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Formation and Stabilization of Rhizosheaths of *Zea mays* L.[1]

Effect of Soil Water Content

Michelle Watt, Margaret E. McCully*, and Martin J. Canny

Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Canada K1S 5B6

Field observations have shown that rhizosheaths of grasses formed under dry conditions are larger, more coherent, and more strongly bound to the roots than those formed in wet soils. We have quantified these effects in a model system in which corn (*Zea mays* L.) primary roots were grown through a 30-cm-deep prepared soil profile that consisted of a central, horizontal, "dry" (9% water content) or "wet" (20% water content) layer (4 cm thick) sandwiched between damp soil (15–17% water content). Rhizosheaths formed in dry layers were 5 times the volume of the subtending root. In wet layers, rhizosheaths were only 1.5 times the root volume. Fractions of the rhizosheath soil were removed from individual roots by three successive treatments; sonication, hot water, and abrasion. Sonication removed 50 and 90% of the soil from rhizosheaths formed in dry and wet soils, respectively. After the heat treatment, 35% of the soil still adhered to those root portions where rhizosheaths had developed in dry soil, compared with 2% where sheaths had formed in wet soil. Root hairs were 4.5 times more abundant and were more distorted on portions of roots from dry layers than from wet layers. Drier soil enhanced adhesiveness of rhizosheath mucilages and stimulated the formation of root hairs; both effects stabilize the rhizosheath. Extensive and stable rhizosheaths may function in nutrient acquisition in dry soils.

Rhizosheaths are coherent entities, formed under the influence of the root, that remain attached to the root when it is removed from the surrounding soil. Work with field-grown corn (*Zea mays* L.) in our laboratory indicates that these sheaths include, in addition to soil particles, a network of root hairs, a native bacterial flora (Gochnauer et al., 1989), and mucilages produced by both the root and the associated bacteria, which act as adhesives maintaining sheath coherence and adherence (Watt et al., 1993). Sheaths overlie the younger portions of the roots where the large, late metaxylem vessel elements are still alive and not yet conducting the transpiration stream (McCully and Canny, 1988). As a likely consequence, the relative water content is higher in the sheathed regions of roots than in the older, bare regions where the late metaxylem vessels are mature and open (Wang et al., 1991).

Casual field observations of maize and other mesophytic grasses growing over the course of several summers have drawn our attention to an interesting characteristic of their rhizosheaths: they are thicker and held to the root with greater tenacity when formed in the drier soils of midsummer, and they are less substantial and more easily removed from roots growing in the wetter soils of early spring. Therefore, although sheathed portions of roots are wet and fleshy zones, sheaths are more fully developed in drier soil conditions. In this study we have quantified this somewhat paradoxical, inverse relationship between the water content of the soil and the extent and tenacity of rhizosheath formation.

We have adapted an experimental system used by Nambiar (1976) to study zinc uptake by roots in dry soil. This experimental system consisted of three layers of soil, with a dry middle layer, containing ^{65}Zn, isolated from two sandwiching moist layers by two hydrophobic yet root-permeable partitions. We were attracted to Nambiar's experimental set-up for three reasons. First, he found that the region of the roots from the dry zone had a tightly adhered annulus of soil, whereas the rest of the root bound relatively less soil. Second, he reported an unexpectedly high amount of labeled zinc taken up by the regions in the dry zone, suggesting a correlation with soil sheath development. Third, the technique would provide us with a way to control soil water content around a small region of the root system, thus ensuring that any changes occurring in that region were due to changes in soil water content and not to changes in root water status. Here, using maize plants, we have pre-set the water content of a layer of soil (to either "dry "or "wet"), separated it from the rest of a soil profile by wax-paraffin partitions, and quantified and observed sheath formation and tightness of soil binding between root samples and along individual roots.

MATERIALS AND METHODS

Cultivation of Plant Material

Corn (*Zea mays* L. cv Seneca Chief) seeds were allowed to imbibe 3 to 5 h and germinated on moist filter paper in sealed Petri dishes for 40 to 48 h at 26°C. Uniform seedlings with radicles 2 to 3 cm in length were each carefully transferred to 2 cm below the surface of the top layer of a prepared soil profile in a growth tube (see below). The plants were left to grow for 5 d in a greenhouse (approximately 23°C, 14 h light/10 h dark), by which time their primary roots had grown

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* Corresponding author; fax 1–613–788–4497.

Abbreviation: *SWC*, soil water content.

through the soil profile. A minimum of 10 plants were grown for each treatment. They were watered with tap water every 1.5 d from the top and on d 3 from the bottom.

