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Responses of four arid zone grass species from varying habitats to drought stress

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Abstract

The effects of 4 or 8 drought cycles on four grass species, *Cenchrus pennisetiformis*, *Leptochloa fusca*, *Panicum turgidum*, and *Pennisetum divisum* were assessed in a pot experiment. There were significant differences between the species in biomass production under water stress. *C. pennisetiformis* and *P. turgidum* produced significantly greater fresh and dry matter than *P. divisum* and especially than *L. fusca*. *L. fusca* had the lowest and *P. divisum* highest osmotic potentials compared with the other species after the completion of 4 or 8 drought cycles. Osmotic adjustment (difference between osmotic potential of droughted/rehydrated plants and control plants) was highest in *L. fusca*. The stomatal conductance was significantly decreased with increased drought stress in *C. pennisetiformis*. The elasticity of *C., pennisetiformis*, *P. turgidum* and *P. divisum* increased with increase in number of drought cycles, whereas that of *L. fusca* remained unchanged. *L. fusca* and *P. turgidum* had the lowest leaf hydration of all species after 8 drought cycles. The chlorophylls *a* and *b* in all species remained unaffected by drought treatments. The proline content of *C. pennisetiformis* and *L. fusca* increased significantly with increased drought stress, whereas that of *P. turgidum* remained unaffected after 4 or 8 drought cycles. *L. fusca* synthesized great amount of leaf soluble proteins during 8 drought cycles, whereas *P. divisum* had low protein content after 4 drought cycles. The protein contents of *C. pennisetiformis* and *P. turgidum* remained unaffected after 8 drought cycles.The leaf epicuticular wax of *L. fusca* increased consistently with increased drought stress, but leaf wax of *P. divisum* increased only at the highest drought stress and that of *C. pennisetiformis* and *P. turgidum* increased after 4 drought cycles. On the basis of these results it was established that *C. pennisetiformis* and *P. turgidum* were the most tolerant, *P. divisum* intermediate, and *L. fusca* the most sensitive to drought stress. The osmotic adjustment did not positively correlate with the degree of drought resistance.

Key words: *Cenchrus pennisetiformis*, *Leptochloa fusca*, osmotic adjustment, *Panicum turgidum*, *Pennisetum divisum*, water relations.

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Introduction

The domestication of highly drought-resistant plant species with high water use efficiency under severe drought conditions, and also of high economic value in terms of yield or biomass production, are recommended for the economic utilization of dry lands.

The relative growth rate of *Leptochloa fusca* is considerably higher compared with most of the other grasses from arid and semi-arid regions and owing to its high salt tolerance, this species is used for reclamation of salt-affected soils (Malik *et al.* 1986).

The present study was undertaken to determine the response of salt-tolerant, wetland *L. fusca* and three grass species, *Cenchrus pennisetiformis*, *Panicum turgidum*, and *Pennisetum divisum*, which commonly occur in deserts and produce relatively high forage under water deficit conditions. The major objective was to compare growth performance and osmotic adjustment because osmotic adjustment is considered to be the most important component of drought tolerance (Blum 1989, Cortes and Sinclair 1986, Cutler *et al.* 1977).

Materials and methods

Seeds of *Cenchrus pennisetiformis* Hochst. & Steud., *Panicum turgidum* Forssk., and *Pennisetum divisum* (Gmel.) Henr. were collected from the Cholistan and Thal deserts in Pakistan, whereas those of *Leptochloa fusca* (L.) Kunth. were collected from a derelict field near the Botanic Gardens of Bahauddin Zakariya University, Multan, Pakistan. After washing with 5 % sodium hypochlorite solution for 10 min seeds of each species were sown in Petri dishes. After two weeks, 6 seedlings of comparable size of each species (except for *P. divisum* for which 4 seedlings) were transplanted equidistant from each other into 28 cm diameter plastic pots containing 5.0 kg sandy loam soil. The experiment was conducted in a greenhouse at 12 h photoperiod and at day/night temperature 28/16 ± 4 °C and relative humidity 54 - 67 %. The pots were placed in a randomized complete block design with four blocks. Each block contained four species and three drought treatments. The drought cycles were started six weeks after seeding. The drought treatments were as follows: T_0, watering each day to field capacity throughout the experiment; T_1, the plants were droughted 4 times until wilting occurred, and then rewatered to field capacity; T_2, the plants were droughted 8 times as in T_1. The plants were considered wilted when 2 - 3 leaves of a plant were wilted and the wilting was simultaneous in all plants within each pot. At the completion of each wilting cycle about 25 g soil was taken from each pot at 6 cm depth for the determination of soil moisture content. Plants from each pot were harvested after rehydration. Plant roots were removed carefully and completely from the soil and were then washed with distilled deionized water, blotted and separated. Fresh masses of shoots and roots were recorded. All the plant samples were then oven-dried at 70 °C for 7 d to constant dry mass.

