S. Afr. J. Bot. 1997, 63(6) 484–490

Rhizosheath occurrence in South African grasses

Catherine Bailey* and Mary Scholes

Department of Botany, University of the Witwatersrand, Private Bag 3, Wits, 2050 Republic of South Africa
e-mail: cbailey@csir.co.za; mary@gecko.biol.wits.ac.za

Received 19 May 1997; revised 1 October 1997

Rhizosheaths are the sandy coatings which cover the entire length of each root of many of the indigenous grass species growing in South Africa. The results of an extensive herbarium survey showed that rhizosheaths occur on more than 80% of the grass species studied, irrespective of the environmental conditions to which the individuals are exposed. Only 23 species did not have any sheath occurrence. The herbarium survey, together with growth experiments using *Anthephora pubescens* Nees, *Digitaria eriantha* Steud and *Eragrostis pallens* Hack, revealed that the extent of the rhizosheaths (the thickness and consolidation of the sheaths) varies not only between but also within species. The within-species variation is a function of soil texture. The higher the sand content in the soil the greater the number of epidermal hairs produced and the greater the extent of the sheaths. *A. pubescens, D. eriantha* and *E. pallens* individuals in soil with 80% sand had 75, 11 and 100 root hairs per centimetre of root length respectively. In comparison, the individuals in soil with only 30% sand had 55, 5 and 45 root hairs per cm of root length respectively. This relationship indicates that while species have a genetic predisposition to sheath development, the extent to which they develop is a facultative response to soil texture.

Keywords: rainfall; rhizosheaths; sheath extent; soil texture.

*To whom correspondence should be addressed: Division of Water, Environment and Forestry Technology, CSIR, P.O.Box 395, Pretoria, 0001 Republic of South Africa.

Introduction

Rhizosheaths are sandy coatings covering the entire length of every root in sheath forming grasses. They have been described as thick soil cylinders formed by modifications of the rhizosphere, hence the name 'rhizosheaths'. The description of rhizosheaths dates back to the turn of the century when three authors noted their presence on grasses collected in Egypt and more widely in Northern Africa (Volkens 1887; Massart 1898; Price 1911). Further work in North America and Australia in the 1980's confirmed the earlier descriptions (Wullstein & Pratt 1981; Buckley 1982). Initially these structures were defined as sandy sheaths if sand grains were held solely in place by the presence of root hairs. They were only defined as rhizosheaths if an adhesive agent was evident. However, as much of the earlier work was done using herbarium specimens, these specimens did not clearly exhibit mucilage which resulted in the definition of these sheaths being broadened to include all sandy structures. It is now accepted that rhizosheaths consist of a mass of sand particles matted together by a mesh-work of prolific hair-like epidermal structures, mucilage and other products released from the roots (Wullstein & Pratt 1981). Mycorrhizal associations are not present in rhizosheaths (Wullstein & Pratt 1981; Buckley 1982; Goodchild & Meyers 1987) but fungal hyphae may contribute to rhizosheath formation. Their role in the function of the rhizosheath is unclear. Soil particles become entangled among the epidermal hairs due to the intertwining growth of the hairs and may also be bound to the root by cell exudates from the hairs. The bonding between soil particles and epidermal hairs is extremely strong. However, the strength of this bonding differs between species, since in certain species the sheaths are easily removed from the root causing little damage to the root.

Limited research has been done on rhizosheaths, particularly with respect to their occurrence in relation to environmental conditions. Early recordings of the existence of rhizosheaths resulted in the assumption that they were peculiar to xeromorphic species (Price 1911; Oppenheimer 1960; Leistner 1967; Wullstein *et al.* 1979; Wullstein & Pratt 1981; Buckley 1982; Goodchild & Meyers 1987) growing in sandy soil conditions (Price 1911; Oppenheimer 1960; Leistner 1967; Wullstein *et al.* 1979; Marneweck 1990). Duell and Peacock (1985) surveyed a number of mesophytic grass species growing in diverse soil and moisture conditions. Rhizosheaths were found on both cool and warm season perennial grasses occurring as either crop or weedy species. Rhizosheaths were also found to occur among species growing in both high and low fertility conditions. There are a number of casual observations concerning the extent of rhizosheaths on South African grasses, not all of these species have distribution ranges restricted to semi-arid nor sandy soil areas.