Preparation of Soil Profiles

Soil profiles were prepared from sandy loam topsoil obtained from a field plot at the Central Experimental Farm of Agriculture Canada, Ottawa. As in Nambiar's (1976) experiment, each profile contained three layers of soil, each isolated from the next by a hydrophobic partition (Fig. 1). These partitions allowed the layers to be maintained at different water contents but did not hinder penetration of the roots through the profile.

Soil profiles were prepared in 5-cm-diameter black plumbing pipes (ABS/DWV T162, Canadian Tire, Ottawa, Canada), cut to 30-cm lengths and slit down one side so the tubes could be hinged open at the time of harvest of the roots. The tubes were held together and sealed along the vertical slit with electrical tape during soil profile preparation and plant growth. Snug-fitting plumbing caps with five holes (1 cm diameter each) for drainage and aeration of soil were used as pot bottoms.

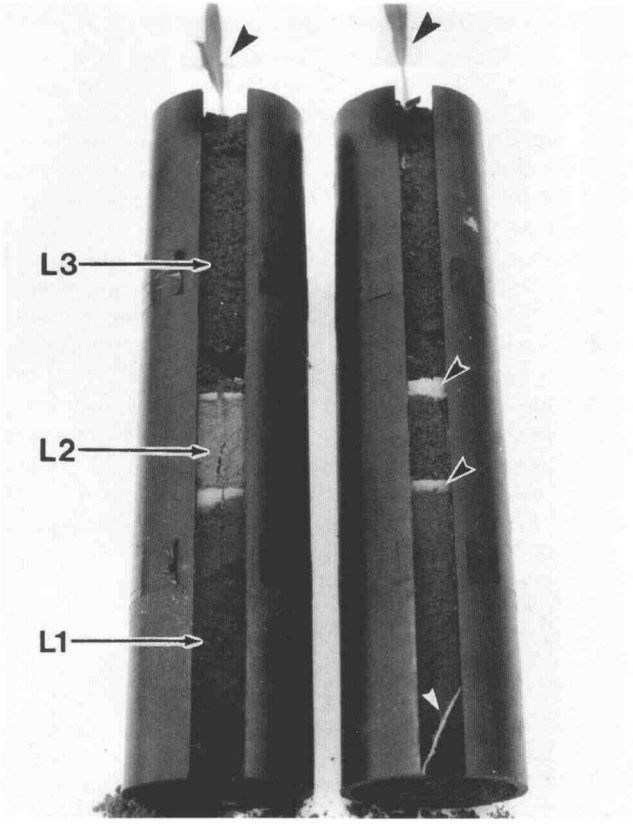

Figure 1. Pots have been hinged open to reveal three-layered profiles of soil through which the primary roots of 7-d-old corn (*Zea mays* L.) plants have grown. Wax-paraffin partitions (black-on-white arrowheads) keep the soil of the middle layers (L2) "dry" (9% *SWC*) (pot on left-hand side) or "wet" (20% *SWC*) (pot on right-hand side) relative to the soil of L1 and L3, but allow penetration of the roots (white arrowhead). Black arrowheads indicate shoots. ×0.3.

The first layer of soil (L1) was gently packed (and its surface flattened) into each tube to a height of 10 cm from the bottom. The water content of the soil was unaltered and similar to that found under normal field conditions (15–17% [w/w] water). Then 15 mL of a molten mixture (melting point 37–39°C) of 1 part bee's wax (Benson Bee Supplies, Metcalfe, Ontario, Canada) and 2.5 parts paraffin oil (viscosity 345–455, S894, J.T. Baker Chemical Co., Phillipsburg, NJ) was poured over the entire surface of L1 and allowed to solidify.

The second, middle layer of soil (L2), 4 cm deep, was gently packed and flattened over the wax:paraffin partition. In contrast to L1, this soil was initially prepared to a desired water content by thoroughly mixing a predetermined weight of air-dried soil with the appropriate amount of tap water. "Dry" samples had 9% (w/w) water, and "wet" samples had 20% (w/w) water. A soil-water characteristic curve showed that water potentials of the dry and wet samples were about −1.5 and −0.06 MPa, respectively (G.C. Topp, Agriculture Canada, personal communication). Another 15 mL of molten wax and paraffin oil was poured over L2, sandwiching the layer of soil of controlled water content between two hydrophobic barriers. Finally, the remainder of each tube (16 cm to top) was filled with unprepared soil similar to that used for L1. This was the seed-bed layer (L3).

