



How do roots penetrate strong soil?

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Abstract

The mechanical and physiological bases for root growth against high mechanical impedance are reviewed. The best estimates of maximum axial root growth pressure (σ_{\max}) in completely impeded pea roots appear to be from 0.5 to 0.6 MPa, which results from a turgor pressure of about 0.8 MPa. When roots are incompletely impeded, a range of responses has been reported. Roots do not change elongation rate in a simple mechanical way in response to changes in mechanical impedance. Instead, ethylene might play a key role in mediating an increase in root diameter and a decrease in elongation rate. These changes persist for some hours or days after impedance is removed. Differences between species in their ability to penetrate strong soil layers are not related to differences in σ_{\max} , but appear to be due to differences in root diameter. In rice, differences between cultivars in the ability of their roots to penetrate strong wax layers are not related to their elongation rates through uniformly strong media. Differences between species or cultivars in their ability to penetrate strong layers may be due to differences in the tendency of roots to deflect or buckle when they grow from a weak to a strong environment.

Introduction

An important factor determining the rate of plant growth is the ability of roots to grow and explore the soil for water and nutrients. Roots experience mechanical impedance and decreased growth rates due to the force required to displace soil particles as they elongate through soil. As soil strength increases, root elongation rate decreases due to the increasing resistance of the soil particles to displacement. Strong soil can be a serious problem in agriculture as it can restrict access of the root system to water and nutrients, and so decrease crop yields. In the field, topsoil may be strong due to a lack of tillage, while tillage operations can compact the soil just beneath the tilled layer and lead to the formation of hardpans. Some subsoils are naturally strong, perhaps due to the presence of gravely horizons (Babalola and Lal, 1977), ironstone pans (Mutsaers et al., 1997) or claypans (Clark et al., 1998).

Drought can increase soil strength in many soil types as soil strength increases with decreasing soil water content (Whiteley and Dexter, 1982). Indeed, drying soils can become strong enough to affect root growth at soil water matric potentials as high as -0.1 MPa (Mullins et al., 1992). Water potentials of -0.1 MPa appear to have little direct effect on root elongation (Sharp et al., 1988) or root growth pressure (Whalley et al., 1998). In many drying soils, the effects of soil strength on plant growth therefore will be greater than the direct effect of low matric potential.

The topic of root growth and mechanical impedance has been the subject of several reviews over the years (Bengough and Mullins, 1990; Bengough et al., 1997; Eavis, 1967; Greacen, 1986). Recently, the use of techniques such as the pressure probe, nanolitre osmometer and shear beam apparatus have greatly increased our understanding of how physiological processes generate mechanical forces in elongating roots (Bengough et al., 1997; Clark et al., 1996). It was often assumed that cell expansion was largely a function of cell turgor pressure, but more recent work

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has shown the importance of cell wall properties in determining expansion and growth rates (Cosgrove, 1993; Frensch and Hsiao, 1995; Tomos and Pritchard, 1994).

Studies of plant responses to mechanical impedance can be broadly divided into two main types. The first is where mechanical impedance is manipulated independently of other physical conditions, such as aeration, generally without using soil as a growing medium (e.g. Clark et al., 2001; Sarquis et al., 1991). This approach has the advantage that plant responses can be largely ascribed to mechanical impedance. The second type of study is where mechanical impedance is varied with other physical conditions, generally by compacting soil, so that roots experience increased impedance, decreased aeration but increased root–soil contact. This approach has the advantage that it is more representative of natural or agricultural environments. For a review of methods of controlling the physical environment of roots, the reader is referred to Whalley et al. (2000).

The aim of this paper is to provide an update on our understanding of the effects of impedance on roots, from the field level down to the cell. How big an impact does impedance have on crop yields under field conditions? What types of impedance occur? Are the roots of some crop species better able to cope with impedance than others? Are the roots of some cultivars better able to cope? If so, how is the better performance achieved? Do individual roots grow better (via increased root growth pressure or greater resistance to buckling for example), or by better performance of the root system as a whole (production of more roots or thinner roots)? If verifiable differences in performance exist and the causes can be identified, then it might be possible to select, breed or engineer improved cultivars ideally suited to difficult soil conditions.

The mechanics of root growth

A theoretical framework

Roots grow by a process of cell division in the apical meristem just behind the tip, and cell expansion in a zone just behind the apex. Water influx into cells generates turgor pressure, which provides the driving force for elongation and hence root growth. Classically, following experiments on cell walls isolated from giant algal cells (Probine and Preston, 1962), cell

elongation has been regarded as plastic flow of the wall material under stress (Lockhart, 1965). Where existing soil channels are smaller than the root diameter, roots must exert a growth pressure in order to displace soil particles, overcome friction and elongate through the soil. The growth pressure (σ) is equal in magnitude to the soil pressure that opposes root growth. In a root tip elongating through soil, cell turgor pressure (P) generates the growth pressure (σ), which results from the difference between P and the wall pressure (W) so that:

$$\sigma = P - W \quad (1)$$

(Greacen and Oh, 1972). In unimpeded roots, σ is by definition zero and P is balanced by W . When roots are completely impeded and cannot elongate, σ attains a maximum value (σ_{\max}). Roots exert growth pressures in both radial and axial directions, but we will only deal with axial growth pressures here.