This study a) described the occurrence of rhizosheaths on 130 species of South African grasses and quantified the extent of the sheaths and b) addressed the hypothesis that the extent of the sheaths increases as the sandiness of the soil increases.

Material and Methods

Herbarium Study

In order to determine whether rhizosheath occurrence is exclusive to individuals growing in sandy soil and/or arid conditions, a herbarium study was undertaken, at the National Herbarium (Pretoria). Due to their hardy nature, rhizosheaths are not easily removed from roots when the plant is extracted from the soil nor when the roots are lightly washed or shaken. They also press well. Therefore, herbarium specimens were ideal for studying individuals from many different localities, soil types and rainfall regions. Sheaths of pressed specimens can be compared to those of fresh specimens as they are not damaged by pressing. The aim of this study was not to determine cause-and-effect but rather to determine whether a relationship existed between sheath occurrence and thickness and environmental conditions. The advantage of the herbarium study was that it allowed a wide spectrum of species to be sampled.

All specimens of grass species, indigenous to South Africa, were studied provided they had intact rhizosheaths showing no damage and recordings of soil texture conditions and grid references. A total of 1 260 specimens from 130 species was studied. For each specimen, for each of the primary roots, the extent of the rhizosheaths, ie the thickness and consolidation of the sheaths was rated using a scale of 5 (maximum thickness and consolidation) down to 0 (no evidence of sheaths):

5 - Sheathed root diameter: greater than 3.5 mm, well consolidated sheath (soil particles adhere tightly to the sheath). Prolific epidermal hairs that are not easily visible with the naked eye due to the large amount of sand in the sheath.
4 - Sheathed root diameter: 2.6–3.5 mm, sheath often less consolidated with more obvious epidermal hairs.
3 - Sheathed root diameter: 1.1–2.5 mm, sheath even less consolidated. Obvious epidermal hairs.
2 - Sheathed root diameter: 0.75–1 mm, sheath easily removed. Prolific epidermal hairs visible with the naked eye.
1 - Beginning of sheath development, with some soil particles held by prolific epidermal hairs.
0 - none of the above sheath characteristics.

The annual rainfall for the area in which each specimen grew was determined using the grid references and rainfall maps of South Africa.

Growth Experiment

Seeds, collected from field sites, of *Anthephora pubescens*, *Eragrostis pallens* and *Digitaria eriantha* were used in this experiment. All individuals of the first two species were found, during the herbarium study, to have distinct rhizosheaths. *D. eriantha* was found to have greater variability in the extent of the sheaths than the other species depending on the soil and rainfall conditions under which the individuals grew. The individuals from which the seeds were collected had thick rhizosheaths.

Seeds were grown in 1L pots in a controlled-climate growth chamber using a 14 hour day (65–80 μmolm^{-2}s^{-1} quantum flux rate) at 25°C, followed by 10 hours of darkness at 16°C. The pots were randomised weekly to eliminate differences due to position in the chamber. Five sets of plants for each species were used, each set was grown in a different soil texture (Table 1).

Each treatment consisted of five pots/replicates, each containing between ten and sixteen individuals per replicate. The sand (80% sand, 20% clay content) was collected from a broadleafed savanna area where *E. pallens* and *D. eriantha* grow. Kaolin powder was added to the sand to make up the clay fraction in treatments 2–5. The texture was accurately determined using a Boucous Hydrometer (Day 1965). The field capacity for each soil treatment was calculated prior to the experiment and the plants were watered regularly to keep the soil at 70% field capacity. It was necessary to water the sandy soil pots more frequently since this soil drains faster than clayey soil. Watering was carried out by weighing each pot and adding the required amount of water. The nutrient concentration in the different soil treatments was not controlled.

