Physics and physiology of plant growth in the soil

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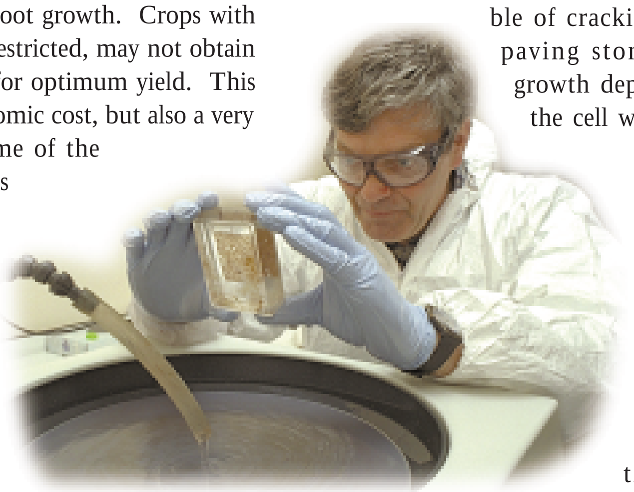
Soil that is too hard, too dry, or too wet provides an adverse environment for root growth. Crops with root systems that have been restricted, may not obtain sufficient water or nutrients for optimum yield. This represents an enormous economic cost, but also a very real human problem, as some of the most physically degraded soils are found in the poorest countries of the world.



Relatively little attention has been paid to the selection of plants with root systems adapted to poor soils. Indeed, most physiological experiments study growth in hydroponics, or in other unrestrictive growth media. By understanding the physiological and biophysical processes of growth in soil, we can provide a rationale for evaluating potential gains from selecting plants with root systems that are better adapted for particular conditions. By determining the physiological responses of roots to adverse conditions we can also relate laboratory experiments to real field conditions.

Root growth occurs as a result of cell expansion. This is a process driven by the hydrostatic pressure, or turgor, within the cells of the root. Large pressures are exerted, of up to 1 MPa, which is about five times greater than the air pressure within an average car tyre. This pressure explains why roots are capable of cracking concrete and lifting paving stones. The rate of root growth depends on the stiffness of the cell walls in the growing zone of the root, the turgor pressure, and the external pressure of the soil (Fig. 1).

When roots grow in compacted soil, the external soil pressure can exceed 1 MPa, slowing the root elongation rate. The roots become fatter and the surface of the root may become distorted where particles of soil exert large point pressures on the root surface (Fig. 2). We have found that the growing zone of the root becomes shorter in compacted soil, so that there is a shorter region of root that is expanding actively. When the root grows out of the hard soil into looser soil, the elongation rate increases only slowly for a period of several days. This shows that the root elongation is not just limited by the external pressure of

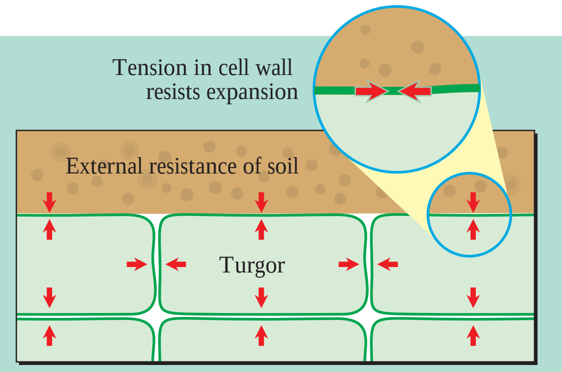


Figure 1 Schematic diagram showing pressures acting in the epidermis of a root growing in soil.

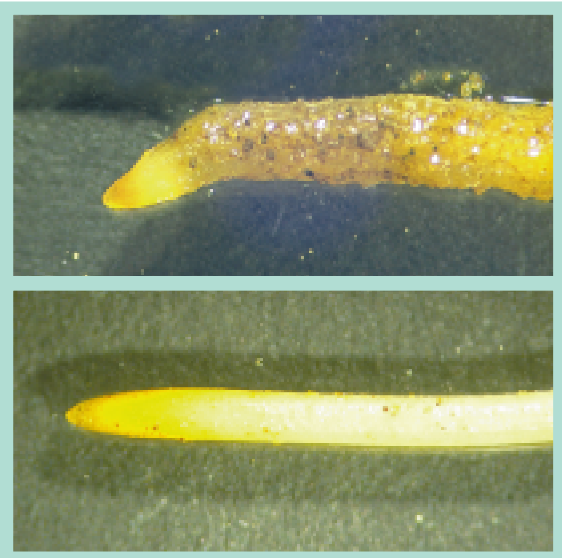


Figure 2 Roots grown in hard soil (top) become thicker and more distorted than those grown in loose soil (bottom).

