



Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth

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Abstract

Root caps provide a protective layer in front of the meristem that protects the meristem from abrasion by soil particles. The continuous production and sloughing of the root cap cells may be an adaptation to decrease the friction at the soil–root interface by acting as a low-friction lining to the channel formed by the root. Experiments were performed which provide the first direct evidence that such cell sloughing decreases frictional resistance to root penetration.

The penetration resistance (force per unit cross-sectional area) to maize roots, which were pushed mechanically into the soil, was compared with the penetration resistance to growing roots and to 1 mm diameter metal probes (cone semi-angles of 7.5° or 30°). The pushed roots experienced only about 40% of the penetration resistance experienced by the 7.5° metal probe that was pushed into the soil at the same rate. Thus, the friction between the soil and the pushed root was much smaller than between the soil and the metal probe. The penetration resistance to the growing root was between 50% and 100% of that to the pushed root, indicating that the relief of friction and slower rate of soil compression were more efficient around the growing root. SEM examination of the surface of roots pushed or grown into the soil showed that numerous root cap cells had detached from the cap and slid for several millimetres relative to the root. The low friction properties of roots may be due largely to the low coefficient of friction between sloughing root cap cells, and may be decreased further by intracellular mucilage secretions.

Key words: *Zea mays*, root cap, frictional resistance, root penetration, cell sloughing.

Introduction

Plant roots may exert pressures of up to 1 MPa in order to penetrate hard soils (Pfeffer, 1893; Misra *et al.*, 1986). Consequently, virtually all plants which grow in soil have evolved root caps which protect the root meristem from physical damage or abrasion by soil particles. Root cap cells are continually being produced by the meristem and, after a period of hours or days, sloughed off from the outer surface of the root cap. These cap cells secrete mucilage and may remain alive for a period of days after detaching from the root cap (Vermeer and McCully, 1982). Thus these cap cells will line the channel created in the soil by the root tip, cushioning the passage of the root surface through the soil. In this paper the possibility that these cap cells play a major role in relieving the frictional resistance to the penetration of soil by roots is considered.

The mechanical resistance of the soil to root growth can be separated into two components: the pressure required to deform a cavity (in the soil) that is large enough for the root; and the pressure required to overcome the frictional resistance between the soil particles and the moving surface of the root.

The resistance of the soil to deformation results in a pressure on the surface of the root which, in turn, is the cause of the frictional resistance between the root surface and the soil. The frictional stress, τ , between soil and the surface of a root is given by the equation

$$\tau = \sigma_N \times \tan \delta + c_a \quad (1)$$

where σ_N is the stress normal to the surface of the root, δ is the angle of friction between the two surfaces, and c_a is the tangential component of adhesion between the surfaces (after Stafford and Tanner, 1977). The direction of the frictional resistance is opposite to that of the

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velocity of the moving surface of the root. The total resistance to the elongation of a root is, therefore, the sum of the components of the cavity expansion pressure ($=\sigma_N$), and τ in the axial direction.

The idea that mucilage exudation and root cap sloughing eliminates practically all the frictional resistance to root growth was first suggested by Greacen *et al.* (1968). The penetration resistance to metal penetrometer probes is generally between 2 and 8 times greater than the axial resistance to plant roots (Bengough and Mullins, 1990). This may be due to the roots experiencing a smaller frictional resistance, but could also be due to the faster rate of penetration used in penetrometer testing.

The aim of this paper was to determine directly whether roots really experience a low frictional resistance. To measure the frictional resistance between root tips and the soil required conditions similar to those that a growing root would experience. To do this, the penetration resistance to plant roots that were pushed into the soil was compared with the resistance to metal probes that were pushed into soil cores at the same rate of penetration. Further comparisons were made with the penetration resistance experienced by roots growing into the same soil. The surface of the roots were examined before and after the experiments using a scanning electron microscope.

Materials and methods

Soil preparation

The soil used (Hallam loam) was from the top 100 mm of a silty loam collected on the Agricultural Reserve at La Trobe University, Bundoora, Victoria, Australia. Typical particle composition of the mineral fraction for this soil is clay ($<2 \mu\text{m}$) 0.13 kg kg^{-1} , silt ($0.02\text{--}0.002 \text{ mm}$) 0.28 kg kg^{-1} , fine sand ($0.02\text{--}0.2 \text{ mm}$) 0.54 kg kg^{-1} , and coarse sand ($0.2\text{--}2.0 \text{ mm}$) 0.05 kg kg^{-1} . Soil ($<2 \text{ mm}$ sieved) was slowly wetted to a water content of 0.23 kg kg^{-1} (which is approximately 0.85 times the Plastic Limit of this soil). Using an hydraulic press, the soil was compacted into core rings ($56 \text{ mm long} \times 72 \text{ mm i.d.}$) to dry bulk densities of 1.0, 1.2, 1.3 or 1.4 Mg m^{-3} . The cores were then sealed and stored for a maximum of 10 d until use.