Leaf conductance (g_{ep}) was measured with an automatic porometer (*MK3 Delta-T*

Device, Cambridge, UK) three times a day and data were pooled to calculate mean g_{ep} per day. The elasticity (e) was estimated following Thomas (1987). A leaf was excised from each plant at 08.00, weighed (W_1), inserted in the pressure bomb and its water potential (ψ_{w1}) measured. Then the leaf was over-pressured to 0.5 MPa over the water potential value of each leaf for 90 s to express a small volume of xylem sap. The pressure was released and the new water potential (ψ_{w2}) was measured. Then the leaf was weighed again (W_2), and dried at 85 °C for 24 h and reweighed (W_d).

$$W_{ref} = W_1 - W_d + (\psi_{w1} - 0.5)\,(W_1 - W_2)/(\psi_{w2} - \psi_{w1})$$
$$\Delta R = (\psi_{w1} - \psi_{w2})/\mathrm{Wref}$$
$$e[\mathrm{MPa}] = (\psi_{w2} - \psi_{w1})/\Delta R$$

This elasticity should not be confused with bulk modulus of elasticity.

Leaf hydration (H) was calculated as the ratio of the mass of water in a turgid leaf to its dry mass.

At 8.00 a.m. following rehydration overnight leaf samples were taken from each plant for the measurement of osmotic potential of the leaves at full turgidity. The leaf material was frozen in 2.0 cm^3 polypropylene tubes for 2 weeks. 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 an osmometer *TP 10B* (*Camlab Limited*, Cambridge, UK).

An apical small portion of one plant tiller having three leaves was excised randomly from each pot, and leaf water potential measurements were made at 9.00-10.00 a.m. with a Scholander type pressure bomb (*Chas W. Cook. & Sons*, Birmingham, UK)

Proline was estimated spectrophotometrically following the ninhydrin method described by Bates *et al.* (1973). Chlorophyll content was estimated by the method of Witham *et al.* (1971). 1 g of leaf fresh mass was triturated in 80 % acetone and absorbance of the extract was read at 645, 652, and 663 nm using a spectrophotometer (*Hitachi, U-2000,* Japan).

For the determination of leaf epicuticular wax content leaves were randomly taken from each plant and their area was measured by the graphic method. The leaf samples (1 g fresh mass) were consecutively washed with 40, 30, and 30 cm^3 of carbon tetrachloride for 30 s per wash. The extract thus obtained was filtered and evaporated to dryness. Wax content was expressed on the leaf area basis. Total soluble proteins were estimated as described by Lowry *et al.* (1951).

The results of all the parameters were subjected to two-way analysis of variance, and the least significant difference (LSD) was calculated following Snedecor and Cochran (1980).

Results

L. fusca wilted at significantly greater ($P < 0.05$) moisture content compared with the other species (Table 1). The fresh and dry mass of the shoots, and root dry mass of all four grass species decreased consistently after both drought treatments (Table 2). *C. pennisetiformis* and *P. turgidum* had significantly greater fresh and dry shoot mass

Table 1. Soil moisture content [%] at the end of each wilting cycle.