Plant Harvest

Plants were easily recovered with their root systems intact from hinged-open tubes provided that the wax partitions were carefully cut away from the contact with the root. To maintain the water status of the excavated roots and their adhering soil, the three regions of the primary roots were immediately covered with soil from the corresponding layer (L1, L2, or L3). Quantitative observations were started within 15 to 30 min of uprooting the plants and qualitative observations of root structure were also performed on fresh plants or plants preserved in formaldehyde (3.7% in tap water).

Quantitative Measurements

SWC

The *SWC* of L2 was determined at soil profile preparation and at plant harvest for each sample. During initial experimental trials, *SWC* was determined for L1 and L3.

A small aliquot of soil (approximately 1–2 g) was quickly scooped into a tared, 10-mL glass vial, which was capped, then the fresh weight (*W1*) of the aliquot was determined. Dry weight (*W2*) of the soil was determined after 4 to 5 d of drying at 105°C. Then *SWC* was calculated from:

$$SWC = \%\ \text{water (w/w)} = [(W1 - W2)/W2] \times 100$$

Relative Volume of Sheath to Volume of Root

The extent of sheath formation around the portion of root from L2 was quantified by measuring the ratio between sheath and root volumes, assuming cylindrical shapes for the piece of root and its surrounding sheath of soil.

The root portion from L2 was cut from the rest of the primary root and, with minimum agitation, measured lengthwise (l) to give the midpoint. From there, three thin (<200

μm) transverse sections were taken (the root portion lay on soft dental wax and a fresh, wet, surgical steel razor blade was carefully drawn through sheath plus root) and mounted in a drop of immersion oil (to prevent dispersion of the sheath) on a microscope slide, and a coverslip was gently placed on top. To prevent squashing and thus distorting the soft root sections, the coverslip was supported by two shims made from a broken coverslip. Using ocular and stage micrometers in a microscope, radii of the root (r_1) and the sheath plus root (r_2) were obtained from their diameters measured at three points (120° apart) on each cross-section circumference. From these radii, the ratio of sheath to root volume (V) was calculated from the derived formula:

$$V_{sheath}/V_{root} = [(r_2)^2/(r_1)^2] - 1$$

Strength of Soil Adhesion

After the transverse sections were removed for relative volume calculations, the remaining halves of the root portion were immediately used to determine how tightly the soil of the sheath was bound to the root. Fractions of the sheath soil of three graded binding strengths were removed by three successive treatments worked out during previous studies of maize rhizosheaths in our laboratory (unpublished data).

For fraction 1 (F1), with the weakest binding, the root halves were placed in a tared 10-mL glass vial filled with distilled water, which was capped and put in a sonicator bath (Bransonic 1200 Ultrasonic Cleaner, Bransonic Ultrasonic Co., Danbury, CT) at room temperature for 10 min. The vial was removed from the bath and the loosened soil was allowed to settle to the bottom. The two root halves were then transferred to another 10-mL vial filled with distilled water and left at 65°C for 48 h (lid on vial). The root halves were then gently shaken free of heat-loosened soil (F2, medium-strength binding) and transferred to a watch glass with about 5 mL of distilled water. There, a small brush was used to gently scrape off any soil remaining bound to the root surface. The water with the mechanically removed soil (F3, strongest binding) was carefully poured (with a funnel) into a third 10-mL vial, adding distilled water to clean off the watch glass and brush.

All vials with their fractions of loosened soil were dried for 48 h at 105°C (drying curves indicated weight stabilization of vials after 24 h and of fractions after 30 h) (lids off). Then the vials plus soil were left to cool to room temperature in a desiccator for 3 h (lids off) and weighed (lids on), and dry weights of soil were determined by subtracting the dry weights of the vials from those of the vials and soil.

Root Hair Observations

Several microscopic techniques were used to observe and quantify root hair density on wet and dry samples. The root portions used for these observations had not been subjected to sheath removal treatments. Transverse or tangential sections, or peels of the epidermal surface of the root portions, were either:

(a) Stained with toluidine blue O (0.05% [w/v] in benzoate buffer, pH 4.4) for about 45 s (O'Brien and McCully, 1981), rinsed (3 × 2 min), and mounted root-hair side up in tap water on a microscope slide under a supported coverslip. Tangential sections (<1 mm^2) were used to determine root hair density by counting the number of hairs per area of epidermal surface. Measurements were made with a calibrated scale in the eyepiece of a bright-field microscope.

(b) Stained with rhodamine B (1:10,000 in aqueous solution) for 3 to 4 min or with acridine orange (1:10,000 in aqueous solution) for 7 min and then mounted in aniline blue (0.05% [w/v] in phosphate buffer, pH 8.6) and observed with fluorescence optics. These fluorescent dyes were used to increase contrast of the root hairs.