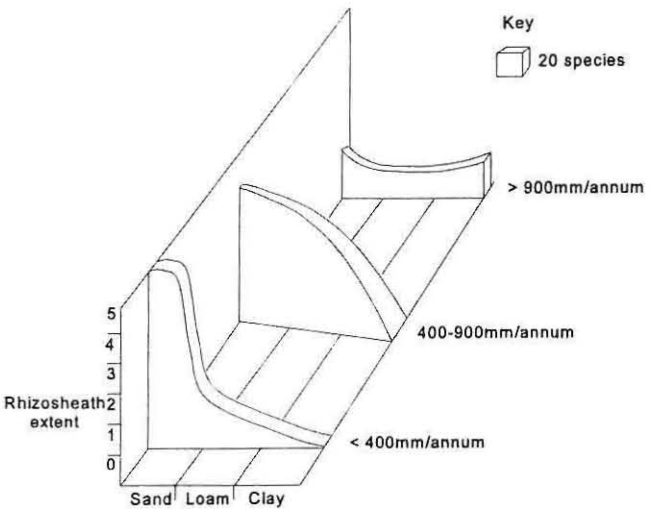

Figure 1 Occurence of species in terms of soil and rainfall conditions and trends in extent of rhizosheaths.

Table 1 Percentage sand and clay content in the soil treatments

Treatment	% sand	% clay
1	80	20
2	70	30
3	60	40
4	50	50
5	30	70

After twelve weeks of growth the plants were uprooted and the presence and extent of rhizosheaths was scored for ten individuals per replicate using the same scale as in the herbarium study. Using a dissecting microscope, the number of epidermal hairs per unit length of root were counted on five of the primary roots of each individual.

Results

Herbarium Study

Rhizosheaths occur on individuals growing in all soil textures and in all rainfall areas (Figure 1). The presence of rhizosheaths is therefore independent of soil texture and rainfall conditions. The presence is also not restricted to certain genera or even tribes (Table 2). Rhizosheaths occurred on 107 of the 130 species studied. Of these 107 species, six did not possess rhizosheaths on all individuals. Neither rainfall nor soil texture appeared to affect the presence of sheaths, or lack thereof, since there were no trends within the six species with regard to these conditions and sheath thickness and consolidation. Within the other 101 species, all individuals possessed sheaths, the only variation being the thickness and consolidation of the sheaths. It has still to be determined to which conditions rhizosheath development is responding. Most of the 23 species on which sheaths did not occur (Table 2), had no representative individuals in arid areas. Those that do, have less than 30% of their individuals in these areas. Relationships appear to exist between the extent of rhizosheaths and soil texture and rainfall conditions (Figure 1).

There is a high representation of species in sandy, arid (rainfall less than 400 mm/annum) areas. Among these species the rhizosheaths are generally thick and well consolidated. There is also a high representation of species in semi-arid areas (rainfall 400–900 mm/annum), especially on clay soil. In both these rainfall categories the individuals in the sandy soil regions generally have more extensive sheaths than those in clay soil. These trends indicate a relationship between the extent of sheaths and soil texture.

The average extent of sheaths in sandy soil is lower in high rainfall (more than 900 mm/annum) areas than that in arid and semi-arid areas. Within high rainfall areas, the sheath-forming species develop sheaths of similar extent irrespective of the soil type. There is also a high number of species without sheaths in these areas. These trends show that a relationship exists between extent of sheaths (thickness and consolidation) and rainfall conditions, especially among individuals found growing on sandy soil.

Growth Experiment

The higher the sand content the greater the number of epidermal hairs produced and the greater the extent of the sheaths (Table 3). Similar trends were evident with regard to the change in number of epidermal hairs and extent of rhizosheaths in response to the percentage sand content in the soil.

The increase in rhizosheath extent appears to be a response to an increase in sand content in the soil. The thicker, more consolidated rhizosheaths occurred on individuals growing in soil with the highest sand content.

