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Sand rhizosheath of an arid zone grass

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Summary The root sheath of the arid zone grass *Zygochloa paradoxa* comprises a dense cylinder of sand grains held mainly by short twisted root hairs. The sand sheath and hypodermal sleeve enclose a thick cortex with a sclerenchymatous inner zone and a partially disintegrated aerenchymatous outer zone. The outer tube comprising sheath and hypodermal sleeve is largely impermeable to water and its primary function is probably to insulate the stele against moisture loss during translocation.

Introduction

Many perennial grasses of arid sandy habitats possess cylindrical sand sheaths encasing their roots[5,12,20,22,24,25]. Such species are particularly abundant in sandy habitats with marked fluctuations in the soil moisture content[9] (Latz pers. comm., El-Sharkarwy pers. comm.), and generally have extensive root systems with shallow laterals up to 20 m long[14,16,17,21,22] and persistent root hairs and a spongy cortex[1,11]. Cortical morphology has been described by Henrici[9], Goossens[8], Beckel[1] and Robards *et al.*[18], but the structure and function of the sand sheath have not been analysed previously, probably because it defies conventional sectioning. The grains may be cemented by mucilage[8,17], probably a pectoglucan complex[15].

There have been four hypotheses regarding the function of these root sheaths. First, Thomas[20] and Oppenheimer[16] suggested that they protect the stele against mechanical abrasion and soil compression, but this is unlikely since the sheath is considerably more fragile than the stele. Second, Henrici[9], Killian[10] and Kutschera[11] suggested that the sheath increases moisture absorption from damp sands, but the sheath was not connected to the stele save by isolated strands of disintegrated cortical cells. Third, *Oryzopsis hymenoides* rhizosheaths contain nitrogen-fixing bacteria[26,27], but nutrient transfer to the plant has not been demonstrated conclusively. The sand filled mounds of *Zygochloa paradoxa* contain more extractable phosphorus than control soils[4], which suggests that the sheaths may be mycorrhizal (Latz pers. comm.) but could also represent secondary soil P enrichment by animals living in the mounds. Fourth, Warming[24], Goossens[8], and Walter[23] suggested that the sheaths insulate the stele against moisture loss. Such insulation could also be provided by the hypodermal sleeve rather than the sand sheath[7,18].

Methods

The species studied here is *Zygochloa paradoxa* R.Br., from the longitudinal dunes of the Simpson Desert, Australia[2,3]. Root systems were first traced to 6 m depth by field excavations. Sheath and cortex structures were investigated by microscopic examination of fractured specimens, of 30 micron epoxy-embedded petrological thin sections, and of wax-embedded microtome sections of sheathless roots from plants growing in loam. I stained the last with toluidine blue 0 or phloroglucinol/HCl to aid morphological interpretation[13], or with lactophenol cotton blue for fungal hyphae. I tested for intergranular cements by treating portions of sheath with water, ethanol, carbon tetrachloride, dilute perchloric acid, and a commercial 'pectinase' comprising pectin esterase, pectin transeliminase, and endopolygalacturonase at relative activities of 275, 800 and 950 μml^{-1}, together with a cellulase. To test whether the outer tube comprising hypodermal/epidermal sleeve and rhizosheath is permeable to

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water, I sealed intact sections of sheath between two sections of plastic tubing, using a low-viscosity glue to penetrate the voids between the sand grains in the sheath. I passed water through the sections under a 20 cm head, and measured the time till first leakage. I subjected additional sections to increasingly greater heads of water and noted the pressure at which leakage first occurred, and the initial leakage rate. I was not equipped to measure sleeve/sheath permeabilities by the method of Robards *et al.*[18], or to measure acetylene reduction by sheath material.

Results

Individual roots of *Zygochloa paradoxa* can reach 6 m in vertical depth and perhaps more, but roots are extremely sparse at such depths, and the majority are clustered near the surface. Numerous adventitious roots arise from the rhizomes within or immediately below the sand mounds. Sheaths are thickest in the top 40 cm but extend to 2 m vertical depth. Shallow laterals have been traced to 10 m from the parent plant, and live Zygochloa roots are sometimes exposed on the dune surface by the shifting sands over 15 m from the nearest plant. Overall, the root system comprises a few deep tap roots together with numerous extensive sparsely-branching laterals.