(c) Left unstained, mounted in tap water, and observed with dark-field optics.

Bright-field, fluorescence, and Nomarski microscopy were with an Olympus Vanox or a Zeiss Axiophot microscope. Dark-field mounts were observed with an Olympus SZH stereo microscope. Some whole-root pieces (cut to length 0.4 cm for cross-sections and 1 cm for observation of the tangential surface) were frozen in liquid nitrogen slush, coated with aluminum (Huang et al., 1994), and observed with a JEOL JSM 6400 cryo-scanning electron microscope. All micrographs were recorded on Kodak TMAX 100 film.

RESULTS

Experimental Design

Plants excavated from the tubes were uniform in size and appeared healthy. The primary roots easily penetrated the wax-paraffin partitions to L1 of the soil profile with no signs of "buckling" at the root tips. The tips reached the tube bottom, plus or minus approximately 1 cm (Fig. 1). On occasion, the root grew along the edge of the pot in L2, in which case the root was not used.

The *SWC* of L2 was approximately the same at soil profile preparation and plant harvest, indicating that the wax-paraffin partitions were hydrophobic yet allowed root penetration. The L2 of dry samples stayed dry, at 9% (±1%) *SWC*, and the L2 of wet samples stayed wet, at 20% (±1%) *SWC*.

Size and Stability of Sheaths

Both the quantitative measurements and the qualitative observations showed clearly that soil sheaths formed in dry soil were larger and more coherent and adhered more tightly to the root than those formed in wet soil (Tables I and II; Fig. 2, A and B; cf. Fig. 3, B and C). If a primary root grown through a profile of soil with a dry L2 was briefly washed

Table I. *Measurements of underlying portions of primary corn roots and their surrounding rhizosheaths formed in dry or wet soil conditions*

Shown are means ± SD; $n = 8$.

	Volume Sheath / Volume Root	Diameter of Root	Thickness of Sheath
		mm	*mm*
Dry (9% *SWC*)	5.0 ± 0.8	0.8 ± 0.1	1.2 ± 0.2
Wet (20% *SWC*)	1.7 ± 0.7	0.8 ± 0.1	0.4 ± 0.2

Table II. *Percentage of soil of the sheath removed after successive disruptive treatments from portions of corn primary roots grown in isolated zones of dry or wet soil*

Shown are means ± SD.

Treatment	Fraction	Percent of Sheath Removed	
		Dry (9% *SWC*)[a]	Wet (20% *SWC*)[b]
Sonication	F1	47 ± 11	91 ± 7
Heat	F2	18 ± 11	7 ± 5
Abrasion	F3	35 ± 5	2 ± 2

[a] $n = 6$. [b] $n = 7$.

with running tap water immediately after excavation, a wide band of sheathing remained in the L2 portion (9% *SWC*) of the root that was greater than the sheathing on the L1 and L3 (15–17% *SWC*) portions. However, after a similar brief washing, a primary root that had grown through a layer of wet soil had little soil adhered in the L2 portion (20% *SWC*) and that part of the root appeared almost bare, whereas the L1 and L3 (15–17% *SWC*) portions had sheathing similar to those found in the L1 and L3 portions of a dry L2 sample.

Quantitative Results

In dry soil (9% *SWC*), the volume of the sheath was 5 times the volume of the subtending root, whereas in wet soil (20% *SWC*), the volume of the sheath was only 1.5 times this volume (Table I). Similarly, Table I shows that the thickness of the sheath surrounding a dry sample was approximately 3 times that of the sheath of a wet sample. The root diameter was the same for dry and wet samples (Table I). The means of the measurements taken from the wet samples have greater SD values because the little soil that adhered to the root was clumped in patches (Figs. 2B and 3B) and therefore was not always a complete cylinder around the root. In contrast, the surface of the sheathing formed in dry soil was relatively uniform (Figs. 2B and 3C).

