

Southern African grasses with foliage that revives after dehydration

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ABSTRACT

A brief survey in Southern Africa revealed 11 grass species and a number of sedges with foliage that recovers from air-drying (equivalent to equilibrium with air at 20-40 % relative humidity at 28° C.). The desiccation tolerance limits were extremely low being equivalent to approximately 0-5 % relative humidity. Some species may have a potential use in agriculture.

INTRODUCTION

Until recently only about nine angiosperm species were considered to have foliage that would tolerate dehydration to the point of air-dryness in a manner similar to lichens on exposed rock surfaces. It has since become clear that this phenomenon is of wider occurrence among the angiosperms than previously thought, particularly in southern Africa where 11 new angiosperm examples were recently reported (Gaff 1971). The fact that some of these were grasses, raised the possibility that some "resurrection" plants might be found that had a potential use in agriculture in arid areas. Consequently, a search was made for further desiccation-tolerant grasses.

METHOD

Grasses were marked while in flower during the moist summer season. Identical voucher specimens were collected and deposited for identification at the National Herbarium in Pretoria. Identifications were also made by the herbaria at Salisbury, Windhoek, Tananarive, and at the Sugar Research Institute of Mauritius, where appropriate. The marked plants were re-examined towards the end of the dry season which, in the regions traversed, extends from about April to September. Wherever possible, plants were collected in a completely air-dry condition—in many cases from shallow soil pans on otherwise bare rock slopes fully exposed to the sun, i.e. extremely xeric sites. If the marked plant had not dried completely, the clump was removed from the soil, placed in an open paper bag, and allowed to dry in the prevailing conditions of low air humidity and moderately high air temperatures.

The air-dry plants were submerged in water to rehydrate for 24 hours in diffuse laboratory light. Plants which became crisp in texture and healthy in appearance were subjected to various tests to establish survival of the leaves (neutral red uptake, Sullivan and Levitt 1959; Evans blue exclusion, Gaff and Okong'o-Ogola 1961; and formation of chlorophyll in nonchlorophyllous tissue).

Water stress levels were assessed as: (a) Relative water content, i.e. the water content of the tissue as a percentage of its water content at full turgor. A 70 °C oven was used to obtain dry mass since higher temperatures caused errors due to decomposition (Paech and Tracey 1955; Loomis and Shull 1937). Twenty-four-hour immersion in water was usually required for attainment of full turgor. (b) Water potential, determined by the gravimetric vapour-exchange method (Slatyer 1958). Errors due to respiratory loss of CO₂ (Kreeb and Onal 1961) were assumed to be negligible in the dry leaves. Drought tolerance levels were determined by allowing the air-dry foliage to equilibrate to air of various relative humidities,

which were maintained constant by saturated salt solutions in contact with the solid salt at 28° C. Concentrated sulphuric acid was used for relative humidities of approximately zero, and various dilutions of this were used for intermediate humidities to 10%. Relative humidity values were based on the data in Robinson and Stokes 1955. The course of equilibration was followed gravimetrically until consecutive masses were constant.

The regions traversed were Rhodesia (Salisbury, Rusape, Matopos, Fort Victoria, Lundi), Transvaal (Messina to Pretoria and the Magaliesberg), the northern Cape Province (Kimberley west to Port Nolloth) and South West Africa (Karasburg to Okahandja, Swakopmund, Maltahöhe), the Malagasy Republic (Tananarive to Ambalavao), and Mauritius. These regions have predominantly summer rainfall with the exception of the Port Nolloth-Karasburg area where rainfall is sporadic rather than seasonal. Unfortunately, it was not possible to examine the winter rainfall areas of the Southern Cape and the succulent karoo.

RESULTS AND DISCUSSION

Air-dry foliage from 11 of the 80 grass species examined revived on rehydration. The water potentials of the air-dry foliage were mainly in the 30-40% RH range (Table 1), i.e. approximately the same range of values as the field-dry "resurrection" plants reported earlier (Gaff 1971). The drought tolerance limits (Table 2) were considerably lower than the water stress levels; most species had tolerance limits of approximately 0% RH. Again this is consistent with the earlier study, even though the times allowed here to ensure full equilibration were some months longer.