The sections revealed the transverse structure shown in Figures 1 and 2. The polyarch stele contains a central pith and sclerenchymatous conjunctive tissue. The uniseriate endodermis is encircled by an inner cortex comprised of radially arranged, heavily sclerotised, slightly flattened intact cells, sharply delimited from an outer cortex of large thin-walled partially-disintegrated cells. These cortical lamellae support the central strand axially in an outer cylinder, round which angular and well-sorted aeolian sand grains are packed regularly and closely. The outer cylinder comprises epidermis, exodermis and hypodermis, and supports a dense piliferous mat of short curly root hairs which invest and retain the sand grains. These root hairs are also revealed well in fractured specimens. A few fungal hyphae run between the grains and penetrate the exodermis, but are too sparse to be described as a mycorrhiza. The root hairs do not extend beyond the grains, and their primary function in the mature root appears to be to hold the grains in place. Few grain contacts were evident in the sections, since the approximately isodiametric grains are much thicker than the section. The sheaths include occasional grains of heavy minerals, but are composed primarily of quartz grains with the red haematite-clay coating characteristic of the central Australian desert sands.

The grains were not dislodged by prolonged gentle washing in water, ethanol or carbon tetrachloride, and remained firmly attached if the sheath was then brushed with a small nylon-bristle brush. Similar treatment in dilute perchloric acid dislodged a few grains, and softened the sheath so that gentle brushing dislodged many more. The commercial pectinase produced a similar effect. This indicates that any cement is probably mucilaginous rather than resinous, but that the root hairs provide the primary means of attachment.

Water can be passed through sections of the outer cylinder for 24 hr without leakage. Sections can also withstand a head of 50 cm water without leakage; when it occurs, leakage is through rootlet junctions and small defects in the sheath, at rates of the order of 1 cm^3/cm^3/cm water/hr under a head of 50 cm water. The outer cylinder is therefore relatively impermeable to water.

Discussion

The structure of the root corresponds with previous descriptions for sheathless aerenchymatous grass roots, referred to earlier. The structure of the sheath has not been described before.

Do the sheaths insulate the stele against moisture loss? Held axially in a sand sheath, the stele is surrounded by a zone of still air and cortical lamellae comparable to expanded foam plastics. These sheaths are sufficiently flexible to accommodate small substrate movements such as those produced by minor slipface slumping, and they invest the conducting strands continuously from the damp sand below 2 m depth to the root bases between the modified leaf sheaths encasing the rhizomes. During prolonged drought, when the dune sands may become completely air-dry to a depth of 1–2 m, the damp sands at the distal ends of the long laterals are connected to the plant stems through many metres of hot dry sand. I suggest that the sheaths minimise moisture loss en route as water is

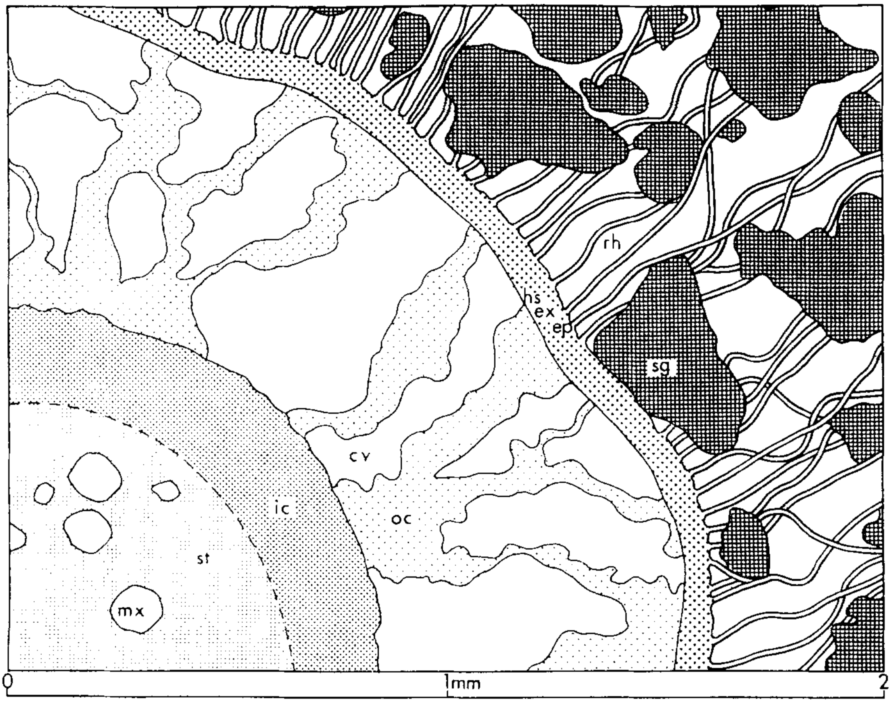

Fig. 1. Section of *Zygochloa paradoxa* root and rhizosheath. Drawn from photomicrograph of ground and polished epoxy-embedded section. Figure diagonal bottom left to top right is complete radius from stele centre to outer margin of root sheath. mx, metaxylem; st, stele; ic, inner cortex; cv, cortical voids; oc, outer cortex; hs, ex, ep, hypodermal sclerenchyma, exodermis, epidermis (not clearly differentiated); rh, root hair; sg, sand grain.