Species	Drought cycles							
	1	2	3	4	5	6	7	8
T_2								
C. pennisetiformis	0.42a	0.42a	0.36a	0.37a	0.45a	0.21a	0.21a	0.20a
L. fusca	0.94b	0.98b	1.19b	0.80b	0.76b	0.77b	0.81b	0.99b
P. turgidum	0.55a	0.31a	0.55a	0.58a	0.36a	0.39a	0.29a	0.35a
P. divisum	0.37a	0.32a	0.47a	0.24a	0.33a	0.29a	0.34a	0.33a
T_1								
C. pennisetiformis	0.35a	0.48a	0.37a	0.42a				
L. fusca	0.96b	0.94b	1.04b	0.86a				
P. turgidum	0.49a	0.45a	0.53a	0.58a				
P. divisum	0.37a	0.38a	0.59a	0.27a				

Values (means of 4 measurements) with the same letter in each column did not differ significantly at $P \leq 0.05$.

Table 2. Growth parameters of four grass species after 0, 4 or 8 drought cycles.

Parameter	Drought cycles	*C. pennisetiformis*	*L. fusca*	*P. turgidum*	*P. divisum*
Shoot fresh mass [g plant^{-1}]	0	20.3 ± 1.2 ax	25.3 ± 1.24ax	23.7 ± 5.5 ax	31:8 ± 0.63ay
	4	13.2 ± 0.9 bx	6.8 ± 0.2 by	14.1 ± 2.1 bx	11.5 ± 1.13bx
	8	11.0 ± 2.4 bx	5.1 ± 0.8 bx	9.6 ± 2.1 bx	8.0 ± 1.0 bx
Shoot dry mass [g plant^{-1}]	0	9.7 ± 0.35ax	11.4 ± 0.7 ax	12.0 ± 2.0 ax	11.5 ± 0.35ax
	4	7.6 ± 0.63abxz	4.1 ± 0.13by	9.2 ± 2.8 abx	6.2 ± 0.40bxz
	8	5.2 ± 1.3 bx	2.1 ± 0.5 by	4.8 ± 0.74bxy	3.6 ± 0.42bxz
Root dry mass [g plant^{-1}]	0	3.0 ± 0.50ax	6.5 ± 1.1 ay	2.5 ± 0.35ax	5.0 ± 0.50ay
	4	3.2 ± 0.64ax	1.1 ± 0.55by	2.4 ± 0.55ay	2.0 ± 0.20by
	8	3.0 ± 0.60ax	0.6 ± 0.10by	1.4 ± 0.30ay	1.5 ± 0.11by
Shoot/root ratio	0	3.2 ± 0.40axy	2.0 ± 0.6 ax	3.9 ± 1.3 ay	2.4 ± 0.2 ax
	4	2.7 ± 0.52abx	3.3 ± 1.0 bx	3.4 ± 1.0 ax	1.3 ± 0.15ay
	8	1.9 ± 0.51bx	3.3 ± 0.3 by	4.3 ± 0.75by	1.7 ± 0.20ax
Number of tillers [plant^{-1}]	0	16.9 ± 1.35ax	16.6 ± 0.92ax	6.1 ± 2.6 ay	6.1 ± 0.9 ay
	4	16.3 ± 0.33ax	15.4 ± 3.6 ax	8.7 ± 1.5 aby	3.1 ± 0.07az
	8	16.2 ± 0.15ax	11.6 ± 0.7 bxy	10.5 ± 1.7 by	3.5 ± 0.35az
Number of leaves [plant^{-1}]	0	14.0 ± 0.0 ax	8.0 ± 0.7 ay	17.0 ± 2.5 ax	27.0 ± 2.4 az
	4	11.0 ± 0.0 abxy	7.0 ± 0.6 ax	14.0 ± 1.8 ay	20.0 ± 0.0 bz
	8	7.0 ± 0.0 bx	6.0 ± 0.5 ax	8.0 ± 1.1 by	21.0 ± 1.1 by

Means with the same letter in each column (a - c) and each row (x - z) did not differ significantly at $P \leq 0.05$.

compared with the other species. *P. divisum* was intermediate and *L. fusca* was the lowest of all species in biomass production.