Table 2 Similarity table based on extent of rhizosheaths. An indication of whether the species are annual (A) or perennial (P), to which tribes the species belong and the number of specimens sampled are given. The key to the tribes is given after the table. However, the key to the numbers follows here:

	% of specimens		% of specimens
1	1–9	4	50–69
2	10–29	5	70–99
3	30–49	6	100

			Extent of rhizosheath:	5	4	3	2	1	0
Tribe	A/P	# specimens	Species						
Chl	P	15	*Eragrostis pallens*	6					
Chl	A	10	*E. cilianensis*	5	2				
Pan	A	10	*Brachiaria brizantha*	5	3				
Ari	P	10	*Stipagrostis namaquensis*	4	4				
Ari	P	9	*S. ciliata* var. *capensis*	4	3				
Chl	A/P	28	*Pogonarthria squarrosa*	4	3				
Chl	P	20	*Eragrostis obtusa*	4	3				
Chl	P	37	*E. curvula*	3	5				
Chl	P	21	*Sporobolus ioclados*	3	4				
Pap	P	35	*Schmidtia pappophoroides*	3	4				
Pan	P	15	*Brachiaria serrata*	3	4				
Pan	P	21	*B. nigropedata*	2	5				
Pan	P	15	*Anthephora pubescens*	2	5				
Chl	P	9	*Sporobolus fimbriatus*	2	5				
Chl	P	19	*S. nitens*	2	5				
Pan	P	16	*Panicum deustum*	4	2	2			
Pan	A/P	25	*P. maximum*	2	3	3			
Chl	P	21	*Fingerhuthia africana*		6				
Pap	P	13	*Schmidtia kalihariensis*		6				
Ari	P	7	*Stipagrostis uniplumis* var. *neesii*		6				
Ari	A	13	*S. uniplumis* var. *uniplumis*		6				
Ari	P	15	*S. obtusa*		5	2			
Ari	P	16	*Aristida diffusa* subsp. *burkei*		5	2			
Ari	P	8	*A. diffusa* subsp. *diffusa*		5	2			
Chl	P	7	*Cynodon hirsutus*		4	4			
Chl	P	15	*Eragrostis capensis*		4	3			
Bro	A	9	*Bromus diandrus*		3	4			
Ari	P	11	*Aristida vestita*		3	4			
And	P	11	*Cymbopogon marginatus*		3	4			
Pap	P	30	*Enneapogon cenchroides*		2	4	3		
Poe	P	16	*Festuca scabra*		2	4	2		
Pan	P	44	*Digitaria eriantha*		1	4	3		
Pan	P	7	*D. natalensis*			5	2		
Pan	P	6	*Urochloa oligotricha*			5	2		
Bro	A	15	*Bromus pectinatus*			6			

