046	0.582±0.191	0.961±0.069	0.561±0.075
	WCA-78	0.267±0.022	0.438±0.109	0.391±0.049	0.869±0.160	1.157±0.120	1.262±0.109

Discussion

In general, K fertilisation is associated with mitigating the effect of water deficit on plant growth because of the positive effect of this nutrient in osmotic adjustment, stomatal regulation, photosynthesis, and protein synthesis (Mengel and Pflüger 1972, Jacoby *et al.* 1973, Flowers and Läuchli 1983, Ashraf and Naz 1994, Quintero *et al.* 1998). But the supra-optimal concentrations of K (9 and 12 mol m⁻³) used in this study were not beneficial in alleviating the effect of drought on the growth of two pearl millet lines since shoot fresh and dry matter of both the lines remained almost unaffected with increasing supply of K under water deficit (Fig. 1). Lack of positive relationship of our results with the earlier studies could be due to difference in K concentrations used, since we have used supra-optimal K levels, *i.e.*, 9 and 12 mol m⁻³ that are significantly higher than 6 mol m⁻³ being used an adequate level in most of the studies reported earlier. For instance, Sen Gupta *et al.* (1989) noted that the effect of drought was much less severe on the growth and photosynthesis of wheat plants supplied with 6 mol m⁻³ K than of those supplied with 2 mol m⁻³ K. The second reason for lack of any effect of enhanced supply of K in pearl

millet under drought stress may have been due to the adaptation of this crop to low nutrient regimes usually encountered under water limiting conditions since this crop is grown on dry-lands throughout the arid and semi-arid regions of the world where nutrient deficiency is one of the important characteristics of such soils (Bidinger *et al.* 1987, Van Oosterom *et al.* 1995). Thus the critical and adequate K supplies for this crop, that are not reported in literature, may be much lower than for crops which are normally grown on well-watered fertile soils, so the K levels used in this study may have coincided with the adequate levels of this crop.

In WCA-78 an ameliorative effect of increasing supply of K on P_N was observed particularly under water deficit. This is parallel to what has earlier been noted in wheat (Sen Gupta *et al.* 1989) that inhibition in photosynthesis of drought-stressed plants was much less severe when they were supplied with enhanced supply of K.

Stomatal conductance has long been considered an important selection criterion for drought resistance (Boyer 1970, Quarrie and Jones 1979). Maintenance of pressure potential facilitates higher g_s at lower water po-

tential (Turner and Jones 1980) in addition to enabling cell elongation and thereby increasing growth. In fact, the leaf pressure potential in both pearl millet lines increased considerably with increasing K in the growth medium under water limiting regime, but the increase in pressure potential did not prove beneficial for enhancing growth of pearl millet under these soil conditions. Reduction in growth can occur even though pressure potential is maintained, as the result of changes in tissue extensibility, yield threshold, and hydraulic conductivity (Matsuda and Rizvi 1981, Mathews *et al.* 1984, Westgate and Boyer 1985).

Although *E* decreased considerably in both lines of pearl millet under water deficit, the effect of enhanced K supply was not prominent. In addition, higher WUE of two lines under water deficit remained almost unaffected in comparison with that at well-watered conditions. This seemed to be due to similar pattern of reduction in P_N and *E* under water limiting conditions.

The leaf osmotic potential was generally decreased with increasing soil K supply. The positive association of K nutrition with plant water relations found here in pearl millet can be explained in view of the reason that K is absorbed both passively and actively and may be important in osmotic adjustment (Jones *et al.* 1980, Premachandra *et al.* 1995). However, the decrease in leaf osmotic potential under water deficit regimes can be related to high accumulation of free amino acids in the leaves of both lines but not with the leaf soluble sugars and soluble proteins. No increase in soluble proteins with increasing

supply of soil K does not conform to the findings of Helal *et al.* (1975) that osmotic stress generally enhances incorporation of N into proteins. The results for soluble proteins in pearl millet are also not parallel to what had been earlier observed in sorghum (Eck and Musick 1979), four *Brassica* species (Ashraf and Mehmood 1990), and *Sesamum indicum* (Vyas *et al.* 1985).

Furthermore, the values of leaf osmotic potential showed that osmotic adjustment had occurred in pearl millet plants subjected to drought. Since pearl millet is prone to grow under water deficit, considerable magnitude of osmotic adjustment was likely to occur.

In general, Chl *a* and Chl *b* contents in both lines of pearl millet were increased markedly after the drought stress treatment, and the enhanced supply of K had an increasing effect on these pigments except in WCA-78 under water deficit. However, the similar increase in both Chls *a* and *b* at watering regimes did not affect Chl *a/b* ratios. This is in contrast to some earlier studies reflecting that increasing Chl *a/b* ratio under water deficit conditions is a common phenomenon in most crop species (García *et al.* 1987, Estill *et al.* 1991, Ashraf *et al.* 1994).

In conclusion, supra-optimal concentrations of K did not prove to be beneficial in alleviating the effect of drought on the growth of pearl millet. In addition, the growth of pearl millet under drought stress and high K regimes was strongly associated with P_N , but not with NAR or RGR. A considerable magnitude of osmotic adjustment occurred in pearl millet plants experiencing water deficit and high K regimes.

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