Increasing drought had no significant effect on the shoot/root ratio in *P. divisum*. However, the shoot/root ratio of *L. fusca* increased, whereas that of *C. pennisetiformis* and *P. divisum* decreased (Table 2). After 4 drought cycles the shoot/root ratio of *P. divisum* was the lowest of all species.

The number of tillers per plant (Table 2) of *L. fusca* was reduced significantly after 8 drought cycles, whereas tillering of *P. turgidum* increased and *P. divisum* decreased and that of *C. pennisetiformis* remained unaffected after both drought treatments, compared with their respective controls. *P. divisum* had a significantly lower number of tillers/plant after 4 or 8 drought cycles compared with the other species.

Drought significantly reduced the number of leaves per tiller (Table 2) of *C. pennisetiformis*, *P. turgidum* and *P. divisum*. *P. divisum* had the highest and *L. fusca* the lowest number of leaves per tiller after 4 or 8 drought cycles.

The repeated drought cycles had no significant effect on leaf water potentials in all grass species (Table 3). Leaf osmotic potential of all species decreased significantly ($P < 0.001$) with the increase in drought cycles. *L. fusca* had the lowest and *P. divisum* the highest osmotic potential after both drought treatments.

Table 3. Parameters of water relations of four grass species after 0, 4 and 8 drought cycles.

Parameter	Drought cycles	*C. pennisetiformis*	*L. fusca*	*P. turgidum*	*P. divisum*
Leaf water potential [-Mpa]	0	2.20 ± 0.09	2.00 ± 0.40	2.42 ± 0.10	2.05 ± 0.15
	4	2.50 ± 0.10	2.50 ± 0.20	2.60 ± 0.23	2.00 ± 0.40
	8	2.62 ± 0.21	2.45 ± 0.23	3.00 ± 0.17	2.42 ± 0.20
Leaf osmotic potential [-MPa]	0	1.40 ± 0.41ax	1.10 ± 0.0 ax	1.35 ± 0.0 ax	1.04 ± 0.12ax
	4	2.30 ± 0.21bx	2.90 ± 0.84by	2.03 ± 0.06bxy	1.65 ± 0.13bz
	8	2.50 ± 0.21bx	3.20 ± 0.84by	2.30 ± 0.06bxz	2.00 ± 0.13bz
Osmotic adjustment[MPa]	4	0.92	1.80	0.70	0.62
	8	1.11	2.12	0.95	1.50
Stomatal conductance [cm s^{-1}]	0	0.15 ± 0.021ax	0.15 ± 0.006ax	0.15 ± 0.013ax	0.11 ± 0.008ax
	4	0.13 ± 0.009ax	0.16 ± 0.023axy	0.18 ± 0.015ay	0.10 ± 0.003az
	8	0.09 ± 0.001bx	0.18 ± 0.021ay	0.19 ± 0.032ay	0.13 ± 0.005ax
Elasticity [MPa]	0	6.15 ± 0.85axy	5.30 ± 0.57ax	5.80 ± 0.9 ax	8.60 ± 2.12ay
	4	6.20 ± 1.39ax	5.30 ± 1.21ax	7.60 ± 1.0 abx	12.14 ± 2.82by
	8	9.90 ± 1.12bx	6.70 ± 0.0 ay	10.32 ± 1.52bxz	12.90 ± 1.9 bz
Leaf hydration [$g(H_2O)\ g^{-1}(d.m.)$]	0	3.60 ± 1.3 ax	5.00 ± 0.7 ay	3.90 ± 0.5 ax	3.90 ± 1.0 ax
	4	3.00 ± 1.0 bx	4.40 ± 0.75by	3.70 ± 0.4 abz	3.40 ± 0.6 bxz
	8	2.90 ± 0.3 bx	2.70 ± 0.9 cxy	3.40 ± 0.04by	2.40 ± 0.25cx

Means with the same letter in each column (a - c) and each row (x - z) did not differ significantly at $P \leq 0.05$. Differences in leaf water potential are not significant.

The osmotic adjustment occurred in all species after drought cycles. *L. fusca* showed higher osmotic adjustment compared with the other three species (Table 3).