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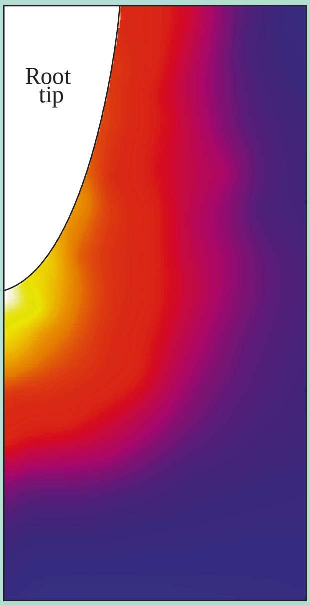

Figure 3 Stress distribution predicted around a simulated pea root (blue represents low stress, yellow high stress).

the soil, but by some physiological response of the root that is present even after the pressure is removed. We measured the turgor pressure in the pea roots that had been impeded, using a pressure probe, and found that the pressure was the same as in unimpeded roots. This shows that the pressure driving cell expansion is the same in the two sets of roots, and suggests that elongation is slower because the tension in the cell wall is greater, due to a stiffening of the cell wall. Tension in the walls of expanding cells often exceeds 100 MPa (about two orders of magnitude greater than the tension in the wall of a car tyre), and it is now thought that cell walls play a major role in controlling cell expansion.

Given that roots can generate large pressures, is there any design of root that transmits this pressure to the soil in a more efficient manner? To answer this, we need to determine the stress distribution in the soil, and how it is affected by the geometry and physical properties of the root surface. In collaboration with CSIRO, Canberra, we are using critical state soil mechanics with finite element models to determine the stresses around a root (Fig. 3). Preliminary findings have shown that doubling of the root diameter can decrease the peak stress at the tip of the root by a factor of two. This means that the thickening of roots in hard soil will decrease the pressure on the centre of the root cap - a result which is of considerable importance regarding the ability of roots to penetrate hard soils. The coefficient of friction between the soil and the root surface has a major effect on the resistance experienced by the root. We have shown experimentally that roots experience much less friction than metal probes, and we believe that sloughing of root cap cells plays a major role in decreasing this component of friction (Fig. 4).

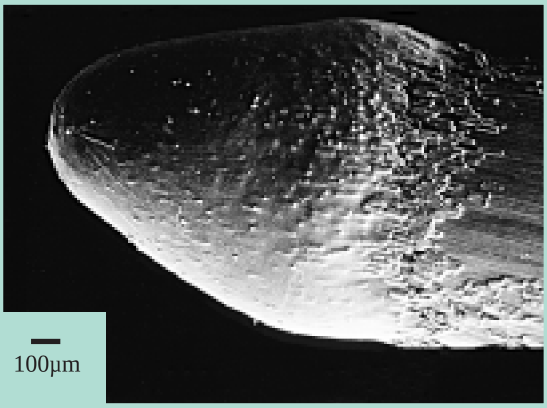

Figure 4 Maize root tip covered in mucilage and sloughing root cap cells (reproduced with permission from *J. Exp Bot* 48, p891).

Shoot growth is often decreased in compacted soils, indirectly *via* a reduction in water and nutrient uptake, and directly *via* root-shoot signalling. The effect of soil hardness is difficult to separate from the effects of water content, because a dry soil is normally a hard soil. To separate out these effects, we measured the leaf extension of wheat and barley grown in sand, and found that compressing the sand (increasing the resistance to root growth) decreased the leaf elongation rate within minutes. The sand was saturated with aerated nutrient solution at atmospheric pressure, and so only the strength of the growth medium changed. The mechanism behind this response is unknown but means that plants grown in hard soils can somehow sense the strength of the soil and communicate this information to the shoot.

We have made considerable progress in understanding the physics and physiology of plant growth in soil. This understanding also gives us valuable information on the mechanics of plant tissues that may be applied in apparently unrelated areas, such as that of fruit and vegetable texture and handling properties - a subject of considerable interest to consumers and the food processing industry.