Some of the remaining species examined, particularly *Aristida* spp., gave a superficial appearance of revival in the young tiller shoots. However, the healthy green appearance deteriorated after a further day of full hydration, and the crispness of the tissue could be attributed to a high fibre content rather than to restoration of cell turgor. The tests with Evans blue and neutral red confirmed that these tissues had not survived. Most of the species listed in the appendix grew in extremely xeric sites, and appeared superficially to be dry and dead during the dry season. However, closer examination usually revealed a few well-hydrated immature tillers persisting in the centre of the otherwise defunct clump. The possibility that some of these species may yet prove desiccation tolerant cannot be ruled out entirely, since the root system of the plant was often extensively damaged as the plant was removed from the soil, and artificial dehydration may have been more rapid than desiccation under field conditions.

Desiccation-tolerant grasses appear to be restricted to the subfamily Eragrostoideae sensu Tateoka (1957). Even here they occur in three tribes which Hutchinson, 1959, considers are related, viz the Eragrosteae (*Eragrostis* and *Tripogon*), Sporoboleae

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(*Sporobolus*) and the Chlorideae (*Oropetium*, *Brachyachne*, *Microchloa*). All these tribes have the eragrostoid type of mesophyll and parenchymatous bundle-sheath arrangement (Carolin, Jacobs & Vesk, 1973) and are Kranz species (Brown and Smith 1972), which presumably exhibit the C4 photosynthetic pathways. It would seem that these groups have some predisposition toward desiccation tolerance that is realized in only a small number of genera, some of which possess a predominance of tolerant species (e.g. *Microchloa**), others only a minor proportion (e.g. *Eragrostis*, *Sporobolus*). This pattern suggests a relatively recent appearance of the adaptation during the evolution of the grass tribes. There is evidence that young, meristematic tissue is more drought tolerant than mature, differentiated tissue on the same plant (reviewed in Levitt 1972). It seems likely that the basal-meristematic pattern of growth in the grass and sedge leaves might allow a gradual extension of extreme drought tolerance developed in the basal meristem to progressively older areas of the leaf. That is, species in which desiccation tolerance is confined to the basal centimetre of the leaf (e.g. *Eragrostis hispida*, *Cyperus bellus*) or the immature leaves (e.g. *Sporobolus lampranthus*), are in an earlier stage of evolutionary adaptation than species in which the full length of the mature foliage is tolerant (e.g. *Eragrostis nindensis*, *Coleochloa setifera*, etc.). Most grasses with tolerant mature leaves retain the chlorophyll in the dry state, and are fully green after imbibition is complete (24 hrs or less). *Eragrostis nindensis* and the two species of *Coleochloa* lose their chlorophyll as they dehydrate, consequently a further 24 hrs is required for regreening after full imbibition. As this would seem a somewhat less efficient level of ecological adaptation, it is tempting to assume that this also is an intermediate evolutionary stage. However, markedly different response patterns in the fine structure of drying cells in the two types (chlorophyll-retainers as opposed to chlorophyll-losers), suggest caution is necessary in accepting this assumption, (unpublished data, Gaff, N. Hallam, S. Zee and T. P. O'Brien).

In general the desiccation-tolerant grasses and sedges appear to be pioneer plants colonizing shallow soil pans. Whereas the two sedges *Coleochloa setifera* and *C. pallidior* commonly grow to 30–50 cm, the grasses are usually low-growing. To a certain extent this is a consequence of the shallowness of the soil (often 1–2 cm deep) and the severity of their habitat; all the grasses show a significant increase in height when grown in pots regularly supplied with a complete mineral nutrient in a greenhouse at 25 °C. In most cases, the increase would be 50–100%, but a threefold increase from about 6 cm to 20 cm occurs in *Microchloa caffra*. Their low growth habit probably places them at a disadvantage when competing with taller species in moister deep soils. Nevertheless, *Eragrostis nindensis*, and *Sporobolus lampranthus* commonly grow as broad tussocks, obviously of considerable age, interspersed between taller grass species on deeper soil flats.