translocated along these laterals. The hypodermis and sheath are together relatively impermeable to moisture loss, supporting the hypothesis that the overall function of the mature aerenchymatous cortex, hypodermal/exodermal sleeve and sand sheath is to minimise such loss. Robards *et al.*[18] concluded similarly that 'the development of the root of *Carex arenaria* seems to afford the central conducting strand strong protection against adverse conditions at the expense of sacrificing any role in water or ion uptake.'

What advantage is conferred by the sand sheath itself? Since I could not separate sand sheath and hypodermal/exodermal sleeve, I could not test their effects independently. It seems likely that the sheath's primary function is to protect the delicate hypodermis and cortex, which insulate the stele against moisture loss, permitting successful translocation of moisture from damp sand through many metres of dry sand during drought. Such sheaths are almost certainly a major factor contributing to the drought tolerance of *Zygochloa paradoxa* and similar species, and thereby to their success on arid sands.

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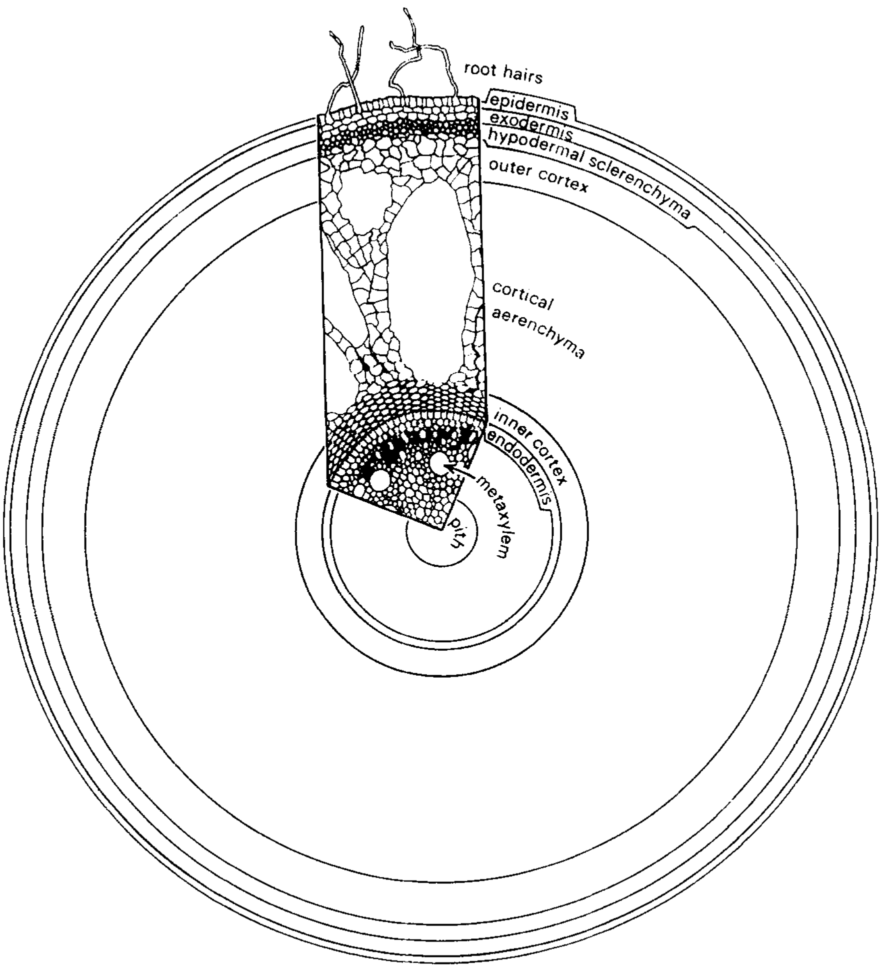

Fig. 2. Section of sheathless *Zygochloa paradoxa* root. Drawn from photomicrograph of wax-embedded microtome section. Total diameter 4 mm.

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