Seed germination

Seeds of maize (*Zea mays* L. cv. SR108; Snowy River Seeds, Orbost, Australia) were soaked for a period of 2–4 h in distilled water that was aerated vigorously. The seeds were then placed on damp blotting paper in the dark at 25°C to germinate for between 1 and 2 d. Seedlings with straight radicles 10–20 mm long were selected for the experiments.

Penetration resistance to metal probes

The resistance to pushing a 1 mm (7.5° or 30° semi-angle) probe into the soil was measured using an electronic balance attached to a computer. The soil core to be tested was placed on the balance that was raised using a loading frame (ELE International, Hertfordshire UK) at a rate of 2.0 mm min^{-1} toward the stationary probe. The probe had a relieved shaft so that only the cone itself contacted the soil, and so there was no

associated shaft friction. Depth readings were recorded at 10 s (0.333 mm) intervals. A 2.5 mm deep hole was made in the top of the soil core using a tapered needle before starting each penetration—this was also done for the root experiments.

Penetration resistance to pushed roots

The radicle of a seedling was inserted into a holder at the base of a modified sample tube (Fig. 1), so that 7 mm of the root tip protruded. The root was then fixed in place using plaster of Paris, and the tube filled with moist vermiculite. The root tip was kept moist and left for a period of 15–30 min to recover from the disturbance. The tube containing the root was then attached to the loading frame so that the root was vertically above a soil core that was placed on the balance. With the exception of a 10 mm diameter hole in the polythene surrounding the site where the root would penetrate, the soil core was covered with polythene to decrease evaporation. A 2.5 mm deep tapered hole was made in the surface of the soil core and the root tip located in the hole so that the root would penetrate the soil instead of sliding along the soil surface. The loading frame was then used to push the root into the soil core to a depth of approximately 6 mm, at a rate of 2 mm min^{-1} , while the force readings on the balance were recorded by a computer. The force required to pull the root out of the soil core was then monitored, to give an indication of the frictional resistance in the region behind the root tip. This was done by lowering the core at 2 mm min^{-1} while recording the force readings on the balance.

Penetration resistance to growing roots

The force exerted by the maize radicle as it grew into a soil core was measured using a balance and a technique similar to that used by Bengough and Mullins (1991; Fig. 1b). The seedling holder was clamped in place above the soil core, and a 2.5 mm deep tapered hole made in the surface of the core. The maize radicle was then inserted into the holder and the root was fixed in place using plaster of Paris. Every 10 min the output of the balance was logged using a computer. After approximately 4 h the root was removed from the soil and the root length and diameter recorded. The temperature was maintained at approximately $22 \pm 2^\circ\text{C}$ throughout the experiments.

Measurement of root diameter

The diameter profile at 1 mm intervals along the apical 6 mm of the 'pushed' and 'grown' roots was measured using a microscope with eyepiece graticule. Measurement accuracy was to $\pm 0.0125 \text{ mm}$.

Examination of root tips using a scanning electron microscope (SEM)

Root tips that had been pushed into soil or grown into soil were compared with root tips of seedlings germinated on blotting paper. For examination, single root tips mounted on stubs were quench frozen in melting nitrogen (-210°C) and inserted into the cold stage (-190°C) of a scanning electron microscope (JEOL JSM-840) through a Hexland cryo-preparation chamber by means of a Hexland CT cryo-transfer system. To assist in revealing detail of the root tips the samples were briefly 'etched' at -80°C (differential removal of ice through sublimation). The sample was returned to the cryo-preparation chamber, gold coated on a cold stage and reinserted into the SEM cold stage. This method was based on van Steveninck and Fernando (1995).