The soil of the sheaths from the dry samples was not removed as easily as the soil of the sheaths from the wet samples. After 10 min of sonication, only 50% of the soil of the dry-sample sheath became loosened (F1) compared with

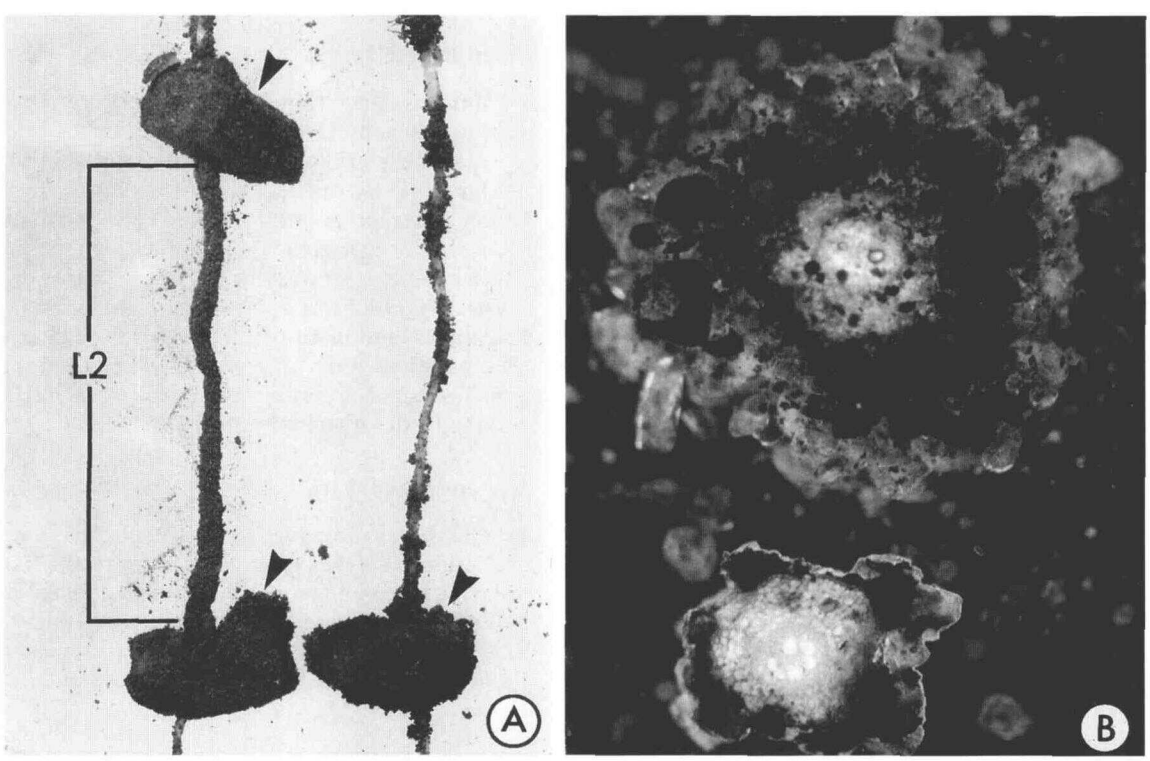

Figure 2. Primary roots of corn that have grown through a soil profile with a dry or wet middle layer, similar to those shown in Figure 1. A, Roots were removed intact from the soil profiles, and parts of the wax-paraffin partitions remain attached to the roots at the L2 boundaries (arrowheads). The left-hand root is from a soil profile with a dry L2 layer; a thick, evenly distributed layer of soil covers the root portion from the dry L2 layer, whereas less soil adheres to the root portions from the wetter L1 and L3 layers (above and below pieces of wax-paraffin partitions). The right-hand root is from a soil profile with a wet L2 layer: uneven patches of soil adhere along the exposed epidermal surface of the root from the wet L2 layer, and more soil is bound in portions from relatively drier L1 and L3 layers. ×1.5. B, Transverse sections of root portions from L2 layers as in A. These sections are similar to those used to measure sheath and root volumes. The upper section, through a root portion from a dry L2 layer, is surrounded by a thick rhizosheath. The lower section, through a root portion from a wet L2 layer, has little attached soil, which does not form a complete sheath. ×28.

90% of the soil of a wet-sample sheath. In addition, after the F2 fraction had been removed, 35% of the soil sheath was left to be brushed off, whereas only 2% of the sheath remained on the wet sample (Table II). Observation of those root pieces to which a large F3 fraction adhered showed soil particles (including sand particles) bound tightly to the surface of the epidermis and to distorted regions of the root hairs.

Root Hair Development

Observations of root hair development indicated that root portions from the isolated dry soil layers had more hairs than those from the wet layers (cf. Fig. 3, D and E). Density measurements confirmed these observations: portions of root from dry L2 layers had 140 ± 53 root hairs/mm^2 of epidermis, whereas those from wet L2 layers had only 31 ± 15 root hairs/mm^2 (means ± SD, n = 15 sections from four plants for each treatment). However, it is important to note that soil adhered to the epidermis proper, as well as to the root hairs (Fig. 3B), so root hair development is not the only determining feature in sheath formation.