* It seems that *Microchloa indica* (L.f.) Beauv. is a marginal case. Plants grown from seed collected in Rhodesia, showed survival of a significant proportion of cells in the young leaves following artificial drying of potted plants. On the other hand, field-dry plants collected in Northern Australia were dead; however the species is clearly annual and these plants had probably senesced prior to dehydration. We were unable to examine *Microchloa ensifolia* Rendle, but from the description of the plant and its habitat in Angola (Launert 1966), it is highly probable that this, too, is a resurrection grass.

The low height of the grasses is in part traceable to their common growth habit; all are perennials which tiller repeatedly to form a dense, compact tussock; very little elongation of the internodes occurs except in the inflorescence. None are stoloniferous or rhizomatous. Possibly the vascular structure of grasses, i.e. largely two metaxylem vessels and a protoxylem canal arranged in widely-separated bundles rather than in a firm, compact mass of tracheids, is more liable to damage as the dehydrating plant shrinks. Consequently re-establishment of water continuity in the xylem from the root to the transpiring leaf on rehydration would be impaired (c.f. Gaff 1972). This factor might have restricted the evolution of desiccation tolerance in grasses which have extensive development of the internodes.

The taller resurrection grasses may be useful components of pastures subject to prolonged drought. Although there has been no systematic assessment of how long the grasses can endure desiccation, dry material of one resurrection plant, *Borya nitida* Labill., has survived 2½ years to date. There seems to be no reason why the grasses should not be equally durable. Rehydration is rapid in all species; most grasses expand to their original dimensions within 4–5 hours and are fully turgid well within the 24-hour period allowed here. This means that green feed is available within a day of a rainfall of 10 mm or more. A further day is required by *E. nindensis* for regreening, since this species loses its chlorophyll on dehydration. Apart from any fodder value, their persistence over long periods without rain should minimize wind erosion.

At present, *E. nindensis* would appear to have the most potential for introduction to semi-arid pastures beyond its present distribution. Although of only moderate height (approximately 12 cm.), its value as a pasture plant has been commented on by Walter and Volk (1954) who drew attention to its rapid resumption of growth after rain, but who do not appear to have realized the desiccation-tolerant nature of the foliage. Their analyses revealed a generally high content of protein and phosphate, which they considered confirmed the good reputation of the species in S. W. Africa. *E. nindensis* tussocks possess a strong, firm root system, which resists wrenching of the plant from the soil by grazing animals. Although the *Coleochloa* species are taller-growing, there was no evidence of grazing. Presumably a high fibre content of the leaves renders them unpalatable or possibly the rock surfaces on which they grow may not readily be grazed by domestic animals.

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OPSOMMING

'n Beperkte ondersoek in Suidelike Afrika het 11 grassoorte en 'n aantal biesies opgelewer, met blare wat herstel van luguitdroging (gelykstaande aan 'n ewewig met lug van 20–40% relatiewe vogtigheid by 28° C). Die grense van die uitdrogingsverdraagsaamheid was besonder laag, naamlik ongeveer 0–5% relatiewe vogtigheid. Sommige van die soorte het dalk moontlikhede vir gebruik in die landbou.

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TABLE 1.—Species with foliage that survives air-drying; and the water stress in their leaves immediately prior to rehydration for the survival tests.