Leaf conductance of *C. pennisetiformis* decreased with increasing number of drought cycles, whereas that of *L. fusca, P. turgidum* and *P. divisum* remained almost constant (Table 3). *P. divisum* and *C. pennisetiformis* had the lowest leaf conductance of all four species after 4 or 8 drought cycles, respectively.

Elasticity of *C. pennisetiformis*, *P. turgidum* and *P. divisum* increased with increase in drought cycles, whereas that of *L. fusca* remained unaffected (Table 3). *P. divisum* had the highest and *L. fusca* the lowest elasticity. The other two species did not differ significantly after either drought treatment.

Drought cycles significantly decreased the leaf hydration of all grass species (Table 3). *L. fusca* and *P. turgidum* had the higher leaf hydration after 4 drought cycles, than *C. pennisetiformis* and *P. divisum*.

Increasing number of drought cycles had no significant effect on chlorophyll (Chl) *a* and *b* content (Table 4). Species differed significantly in Chl *a* and *b* content ($P < 0.05$), but this difference was inherent.

Table 4. Chlorophyll *a* and *b*, soluble proteins, proline and epicuticular wax contents in leaves of four grass species after 0, 4 or 8 drought cycles.

Parameter	Drought cycles	*C. pennisetiformis*	*L. fusca*	*P. turgidum*	*P. divisum*
Chl *a*	0	2.61 ± 0.08	2.89 ± 0.04	2.44 ± 0.08	3.04 ± 0.21
[mg g^{-1}(d.m.)]	4	2.35 ± 0.35	2.15 ± 0.02	1.84 ± 0.11	2.06 ± 0.38
	8	2.86 ± 0.42	3.28 ± 0.23	2.40 ± 0.21	2.42 ± 0.54
Chl *b*	0	1.71 ± 0.23	2.22 ± 0.42	1.39 ± 0.10	1.66 ± 0.21
[mg g^{-1}(d.m.)]	4	1.29 ± 0.21	1.65 ± 0.17	1.22 ± 0.33	1.31 ± 0.25
	8	1.57 ± 0.23	2.43 ± 0.26	1.60 ± 0.39	1.54 ± 0.28
Proteins	0	2.51 ± 0.04axy	2.66 ± 0.13ax	2.18 ± 0.02ay	2.76 ± 0.31ax
[mg g^{-1}(d.m.)]	4	1.91 ± 0.22bx	1.65 ± 0.05by	1.53 ± 0.06bx	1.12 ± 0.13bx
	8	2.18 ± 0.04abx	3.89 ± 0.72cy	2.00 ± 0.23ax	2.00 ± 0.41cx
Proline	0	3.45 ± 0.31ax	8.10 ± 1.26	4.04 ± 1.08ax	2.79 ± 0.03ax
[μmol g^{-1}(d.m.)]	4	6.79 ± 0.14bx	10.40 ± 1.96ay	5.97 ± 1.42ax	1.87 ± 0.02az
	8	11.87 ± 1.31cx	20.17 ± 0.93by	6.80 ± 1.51ax	6.49 ± 0.12bz
Wax	0	61.7 ± 15.7axy	34.5 ± 4.8ax	97.7 ± 21.3ay	185.0 ± 4.2az
[μg cm^{-2}]	4	158.5 ± 22.8bx	281.8 ± 69.8by	209.2 ± 31.7bz	183.7 ± 7.1az
	8	53.2 ± 16.9ay	321.9 ± 26.8cx	118.7 ± 27.3ay	222.4 ± 25.0bz

Means with the same letter in each column (a - c) and each row (x - z) did not differ significantly at $P \leq 0.05$. Differences in Chl *a* and *b* are not significant.

The total leaf soluble proteins in *L. fusca* (Table 4) increased after 8 drought cycles, whereas those of *P. divisum* and *C pennisetiformis* decreased after 4 or 8 drought cycles. *L. fusca* synthesized significantly ($P < 0.05$) more proteins during 8 drought cycles compared with the other grass species.