DISCUSSION

The results of our experiments confirm observations of corn plants and other mesophytic grasses growing in the field. That is, rhizosheaths are larger and adhere to the root more tightly when formed in dry soils, whereas rhizosheaths formed under wetter soil conditions are neither as coherent nor as tightly bound to the root surface (Fig. 2; Tables I and II). The results also correspond with longstanding observations that highly developed rhizosheaths are a feature of grasses growing in dry, sandy habitats (Price, 1912; Arber, 1934; see Buckley, 1982, for additional refs.; Huang et al., 1993).

No previous study has confirmed the relationship between grass rhizosheath development and the water content of the surrounding soil. However, a study of soybean plants growing under water stress in sand culture reported similarly increased adhesion of soil to the roots in drier conditions (Sprent, 1975). More recent work with the desert plants *Ferocactus acanthodes* and *Opuntia ficus-indica* shows that rhizosheaths on both intact and excised roots become more tightly bound when the surrounding soil is dried out. Their sheaths are easily slipped from the root when in wet soil (North and Nobel, 1992; Huang et al., 1993).

Effect of *SWC* on Mechanisms of Rhizosheath Adhesion and Cohesion

Mucilages

Mucilages of plant and microbial origin are known to form and stabilize soil aggregates (Cheshire, 1979), and in vitro addition of isolated corn root-cap mucilage to soil with microbes will cause the formation of water-stable aggregates (Morel et al., 1991). Stained sections through field-grown corn rhizosheaths, viewed with the optical microscope, show mucilages coating surfaces of the root and the soil particles (see micrographs of Vermeer and McCully, 1982; McCully and Canny, 1988; Gochnauer et al., 1989). These mucilages are produced by the root-cap cells (and left in situ as the root grows through the soil) and by mucilage-producing bacteria, such as *Cytophaga*, which are native to the sheath. A recent study of the soil-binding properties of the root-cap and bacterial mucilages of the rhizosphere indicates that each mucilage can bind soil (Watt et al., 1993). Thus, the adhesive agents of the rhizosheath include both root and bacterial mucilages.

Drying of the mucilage is a crucial element for soil adhesion (Watt et al., 1993). The pedal mucus of mollusks behaves in a similar way (Denny, 1984). Therefore, when the root is growing under dry conditions, it would be expected that the high negative tension of the surrounding dry soil would draw water from the rhizosheath, causing mucilages to gel, stabilize soil aggregates, and dry down with root and soil surfaces. We saw this in our dry samples, where rhizosheaths were larger (Table I) and more difficult to disrupt and remove from the root surface (Table II).

Conversely, when the root is growing in wet conditions, the mucilages do not dry on the root surfaces and the soil particles. In fact, the high water content of the soil in the wet samples may cause the mucilages to dissolve and diffuse out into the surrounding soil. Since the large late metaxylem vessels are still living, and thus are not conducting large volumes of water in the portion of the root studied (St. Aubin et al., 1986), there is little transpirational pull (i.e. drying potential) from inside the root, especially since the plants used had only two emerged leaves. Therefore, this tension contributes little to the drying of the sheath (Wang et al., 1991).

Root-cap mucilage, which accumulates in the corn rhizosphere as the tip extends through the soil, is composed of polysaccharide molecules with many complex oligosaccharide branches that have neutral sugars at their terminals (Miki et al., 1980; Vermeer and McCully, 1982; Watt et al., 1993). Soil adhesion by this mucilage is primarily via hydrogen bonds between the hydroxyl groups of these neutral sugars and the soil particles (Watt et al., 1993). In both the sonication and the hot-water treatments, it is likely that adhesion and cohesion of the rhizosheath are reduced by breakage of such oligosaccharide branches, with their binding terminal sugars, from the backbones of the mucilage molecules. Some mucilage was not disrupted by these treatments, notably in the dry samples, and soil remained bound at points along root hairs and the epidermis proper. Interestingly, there is a low pectic component in the root-cap mucilage (3% of total polysaccharides, from Bacic et al., 1986), and as a result it is not hydrophilic (Watt et al., 1993). Therefore, dried, hydrophobic mucilage, trapped and binding soil particles in, for example, distortion points on root hairs or grooves in the epidermal surface, would actually repel water, and such soil could be removed only by persistent abrasion.