Species	Initial water potential (equivalent relative humidity at 28° C) %	Relative water content %	Collected dry in field or artificially dried	Comments
GRASSES				
<i>Brachyachne patentiflora</i> (Stent & Rattray) C. E. Hubb.....	40	5	field	Rhodesia
<i>Eragrostis hispida</i> K. Schum.....	37	6	field	basal 1 cm of leaf only
<i>Eragrostis nindensis</i> Fic. & Hiern (= <i>E. denudata</i>).....	23	—	field	
<i>Eragrostis paradoxa</i> Launert.....	46	8	field	S.W. Africa
<i>Microchloa caffra</i> Nees.....	—	9	field	basal 1,5 cm of leaf only
<i>Microchloa kunthii</i> Desv.....	28	3	transplanted to greenhouse; lab. dried.	S. Africa
<i>Oropetium capense</i> Stapf.....	33	8	field.	Rhodesia
	—	7	greenhouse plant, lab. dried	S.W. Africa
<i>Sporobolus festivus</i> Hochst.....	36	5	field	
<i>Sporobolus lampranthus</i> Pilg.....	45	11	field	full length of immature leaves. Half length of mature leaves. Rhodesia
<i>Sporobolus stapfianus</i> Gandoger.....	—	9	field	basal cm and immature leaves. S. Africa
	36	13	greenhouse plant, lab. dried.	S. Africa
<i>Tripogon minimus</i> (A. Rich.) Hochst. ex Steud.	42	7	field	Rhodesia
SEDGES				
<i>Coleochloa setifera</i> (Ridley) Gilly.....	39	9	field	S. Africa
<i>Coleochloa pallidior</i> Nelmes.....	29	10	field	Rhodesia
<i>Cyperus bellus</i> Kunth*.....	—	10	field	basal cm of leaf. S.W. Africa
<i>Kyllinga alba</i> Nees.....	—	11	field	basal cm of leaf. S.W. Africa
<i>Mariscus capensis</i> Schrad.....	—	6	field	basal cm of leaf. S. Africa.

* misidentified as *Ficinia filiformis* Schrad. in Gaff 1971.

TABLE 2.—Drought Tolerance of foliage. The minimum relative humidity (at 28 °C.) which allows survival of 50% or more of the foliage equilibrated to it.

Species	Drought tolerance	Mode of drying	Time left in equilibration chambers (months)
GRASSES			
<i>Brachyachne patentiflora</i>	approx. 0% R.H.	field	6
<i>Eragrostis hispida</i> leaf bases	approx. 0% R.H.	field	4
<i>E. nindensis</i>	0%–2% R.H.	field	4
<i>E. paradoxa</i> leaf bases	approx. 0% R.H.	field	6
<i>Microchloa caffra</i>	5% R.H.	field	6
<i>M. kunthii</i>	approx. 0% R.H.	field	6
<i>Oropetium capense</i>	approx. 0% R.H.	field	3
<i>Sporobolus festivus</i>	approx. 0% R.H.	field	6
<i>S. lampranthus</i> leaf bases	approx. 0% R.H.	field	4
<i>S. stapfianus</i>	2% R.H.	field dry rehydrated and air-dried	7
<i>Triopogon minimus</i>	approx. 0% R.H.	field	7
SEDGES			
<i>Coleochloa setifera</i>	approx. 0% R.H.	field	2
<i>C. pallidior</i>	approx. 0% R.H.	field	6
<i>Cyperus bellus</i> leaf base	10% R.H.	field	6
<i>Mariscus sp.</i> leaf base	approx. 0% R.H.	field	5

APPENDIX

Species examined in which the air-dry foliage failed to survive. Collector's (R. P. Ellis) numbers are given together with abbreviated collection localities: MAUR—Mauritius MLG—Malgasy Republic NC—Northern Cape Province RH—Rhodesia SWA—South West Africa TVL—Transvaal

Antheophora argentea Goosens, 877, NC.

A. pubescens Nees, 927, SWA.

Aristida adscensionis L., 800, 845, 864, NC & RH.

A. aequiglumis Hack., 1036, TVL.

A. congesta Roem. & Schult. subsp. *barbicollis* (Trin. & Rupr.) De Wint., 841, NC.

A. decaryana A. Camus, MLG.

A. effusa Henr., 1064, SWA.

A. engleri Mez, 879, NC.

A. meridionalis Henr., 865, NC.

A. spectabilis Hack., 833, TVL.

A. transvaalensis Henr., 1027, TVL.

A. vestita Thunb., 844, NC.

Asthenantherum glaucum (Nees) Nevski, 872, NC.

Brachiaria nigropedata (Munro ex Fical. & Hiern) Stapf, 834, TVL.