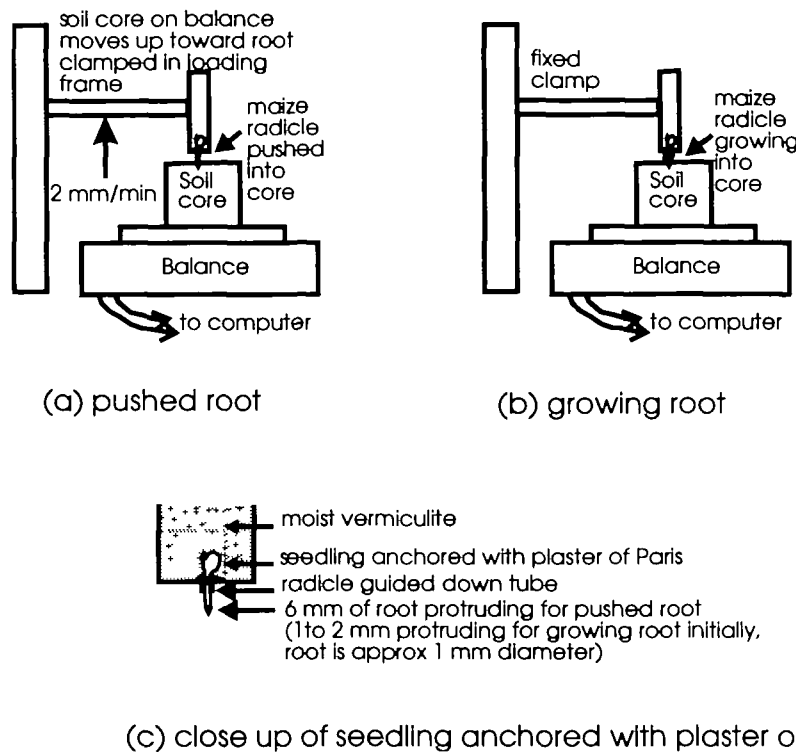


Fig. 1. Schematic diagram of apparatus for measuring force exerted by pushed (a) and growing (b) roots. The method of anchoring the seedling in place is shown in (c).

Results

Calculation of penetration resistance

The penetration resistances, Q_p , to the penetrometer probe, and to the 'pushed' and 'grown' roots were calculated as

$$Q_p = F_p / A_p \quad (2)$$

where F_p is the force exerted by the probe or root in penetrating the soil, and A_p is the cross-sectional area of the probe or root. The average force experienced by the root was calculated from the measurements taken when the root had penetrated between 3.5 and 5.5 mm into the soil. This depth range was sufficiently deep to avoid edge effects with the surface. The depth of penetration of the 'grown' root was calculated from the final root length, assuming a constant root elongation rate during each 4 h experiment.

To calculate the resistance to the 7.5° semi-angle probe after deducting the frictional resistance, the equation (after Greacen *et al.*, 1968; Bengough, 1992) was used.

$$\sigma_N = \frac{(Q_p - c_a \tan \delta)}{(1 + \cot \alpha \tan \delta)} \quad (3)$$

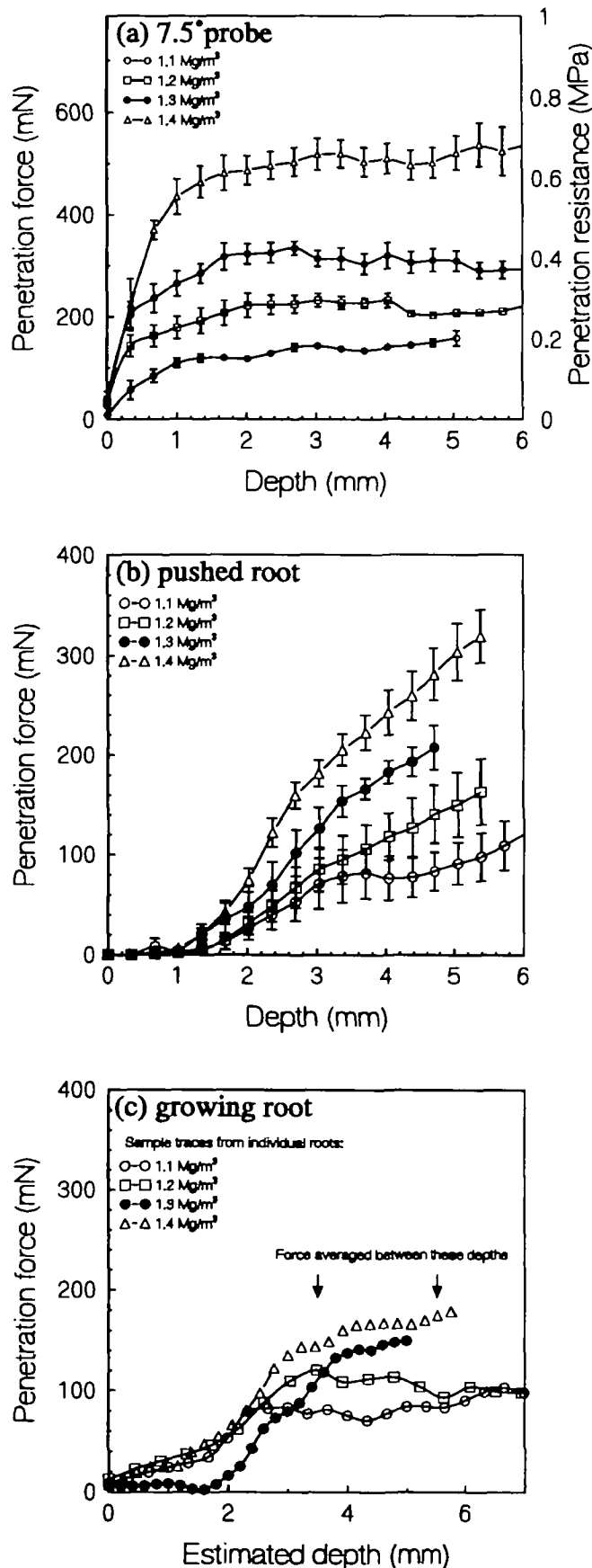
where α is the cone semi-angle, δ is the angle of soil-metal friction, c_a is the soil-metal adhesion, and σ_N is the normal stress on the surface of the probe. In a separate experiment the values of δ and c_a were measured between soil and