The proline contents of *C. pennisetiformis*, *P. divisum* and *L. fusca* (Table 4) increased significantly ($P < 0.05$), whereas those of *P. turgidum* remained unaffected after both drought treatments. *L. fusca* synthesized significantly greater amount of proline after 4 or 8 drought cycles compared with the other three species. By contrast, *P. divisum* had the lowest proline content of all species after 4 drought cycles.

Leaf epicuticular wax of *L. fusca* (Table 4) increased consistently with increase in drought stress, whereas that of *P. turgidum* and *C. pennisetiformis* increased after 4 drought cycles and that of *P. divisum* increased after 8 drought cycles. The leaf wax content of *L. fusca* was the highest of all four species after both drought treatments.

Discussion

From the results for soil moisture content at each wilting cycle (Table 1) and for biomass production (Table 2) it is evident that *C. pennisetiformis* and *P. turgidum* were relatively resistant to repeated cycles of drought. By contrast the lower fresh and dry mass of *L. fusca* and its relatively greater soil moisture content at wilting shows its susceptibility to drought stress. *P. divisum* was intermediate in its response to drought.

The relatively greater drought resistance of *C. pennisetiformis* and *P. turgidum* is expected in view of the fact that these two species are natural colonizers of the desert where severe water deficit conditions are predominant (Ashraf and Bokhari 1987). The susceptibility of *L. fusca* to drought is also expected as the species commonly occurs on waterlogged sodic soils (Malik *et al.* 1986).

Although *P. divisum* has been recorded from Thal desert, its density is very low compared with other grass species in the area (Bokhari, personal communication); in extreme drought conditions during the summer months it remains dormant and starts growing vigorously soon after the commencement of the rainy season. The lower drought resistance of *P. divisum* is probably a factor which restricts its wide occurrence in the desert.

It is now well documented that osmotic adjustment plays a crucial role in plant adaptation to drought (*e.g.* Hsiao 1973, Turner and Jones 1980, Quisenberry 1982). It might be effective in plant tolerance to salinity and freezing, which also involve water deficit (Blum 1988, 1989). In these experiments the osmotic potential was taken of the sap which was expressed from disrupted tissue, which may be a mixture of apoplastic and symplastic water (Turner and Jones 1980). Since the redistribution of cell water was not assessed, the results for osmotic adjustment must be interpreted with some caution.

The osmotic potentials of plants which experienced repeated cycles of drought were significantly lower than those of well watered plants in all four species. This might be due to the accumulation of osmotically active solutes. It further suggests that osmotic adjustment had occurred in all species subjected to drought. The extent of osmotic adjustment was significantly higher for *L. fusca* and *P. divisum* than for

C. pennisetiformis and *P. turgidum*. The results are surprising in view of their contrasting capacity to resist drought stress. However, there may be other characters which contribute to enhanced drought resistance in *C. pennisetiformis* and *P. turgidum*. For example leaf conductance was lowest in *C. pennisetiformis*.

Elasticity is an important parameter in cell water relations (Baker 1984, Dainty 1976). In this study, different drought cycles had no significant effect on the elasticity of drought-sensitive *L. fusca*, whereas the elasticity of the remaining three more drought-resistant species increased. Therefore, leaf elasticity can be related to the differential drought resistance of the studied species similarly as was found in other species (Noy-Meir and Ginzburg 1969, Steudle *et al.* 1977, Turner 1979).

It is now well established that deposition of wax on leaf surfaces plays a crucial role in minimizing water loss (Johnson *et al.* 1983, Jordan *et al.* 1984) and all four species accumulated considerably higher quantities of wax while experiencing drought cycles. *L. fusca* and *P. divisum* had the higher epicuticular wax content than other two species, which indicates a negative correlation between epicuticular wax content and drought resistance in studied species. These results are not in agreement with those of Ashraf and Mehmood (1990) who found a positive correlation between the deposition of wax on leaf surfaces and drought resistance in *Brassica* species.

Leaf proline content of all four species increased with increase in drought, but a greater increase was observed in drought-sensitive *L. fusca*. A negative correlation between proline accumulation and salt tolerance was also observed in soybean (Moftah and Michel 1987) and *Vigna mungo* (Ashraf 1989).

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