Table 2 Continued

			Extent of rhizosheath:	5	4	3	2	1	0
Tribe	A/P	# specimens	Species						
Pap	P	7	*Enneapogon pretoriensis*			6			
Pap	P	11	*E. scaber*			6			
And	P	7	*Cymbopogon prolixus*			6			
Sti	P	4	*Stipa dregeana* var. *dregeana*			6			
Tri	A	8	*Hordeum murinum* subsp. *glaucum*			6			
Tri	A	6	*H. murinum* subsp. *leporinum*			4	4		
Tri	A	3	*H. murinum* subsp. *murinum*			4	3		
Ari	P	21	*Aristida congesta* subsp. *congesta*			4	3		
Ari	P	16	*A. junciformis* subsp. *junciformis*			4	3		
And	P	6	*Bothriochloa radicans*			4	3		
Ave	P	11	*Helictotrichon turgidulum*			2	3	2	
Poe	A	8	*Lolium rigidum*			2	4	2	
And	P	25	*Cymbopogon plurinodis*			3	4		
And	P	11	*Hyparrhenia dregeana*			3	4		
And	P	24	*Urochloa mosambicensis*			3	4		
Pan	P	15	*Panicum coloratum*			3	4		
Pan	A	9	*Setaria nigrirostris*			3	4		
Pan	P	16	*S. sphacelata* var. *sphacelata*			3	4		
Pan	P	14	*S. verticillata*			3	4		
Ave	A	8	*Phalaris minor*			3	5		
Pan	P	25	*Setaria sphacelata* var. *torta*			2	5		
Pan	P	16	*S. incrassata*			2	5		
Pan	A	7	*Digitaria ternata*			2	5		
And	P	15	*Bothriochloa insculpta*			2	5		
And	P	17	*Cymbopogon validus*			2	5		
And	P	12	*Hyparrhenia anamesa*			1	5		
And	P	15	*H. filipendula* var. *pilosa*			1	5		
Pap	P	17	*Enneapogon scoparius*			1	5		
And	A	11	*Urochloa brachyura*			1	5		
Ave	A/P	13	*Agrostis lachnantha* var. *lachnantha*			1	5		
Poe	A	4	*Vulpia fasciculata*				6		
Chl	A	6	*Triraphis purpurea*				6		
And	P	11	*Bothriochloa bladhii*				6		
And	P	5	*Schizachyrium jeffreysi*				6		
And	P	3	*S. ursulus*				6		
And	P	24	*Hyparrhenia hirta*				6		
Bro	A/P	13	*Bromus catharticus*				5	1	
And	P	7	*Hyparrhenia filipendula* var. *filipendula*				5	2	
Mel	P	4	*Melica racemosa*				5	2	
Chl	A/P	11	*Chloris pycnothrix*				4	3	
Aru	P	6	*Danthoniopsis pruinosa*				4	4	

Table 2 Continued

			Extent of rhizosheath:	5	4	3	2	1	0
Tribe	A/P	# specimens	Species						
Poe	P	6	*Lolium perene*				4	4	
Chl	P	6	*Fingerhuthia sesleriiformis*				4	4	
Chl	P	11	*Eragrostis racemosa*				3	4	
Pan	A	21	*Urochloa panicoides*				3	4	
And	P	12	*Hemarthria altissima*				3	4	
Mel	P	3	*Melica decumbens*				3	4	
Bro	P	3	*Bromus leptoclados*				3	4	
Ave	A	14	*Polypogon monspeliensis*				2	5	
Ave	P	4	*Agrostis eriantha* var. *eriantha*				2	5	
Aru	P	20	*Tristachya leucothrix*				2	5	
Poe	A	8	*Vulpia myuros*				2	5	
Poe	A	4	*V. muralis*					6	
Poe	A/P	8	*Lolium multiflorum*					6	
Aru	P	12	*Loudetia flavida*					6	
Aru	P	8	*Tristachya rhemannii*					6	
Tri	A	4	*Hordeum capense*					6	
Bra	P	10	*Brachypodium distachyon*					6	
Bra	P	4	*B. flexum*					6	
Ave	P	4	*Phalaris arundinaceae*					6	
Ave	P	4	*Helictotrichon hirtulum*					6	
Ave	P	5	*Helictotrichon longifolium*		2		5		
Ehr	A/P	15	*Ehrharta calycina*		2		3	3	
Pan	A	13	*Panicum schinzii*			2	3	2	
Chl	P	20	*Chloris virgata*			2	3	2	
Chl	P	9	*Cynodon incompletus*		2			5	
Chl	P	30	*C. dactylon*		2	2		3	3
Chl	P	18	*Sporobolus virginicus*			2			5
Chl	A	10	*S. pyramidalis*	2	2				5
Pan	P	13	*Digitaria monodactyla*					2	5
Aru	P	3	*Danthoniopsis parva*					4	3
Aru	P	20	*Loudetia simplex*					3	5
Aru	P	7	*Trichopteryx dregeana*						6
Aru	P	17	*Arundinella nepalensis*						6
Aru	P	5	*Tristachya biseriata*						6
Chl	P	17	*Triraphis andropogonoides*						6
Chl	P	7	*T. schinzii*						6
Pan	P	15	*Panicum natalense*						6
Pan	P	11	*Digitaria argyrograpta*						6
And	P	20	*Cymbopogon excavatus*						6
And	P	21	*Schizachyrium sangiuneum*						6
And	P	31	*Elionurus muticus*						6