metal surfaces under applied normal stresses of 0.03 MPa and 0.1 MPa. On replicate samples, δ was measured as 15.6° and 19.2° , with c_a as 4.89 and 4.50 kPa, respectively.

Penetration resistance to penetrometer probes, 'pushed' and 'growing' roots

Penetration resistance to the roots and to the metal probes increased with increasing soil bulk density. Penetrometer resistance to both probes increased with depth until a depth of 2 mm, after which resistance plateaued (shown for 7.5° probe in Fig. 2a), indicating that soil strength was approximately constant between 2 and 6 mm depth in the core. The force experienced by the pushed root continued to increase with depth (Fig. 2b), whereas the force exerted by the growing root reached more of a plateau (Fig. 2c).

The penetration resistance to the pushed root was calculated by averaging the force between 2.5 and 5.5 mm depth, after subtracting the force required to remove the root from the soil (typically 10–20% of the force required to push the root into the soil). This subtraction was necessary to make valid comparisons between the pushed root and the 7.5° penetrometer probe: in the case of the pushed root there was friction on the surface of the root between 2 and 6 mm behind the root tip. That friction was not experienced by the relieved shaft of the penetrometer probe.



The maximum resistance to the 'growing' root was approximately 0.15 MPa, which compares with maximum pressures of approximately 1 MPa that have been recorded for maize (Misra *et al.*, 1986). This therefore represented a relatively small mechanical impedance to root growth, and one which caused no detectable change in the shape of the root (Fig. 3). Penetration resistance was greatest to the 7.5° semi-angle probe and least to the growing root. The various penetration resistances were correlated positively with each other (Figs 4a–d), being approximately 2.5 times greater for the 7.5° probe than for the pushed root. The resistance to the 7.5° probe was about four times greater than that to the growing root. The value of σ_N (the resistance to a frictionless adhesionless probe) is indicated as a second x-axis scale in Fig. 4a and b. This showed that the resistance to the pushed root was always greater than σ_N (Fig. 4a), while the resistance to the growing root was comparable, or sometimes less than σ_N (Fig. 4b).

SEM results

The maize radicles germinated on filter paper (Plate 1a) showed abundant root cap cells encased in a layer of mucilage. When the root was pushed or grown into the soil, these cells detached from the cap and were held in the soil as the surface of the growing or pushed root slid passed them. Particles of soil separated from the root surface by clumps of root cap cells were observed in both the pushed (Plates 1b, c) and grown (Plate 1d) roots. No obvious damage to the epidermis of the root was apparent as a result of pushing the root into the soil, although it was evident that numerous cap cells had detached (Plate 1e).

Discussion

Penetration resistance and friction

In considering the penetration resistances experienced by the pushed and growing roots, it is necessary to consider the mechanisms of penetration in more detail. The root caps of the growing roots were moving through the soil at approximately 1 mm h⁻¹. The velocity of the root surface relative to the soil decreases in the elongation zone with increasing distance from the root apex. Friction between the soil and root surface may be experienced along all the moving surface of the root, but especially at the root cap, where the pressure on the root surface is likely to be greatest (in the maize roots, all the radial expansion occurred between 0 and 1 mm from the root

Fig. 2. Penetration force as a function of depth at four soil dry bulk densities, for the (a) 7.5° probe (± 1 SE, $n=5$ per density), (b) pushed maize radicle (± 1 SE, $n=5$ per density), and (c) growing maize radicle (examples for individual roots).