Bulbostylis burchellii C. B., 1038, TVL.

B. oritrephes (Ridl.) C. E. Hubb., TVL.

B. boekleriana (Schweinf.) Beetle, TVL.

Craspedorachis rhodesiana Rendle, 817, RH.

Cymbopogon excavatus (Hochst.) Stapf ex Burt-Davy, TVL.

C. marginatus (Steud.) Stapf ex Burt-Davy, TVL.

Cyperus exilis Willd. ex Kunth., MAUR.

C. obtusiflorus Vahl, TVL.

C. smithii McClean, TVL.

Dolichochoetae biseriata (Stapf) Phipps, TVL.

Danthoniopsis ramosa (Stapf) W. D. Clayton, 1054, SWA.

Digitaria monadactyla (Nees) Stapf, TVL.

Diheteropogon amplectens (Nees) Clayton, TVL.

Diplachne biflora Hack., TVL.

Enneapogon desvauxii Beauv., 856, 842, NC.

E. pretoriensis Stent, 835, TVL.

E. scaber Lehm., 861, NC.

Eragrostis annulata Rendle ex S. Elliot, 921, SWA.

E. brizantha Nees, 910, SWA.

E. capensis (Thunb.) Trin., NC.

E. chapelieri (Kunth) Nees, 816, RH.

E. curvula (Schrad.) Nees, 860, NC.

E. lappula Nees, 815, RH.

E. lehmanniana Nees, 840, 867, NC.

E. patens Oliver, 808, RH.

E. porosa Nees, 871, 923, NC, SWA.

E. pseudo-obtusa de Wint., 839, NC.

E. racemosa (Thunb.) Steud., 1023, TVL.

E. rigidior Pilg., 1052, RH, TVL.

E. stapfii de Wint., 1037, TVL.

E. tenuifolia Hochst., UGANDA.

E. tenella (L.) Beauv. ex Roem. & Schult., MAUR.

Fimbristylis exilis Roem. & Schult., SWA.

F. glomerulata Nees, MAUR.

F. obtusifolia Kunth, MAUR.

Heteropogon contortus (L.) Beauv. ex Roem. & Schult., 849, NC.

Loudetia flavida (Stapf) C. E. Hubb., 798, RH.

L. ramosa (Stapf) C. E. Hubb., TVL.

L. simplex (Nees) C. E. Hubb., TVL.

Monelytrum luderitzianum Hack. emend Schweick., SWA.

Panicum arbusculum Mez, 878, NC.

Rhynchelytrum brevipilum (Hack.) Chiov., 1056, SWA.

R. repens (Willd.) C. E. Hubb., TVL.

R. setifolium (Stapf) Chiov., 1055, SWA.

Schmidtia kalihariensis Stent, 862, NC.

S. pappophoroides Steud., 837, NC.

Setaria appendiculata (Hack.) Stapf, 905, SWA.

S. lindenbergiana (Nees) Stapf, 1029, TVL.

S. perennis Hack., TVL.

Sporobolus coromandelianus (Retz.) Kunth, 912, SWA.

S. fimbriatus Nees var. *latifolius* Stent, 914, SWA.

S. pectinatus Hack., 1076, TVL.

S. pyramidalis Beauv., 846, NC.

Stipagrostis ciliata (Desf.) de Wint., 863, NC.

S. hirtigluma (Steud.) de Wint., 908, SWA.

S. hochstetterana (Boeck. ex Hack.) de Wint., 909, SWA.

S. namaquensis (Nees) de Wint., 881, SWA.

S. obtusa (Del.) Nees, 854, NC.

S. uniplumis (Licht.) de Wint. var. *neesii* (Trin. & Rupr.) de Wint., SWA.

Sutera canescens (Benth.) Hiern., 1041, NC.

Themeda triandra Forsk., TVL.

Tricholaena monachne (Trin.) Stapf et C. E. Hubb., TVL.

Trichoneura grandiglumis (Nees) Ekman, TVL.

Urochloa panicoides Beauv., 916, TVL.

Zoysia tenuifolia Willd., MAUR.