Less is known of the chemical composition of bacterial mucilage in the rhizosphere. However, it has a higher protein component and binds soil by different mechanisms than root-cap mucilage (Watt et al., 1993). It has different gelling properties and is more hydrophilic than root-cap mucilage. Therefore, we might expect the bacterial mucilages to differ

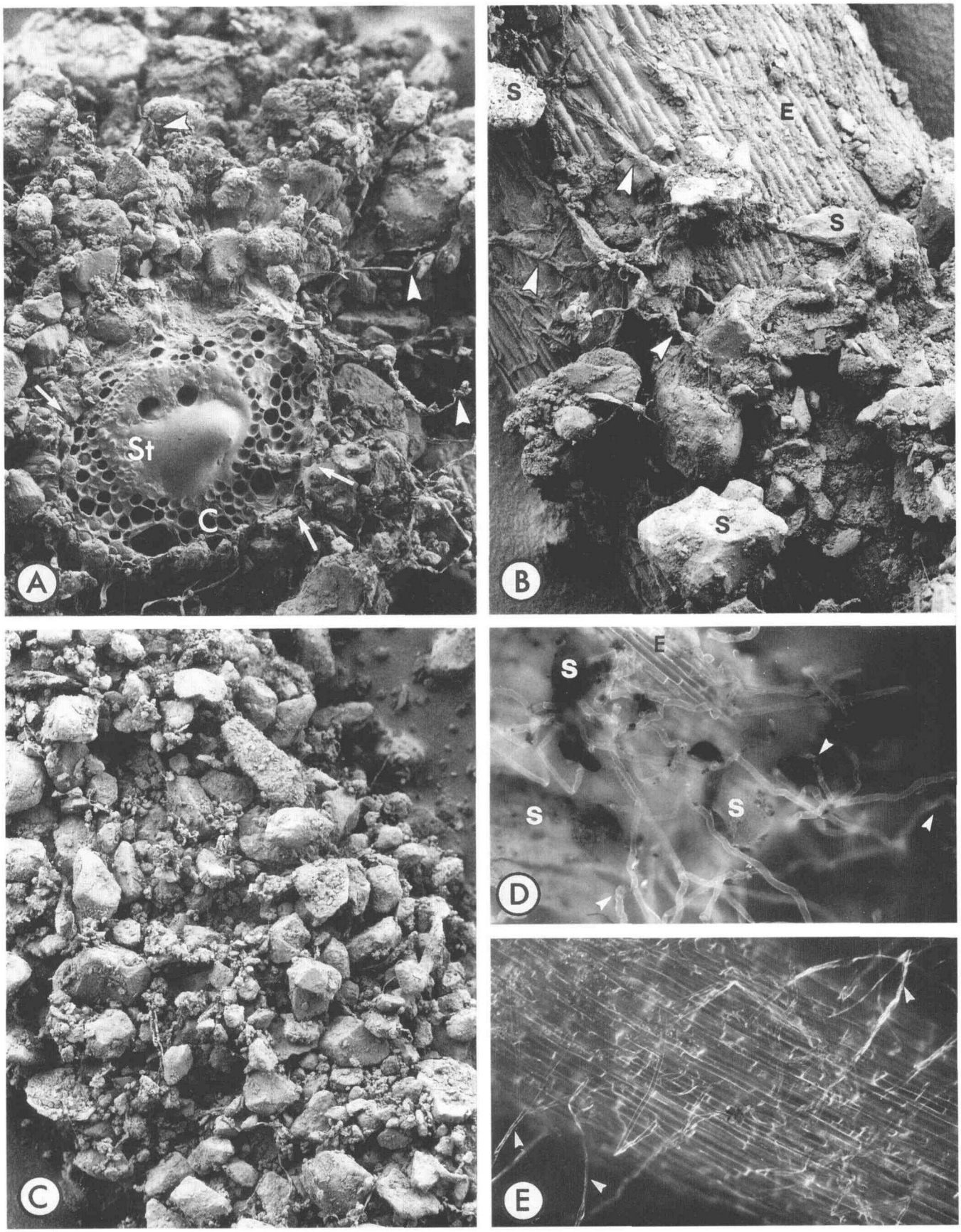

Figure 3. (Legend appears on opposite page.)

from root-cap mucilage in the stabilization of the sheath under wet and dry conditions.