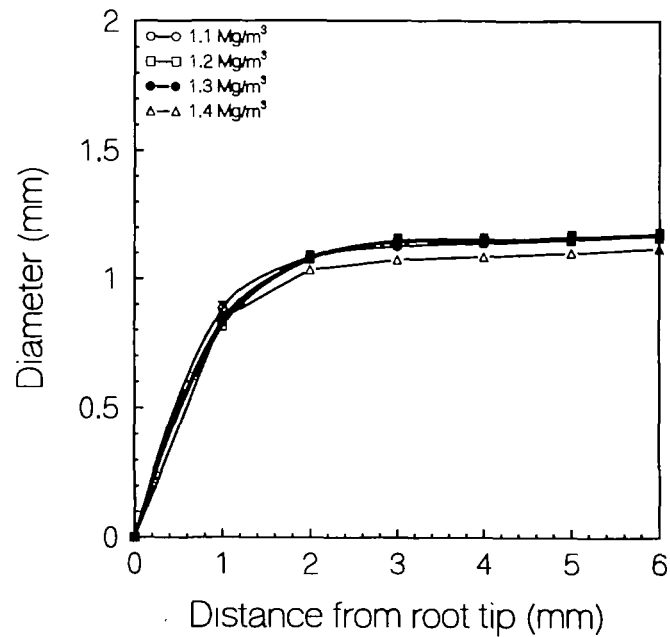


Fig. 3. Root diameter profiles for the roots grown in soil packed to different densities (± 1 SE, $n = 5$ per density).

apex, Fig. 3). Outer cap cells which become detached, will be replaced continually by new cells.

The pushed roots penetrated the soil at 2 mm min^{-1} , the same rate as the metal probes. The velocity at the soil-root interface was therefore 2 mm min^{-1} over the whole of the elongation zone. The supply of cap cells could not be replenished by new cell production during the 3 min penetration test. This may have resulted in a gradual increase in the frictional resistance to the pushed root, causing penetration force to increase with depth for the pushed roots (Fig. 2b) more than for the growing roots (Fig. 2c). This increase in resistance with depth was more noticeable in the denser soil cores, which is again consistent with this hypothesis.

The pushed roots experienced less than half of the resistance experienced by the 7.5° probe, suggesting that less friction was experienced by the pushed roots. Smaller resistance still was encountered by the growing roots, due to a combination of a smaller frictional resistance and a slower rate of penetration. The smaller frictional resistance experienced by roots is probably due to root cap cells detaching and lining the channel around the growing root. The penetration resistance to the growing root was more similar to the calculated values of σ_N for the 7.5° probe (i.e. the resistance to the 'frictionless' probe; Fig. 4b).

The diameters of the growing roots (from 1–6 mm from the apex) were independent of the bulk density of the soil for the range of bulk densities used (Fig. 3). Thus the mechanism proposed by Abdalla *et al.* (1969), that enhanced radial expansion of the root tips creates a zone

of stress relief in front of the penetrating root, did not play any part in reducing the resistance to growth in these experiments. It is also unlikely that, given the relatively uniform nature of the packed soil cores and the short elongation of the root, the roots are able to take advantage of pathways of smaller penetration resistance in the soil.

Mechanisms for decreasing soil-root friction

The adaptations that may give rise to a low coefficient of soil-root friction are mucilage production by the root tip and sloughing of root cap cells from the root cap.

Mucilage secretion: The role of mucilage in lubricating the passage of the root through the soil will depend on the degree of hydration of the mucilage. When wet, mucilage expands to 1000 times its dry volume (Guinel and McCully, 1986). However, few estimates exist of the degree of expansion of mucilage as a function of soil matric potential. By comparison with 1% and 2% agar, Guinel and McCully (1986) suggest that mucilage loses most of its volume when the soil is drier than *c.* -24 kPa , although the mucilage may rehydrate at night when transpiration is low (Sealey *et al.*, 1995). It is likely that mucilage would be well hydrated around the roots grown in soil in these experiments.

In soils much drier than -24 kPa matric potential, mucilage in contact with the soil will be dehydrated, and it has been suggested that it will, therefore, have only a minor role in decreasing soil-root friction (Guinel and