Table 2 Continued

			Extent of rhizosheath:	5	4	3	2	1	0
Tribe	A/P	# specimens	Species						
And	P	15	*Urelytrum agropyroides*						6
Bra	P	3	*Brachypodium bolusii*						6
Ave	A	10	*Polypogon strictus*						6
Ave	A	12	*P. viridis*						6
Poe	P	5	*Festuca caprina*						6
Poe	P	4	*F. costata*						6
Poe	A	6	*Vulpia bromoides*						6
Poe	A	9	*Poa annua*						6
Poe	P	8	*P. binata*						6
Ehr	P	5	*Ehrharta capensis*						6
Ehr	A	7	*E. delicatula*						6
Ehr	P	7	*E. erecta* var. *natalensis*						6
Pry	P	12	*Leersia hexandra*						6

Key to abbreviations

	Tribe
And	Andropogoneae
Mel	Meliceae
Ari	Aristideae
Pry	Oryzeae
Aru	Arundinelleae
Pan	Paniceae
Ave	Aveneae
Pap	Pappophoreae
Bra	Brachypodieae
Poe	Poeae
Bro	Bromeae
Sti	Stipeae
Chl	Chlorideae
Tri	Triticeae
Ehr	Ehrharteae

Table 3 Extent (ext.), i.e. thickness and consolidation of the sheaths, and mean number and standard deviations (std) of epidermal hairs per cm of root (# hairs), found on 10 individuals of each of the three grass species growing on five different soil textures

Treatment		*A. pubescens*			*D. eriantha*			*E. pallens*		
% sand	% clay	ext	# hairs	std	ext	# hairs	std	ext	# hairs	std
80	20	5	75	0.93	3	11	1.08	5	100	0.96
70	30	4	67	0.95	2	8	1.84	4	100	0.70
60	40	2	55	0.90	1	5	1.60	3	60	0.71
50	50	2	55	0.90	1	5	1.81	3	60	1.93
30	70	2	55	1.88	1	5	1.70	2	45	0.78

Discussion

The majority of South African grass species have a genetic predisposition to develop rhizosheaths. There is no relationship between occurrence and thickness of sheaths and soil texture or rainfall conditions. Sheaths occur on individuals regardless of the soil texture. Similarly, sheaths occur on individuals from all rainfall regions studied. There is also no correlation between sheath occurrence and whether the species is an annual or a perennial.

A distinction must be made between the presence of sheaths and the extent of the sheaths. While species have a genetic predisposition to develop sheaths, in all except six species, the extent of the sheaths is a facultative response to soil texture and rainfall conditions which directly affect soil water content. The general trend in all rainfall regions is that in sandy soil the individuals have more extensive sheaths than individuals in more clayey soil. This is particularly marked within the lower rainfall regions (900 mm/annum or less). Since different soil textures have different chemical as well as physical properties they present the plants with different environmental conditions, which result in more or less favourable growth conditions for the plants. For example, sandy soil has a lower water holding capacity and nutrient content than clay soil. Sheath occurrence may be an indirect response not only to the different textures but also to the different water holding capacities and nutrient availabilities of the soils. This hypothesis is supported by the observation that, compared with the situation in low rainfall areas, in high rainfall regions (more than 900 mm/annum) the extent of the sheaths is similar in individuals on all soil types. This suggests that the occurrence of thicker sheaths may be a response to lower soil water contents.