Both root-cap and bacterial mucilage must be initially wetted before they will bind soil particles (Watt et al., 1993). Therefore, especially for dry soils, water must leave the root to provide the necessary hydration of the adhesive mucilages. Water leaked from the root (perhaps during the night) would cause expansion of the mucilage, and subsequent drying (during the day) would gel the mucilage and tightly bind rhizosheath soil. In fact, sheathed corn roots have higher water contents than older, bare regions (Wang et al., 1991), and rhizosheaths of *Oryzopsis hymenoides* have more water than the surrounding soil (Bristow et al., 1985). Increasing experimental evidence with both xerophytic and mesophytic plants indicates that water can move from their roots into the surrounding soil, pulled out, passively, by the lower water potential of the soil (Shone and Flood, 1980; van Bavel and Baker, 1985; Caldwell and Richards, 1989; Blum and Johnson, 1992; Dawson, 1993) or pumped out, actively, by the root (Schwenke and Wagner, 1992). However, the experimental design used here did not allow us to distinguish between these two mechanisms.

Root Hairs

The other component of the rhizosheath that has been recognized as important in its formation and stabilization is the root hairs (Sachs, 1865; Goodchild and Myers, 1987; McCully and Canny, 1988; Huang et al., 1993). They provide an important physical framework for the extending sheath. There were more root hairs on corn root portions in dry soil than in wet soil (Fig. 3, D and E). North and Nobel (1992) also report more root hairs in rhizosheaths of two desert plants formed in drier soil.

Root hairs were present on wet samples but they were fewer and much straighter than those on dry samples. Fewer root hairs and fewer distorted regions on them would provide fewer stable anchor points for the soil of the rhizosheath. Unpublished studies in our laboratory show that certain native bacteria of the corn rhizosheath are able to distort root hairs in the absence of soil. Perhaps the environment at the surface of the wet samples inhibited the growth and function of these specific bacteria, thus reducing rhizosheath formation and stabilization. In any event the presence of root hairs per se does not ensure rhizosheath stabilization.

Possible Functions of Rhizosheaths

The fact that rhizosheaths are more developed on mesophytic grasses in drier conditions, and are a feature of xerophytic grasses, implies that they may be an adaptive feature of some water-stressed plants and may aid in the functioning of the plant. For example, rhizosheath formation may enhance nutrient acquisition by the roots. Nambiar (1976) reports a surprisingly high uptake of labeled zinc by sheathed portions of roots despite growth in soil of low water content. If water is leaving the root in the sheathed zone, as recent evidence suggests (see refs. above), a greater zone of diffusion would be produced for nutrients dissolved from the surfaces of tightly bound soil particles and moving into the root. These nutrients (ions) may accumulate in the large late metaxylem vessels to be transported to the shoot when the vessel elements mature or may be immediately provided to the growing tip (McCully and Canny, 1988).

On the other hand, rhizosheaths may aid in plant-water conservation by acting as zones of resistance to water flow from the sheathed root into the surrounding dry soil (suggested by Bristow et al., 1985; North and Nobel, 1992; Huang et al., 1993). Such resistance is said to be created in dry soils by the formation of air gaps between a shrunken root and the surrounding soil (Nobel and Cui, 1992) or by the possible formation of air gaps between the sheath and its surrounding soil (Huang et al., 1993). In the studies presented here we saw no reduction in root diameter between the wet and dry samples (Table I), and cryo-scanning views of sheathed roots show tight association between root surfaces and soil particles. However, only a short region of the root was affected by the low *SWC*, which may not show the effects seen on an entire root system in dry field conditions. We have not yet looked for a space between the sheath and the surrounding soil.

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Figure 3. (Figure appears on opposite page.) Portions of corn primary root that have grown through either a dry or wet L2 layer of the soil profiles as in Figure 1. A, Transverse section of the root portion from a dry L2 layer. An extensive rhizosheath of tightly packed soil is closely associated with the epidermis proper (arrows). Root hairs (arrowheads) extend into the sheath and are intertwined with soil particles. A small amount of liquid (likely from the living late metaxylem vessels) has collected on the stele (St) during preparation. In the photo, C indicates cortex. Scanning electron micrograph; ×60. B, Surface view of the root portion from a wet L2 layer. Much of the epidermis (E) is exposed between attached soil particles (S). Root hairs (arrowheads) are either bare or have attached soil. Scanning electron micrograph; ×115. C, Root portion from a dry L2 layer. Similar view to that in B except presented at a lower magnification to show the large, even coating of attached soil and protruding root hairs. Scanning electron micrograph; ×55. D, Tangential section of the root portion from a dry L2 layer, stained with rhodamine B, mounted in aniline blue, and viewed with fluorescence optics. Long root hairs extend from the epidermis (E), and soil particles (S) are anchored at distorted regions along them (arrowheads). ×80. E, Tangential section of root from a wet L2 layer viewed with Nomarski optics. Compared with the section in D, fewer root hairs are present and these have few distortions (arrowheads). Little soil remains attached. ×80.

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