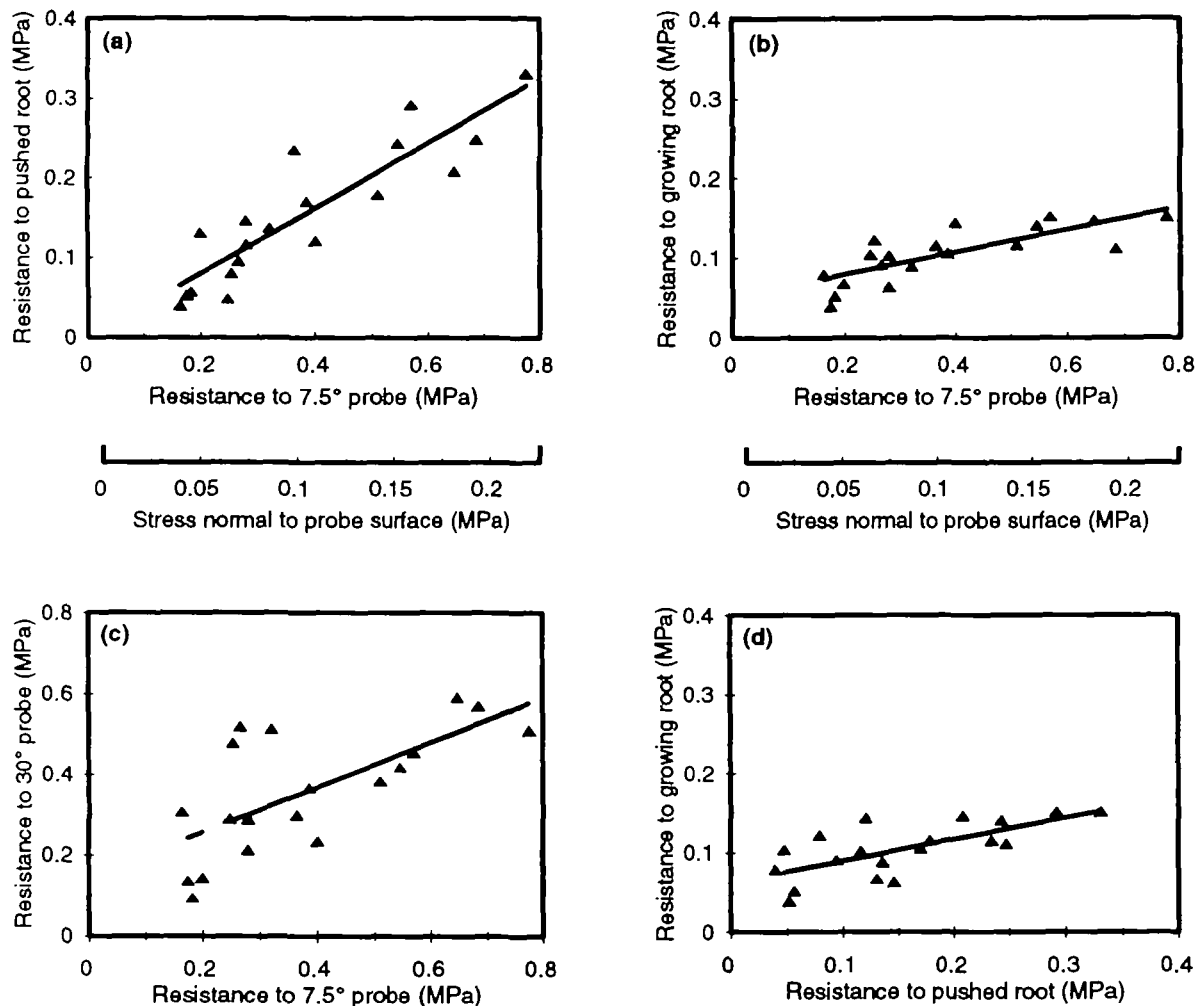


Fig. 4. Correlations between penetration resistances (force/cross-sectional area) for growing and pushed roots, and 7.5° and 30° semi-angle probes: (a) pushed root versus 7.5° probe, (b) growing root versus 7.5° probe, (c) 30° probe versus 7.5° probe, and (d) growing root versus pushed root. Lines are linear regressions. In (a) and (b) the stress normal to the probe surface, σ_N , is shown on the lower x -axis.

McCully, 1986). In some circumstances, however, non-liquid lubricants may be very effective at decreasing friction (e.g. PTFE, graphite), and so it is important that the frictional properties of these dry films of mucilage are determined. It is also conceivable that mucilage may be partially hydrated under the surface layer of cells in the root cap, and so may lubricate the passage of cap cells alongside the root cap and epidermis.

Root cap sloughing: A root cap cell will only move relative to the root if the friction between the cap cell and the surface of the root is smaller than the friction between the cap cell and the surrounding soil. Thus in order for a cap cell to move relative to the root, the coefficient of friction between the cap cell and root surface (including any adhesive forces) must be smaller than between the cap cell and the soil. Hence, by definition, a sloughed cap cell has decreased the frictional resistance to soil penetration.