The growth experiments confirmed the hypothesis that the extent of sheaths increase in response to increased sandiness of the soil. It must however be remembered that the nutrient concentration of the soil used in the experiment was changed by the addition of clay. Adding variable amounts of nutrients to each pot to compensate for the addition of nutrients in the clay fraction would not have been easy and would probably have confounded the experiment. The kaolin addition may also have affected the pH and thereby influenced root growth, since higher amounts of calcium and thus a higher pH may have increased root production.

Although the extent of the sheaths varied between the three species, the trends were similar within a species. Within each species the most extensive sheaths occurred in the individuals growing in sandy soil. The higher the sand content in the soil the higher the density of epidermal hairs that were produced and the thicker, more consolidated the sheath. This finding is in accordance with previous work which showed that the density of epidermal hairs is greater in sandy soil (Kutchera 1960 in Leistner 1967). It has been observed that roots in sandy soil produce more epidermal hairs than roots of the same species in less sandy soil (Fey, pers comm). The more hairs there are the greater the number of tightly bound soil particles there are. This bonding between soil particles and epidermal hairs is extremely strong, especially when formed in sandy soil. This work confirms that of Duell and Peacock (1985), who showed that the occurrence of rhizosheaths is not confined to a few species of grasses growing under xeric conditions in sandy soils.

The significance of these rhizosheaths needs to be elucidated. There has been some suggestion that rhizosheaths aid in seedling establishment under harsh environmental conditions. There is little data to support this suggestion. Duell and Peacock (1985) reported that seedlings had to attain a critical size before rhizosheaths were discernible on nodal roots. Rhizosheaths were never found on seminal roots. The need for an improved mechanism for overcoming drought stress, as has been suggested in the case of desert species (Buckley 1982), would not seem applicable to mesophytic grasses.

It is also suggested that these rhizosheaths are instrumental in the supply of phosphorus to plant roots by creating an environment favourable for soil mirco-organisms. Phosphorus, being relatively immobile, relies on diffusion for uptake and rhizosheaths may aid this process. Studies to address this hypothesis are in progress.

References

BUCKLEY, R. 1982. Sand rhizosheath of an arid zone grass. *Plant and Soil* 30: 105–108.

DAY, P.R. 1965. Particle fractionation and particle-size analysis. In: Methods of soil analysis. Part 1 Physical and mineralogical properties, eds. C.A. Black, D.D. Evans, L.E. Ensinger, J.L. White and F.E. Clarke. American Society of Agronomy, Wisconsin, USA.

DUELL, R.W. & PEACOCK, G.R. 1985. Rhizosheaths on mesophytic grasses. *Crop Science* 25: 880–883.

GOODCHILD, D.J. & MEYERS, L.F. 1987. Rhizosheaths - a neglected phenomenon in Australian Agriculture. *Aust. J. Agric. Res.* 38: 559–563.

LEISTNER, O.A 1967. The plant ecology of the southern Kalahari. *Botanical Survey South African Memoir* 38.

MASSART, J. 1898. Un voyage botanique au Sahara. *Bulletin of the Botanical society, Belgium* 37: 237–240.

MARNEWECK, G.C. 1990. The structure and distribution of sand grain root sheaths in southern African grasses. Honours thesis. University of the Witwatersrand.

OPPENHEIMER, H.R. 1960. Adaptation to drought: Xerophytism. *Arid Zone Research* 15: 105–138.

PRICE, S.R. 1911. The roots of some north African desert grasses. *New Phytologist.* 10: 328–339.

VOLKENS, G. 1887. Die Flora der aegyptisch-arabischen. Wuste auf Grunlage anatomisch-physiologischer Forschungen. Gebruder Borntraeger, Berlin.

WULLSTEIN, L.H., BREUNING, M.L. & BOLLEBN, W.B. 1979. Nitrogen fixation associated with sand grain root sheaths (Rhizo sheaths) of certain xeric grasses. *Physiologia Plantarum* 46: 1–4.

WULLSTEIN, L.H & PRATT, S.A. 1981 Scanning electron microscopy and rhizosheaths of *Oryzopus hymenoides*. *American Journal of Botany* 68: 408–419.