There have been no estimates of root cap sloughing in an abrasive medium such as soil. The only estimates are from maize roots grown in sphagnum moss (Barlow, 1978*a, b*; Clowes, 1971). These papers suggested that the rate of production of new root cap cells was between 2500 and 10 000 per root apex per day. Eighty per cent of the increase in root radius occurred between 0 and 1 mm from the root apex. The normal stress exerted by the soil on the root surface will be greatest in this region, which corresponded approximately to the extent of the root cap. To assess the importance of sloughed cap cells on decreasing the frictional resistance, the fraction of the root cap surface that would be covered by sloughed cap cells if they were spread over the cap in a layer 1 cell deep was considered. The time, t_c , taken for the root to grow the length, l_c , of the root cap is given by

$$t_c = l_c / E \quad (4)$$

where E is the elongation rate of the root. The number

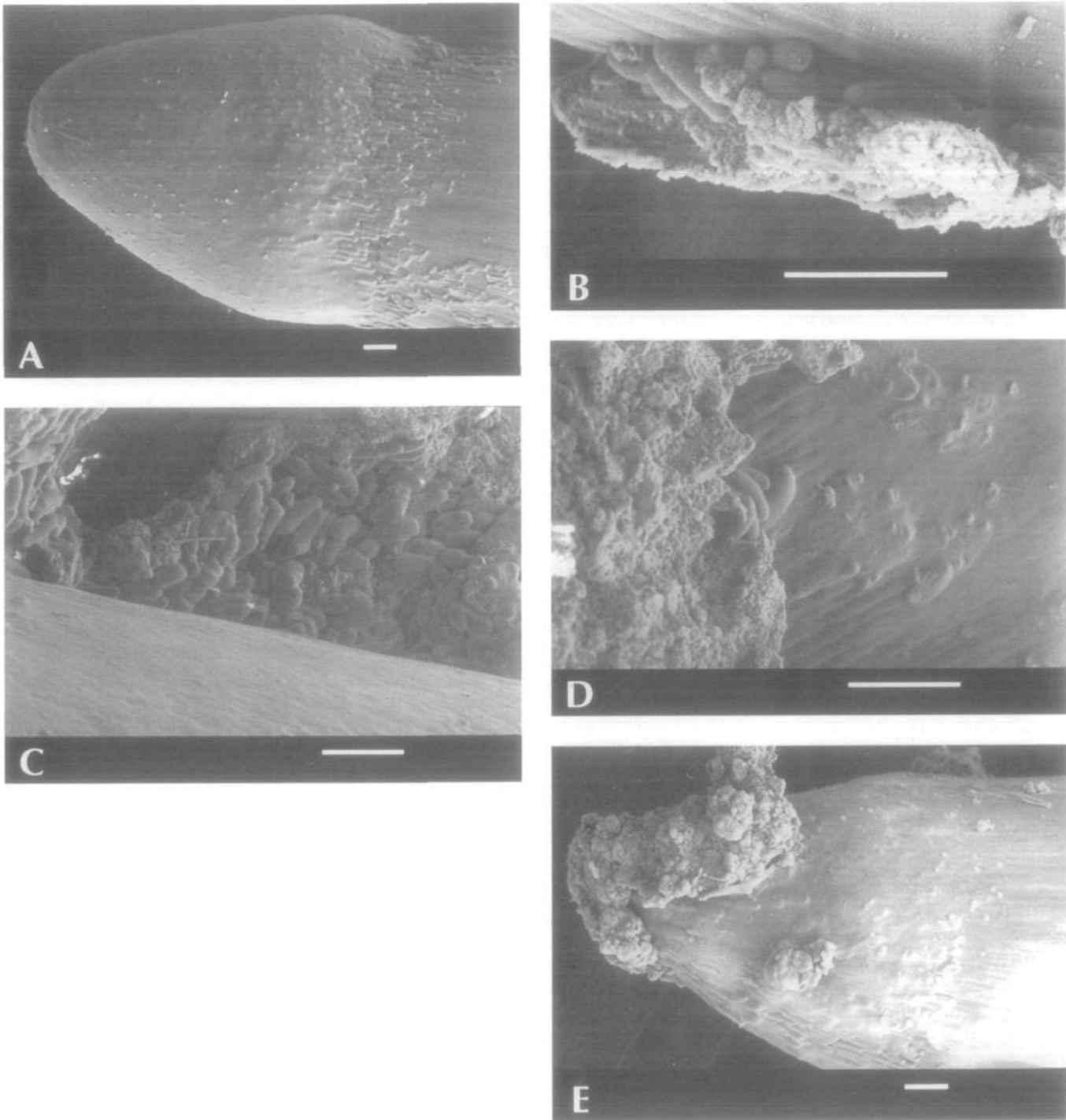


Plate 1. Scanning electron micrographs showing (A) maize radicle grown on filter paper, (B) detached cap cells between soil particle and 'pushed' root epidermis, (C) detached cap cells on exposed underside of soil particle next to root epidermis, (D) detached cap cells between soil particle and root epidermis on 'grown' root, (E) tip of radicle excavated after being pushed into the soil. Bars represent 100 μm .

of cap cells produced in that time, N_c , is

$$N_c = N \times l_c / E \quad (5)$$

where N is the cell production rate (number of cap cells per unit time). The total surface area of the cap covered

by the sloughed cells is then

$$A_s = a_s \times N \times l_c / E \quad (6)$$

where a_s is the mean longitudinal cross-sectional area of a root cap cell. Assuming that the root cap is

approximately a half spheroid (Sealey *et al.*, 1995) the surface area of the root cap A_c can be calculated from the surface area of half the spheroid formed by rotating an ellipse about its major axis (l_c = half of the length of the major axis). Thus,

$$A_c = [\pi r(l_c^2 - r^2)^{1/2}] \left[\sqrt{\frac{l_c^2}{(l_c^2 - r^2)} - 1} + \frac{l_c^2}{(l_c^2 - r^2)} \arcsin\left(\frac{\sqrt{l_c^2 - r^2}}{l_c}\right) \right] \quad (7)$$

where, r is the root radius (i.e. half of the length of the minor axis of the spheroid). The fraction of surface area of the cap covered by sloughed cells, A_f , is then given by

$$A_f = A_s/A_c \quad (8)$$

For a root cap of diameter 0.86 mm and length 1 mm, A_c is 2.27 mm². A_f is illustrated as functions of N and E in Fig. 5, assuming a_s is 600 μm². Thus, with reported rates of cap cell production, anything up to 100% of the root cap may be covered with detached cap cells. These cells will also be most likely to detach at locations on the root cap where the friction between soil particles and the cap cells is greatest and, from the micrographs, these cells will often detach in small groups. When a root is mechanically impeded, the elongation rate will be slowed, the shape of the root tip may become distorted, and the root diameter may increase by up to a factor of two.

The relative importance of sloughed cells, therefore, depends on the production rate of cap cells relative to the growth rate in an abrasive medium such as soil. It is possible that N/E may increase in hard soil, making sloughed cap cells of greater relative importance in decreasing the frictional resistance to growth. Slowed

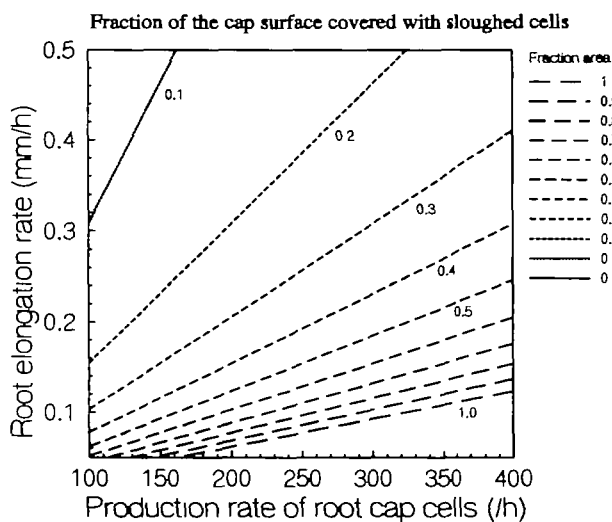


Fig. 5. Contour plot showing the fraction of the root cap surface area covered by detached cap cells in relation to the root elongation rate and the rate of production of new cap cells.

rates of cortical cell production have been found in mechanically impeded roots (Croser *et al.*, 1995), but it is not known whether the rate of cap cell production also changes.

Limitations to the technique used

The technique for measuring the resistance to 'pushed' root tips is only of limited use for measuring the resistance to root growth in soil. The technique is only effective in relatively soft soil. At soil strengths greater than about 0.8 MPa penetration resistance, the plant roots sometimes began to buckle as they penetrated the soil. Thus, at larger soil strengths, the force measured would be that required to buckle the root, as opposed to that required to push the root into the soil.

The rate of penetration used was chosen as 2 mm min⁻¹ for both the pushed roots and metal probes. The aim was to compare the penetration resistance experienced by pushed roots and probes at the same rates of penetration, and therefore it did not matter that the rate was much faster than that of root growth. The rate of penetration for the pushed roots had to be relatively fast to prevent dehydration of the exposed root surface, and to ensure that the amount of root growth during the experiment was negligible.

Conclusions

The frictional resistance experienced by roots is a small, but not negligible, fraction of that experienced by metal probes. The friction is probably relieved by root cap cells detaching and forming a low-friction lining to the cavity enlarged by the root. To test this hypothesis further, measurements are needed of the rate of rate of production and sloughing of root cap cells in abrasive growth media, such as soils with a large penetration resistance.

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