When water transport into growing cells is not limiting, root elongation rate can be considered in terms of a simplified Lockhart equation (Lockhart, 1965), as modified by Greacen and Oh (1972) to take account of the soil impedance:

$$R = m[W - W_c] = m[P - W_c - \sigma], \quad (2)$$

where R is the elongation rate, m is a cell wall extensibility coefficient, W is the wall pressure, W_c is the cell wall yield threshold (also known as Y), P is the turgor pressure and σ is the soil impedance (or growth pressure). This assumes that there is no growth-induced water potential gradient between symplast and apoplast, which is generally considered to be a good approximation in roots. In this simple mechanical model, the growth rate is therefore a function of P , soil resistance and the rheological properties of the cell walls. The extent to which this model of root growth adequately deals with the response of roots to mechanical impedance will be considered later.

How to measure mechanical impedance

Maximum root growth pressure

In completely impeded roots, it is relatively straightforward to measure the force exerted by an impeded root, and then calculate the maximum root growth pressure (σ_{\max}), which is equal to the impedance to root growth. The first measurements of σ_{\max} were made by Pfeffer in 1893 (reported by Gill and Bolt, 1955) and since then, a number of groups have measured σ_{\max} in different species. These measurements

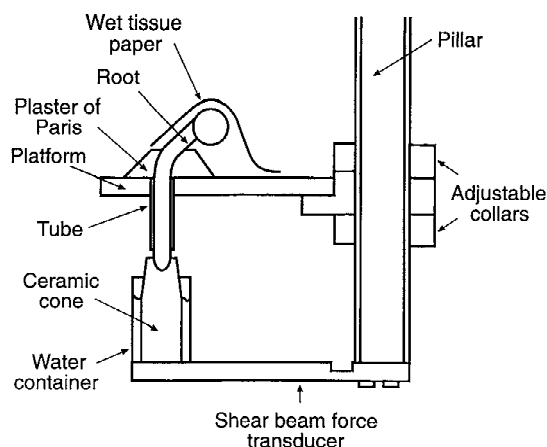


Figure 1. Shear beam apparatus used for measuring the axial growth force of roots. The pillar is mounted on a pivot so that the apparatus can be rotated through 90° in order to measure the root diameter under a microscope. Reprinted with permission from Clark et al. (1996), © Blackwell Science Ltd.

are obtained by dividing the maximum axial growth force (F_{\max}) of a completely impeded root by its cross-sectional area, although σ can reach a maximum before the axial growth force (F), as the root continues to thicken radially (Clark et al., 1996). Taylor and Ratliff (1969) measured mean σ_{\max} of 1.31 MPa for pea seedlings, 0.95 MPa for cotton seedlings and 1.16 MPa for peanut seedlings. They used a force transducer to measure the F_{\max} . Eavis et al. (1969) obtained similar results: they measured a σ_{\max} of 1.2 MPa in pea seedlings and 1.1 MPa in cotton seedlings. They used a dead-load technique to measure F_{\max} , where the weight required to prevent a seedling root from elongating is measured. Misra et al. (1986a) measured F_{\max} by growing roots against a plaster cone on an electronic balance and obtained much smaller values of σ_{\max} . This approach gave σ_{\max} values of 0.50 MPa for pea seedlings, 0.29 MPa for cotton seedlings and 0.24 MPa for sunflower seedlings. Few measurements of σ_{\max} have been made on lateral roots, but Misra (1997) found that lateral roots of pea had similar σ_{\max} to the main root axis.

The differences in σ_{\max} obtained by different workers for the same species are probably caused by the method of measurement. Despite the suggestion of Greacen (1986), these differences appear not to be accounted for by temperature, which has little effect on σ_{\max} in pea (Bengough et al., 1994; Whalley et al., 1994). Clark et al. (1999) tested the effect of different types of apparatus on measurements of σ_{\max} in pea cultivars. Cultivar differences were relatively small,

but different designs of apparatus gave quite different values of σ_{\max} with the same plant material, which varied from 0.53 to 0.87 MPa in cv. Meteor. The main problem appeared to be errors associated with measurement of the root diameter: some types of apparatus have to be dismantled in order to measure root diameter. In the shear beam apparatus (Figure 1), it was possible to measure the diameter of the impeded root *in situ*, and compare these measurements with those taken from cross-sections after dismantling. Measurements from cross-sections were consistently smaller, leading to over-estimates of σ_{\max} . We concluded that the shear beam apparatus gave the best estimate of σ_{\max} in pea (about 0.55 MPa in cv. Meteor). It should be noted that the values of σ_{\max} reported by Taylor and Ratliff (1969) and Eavis et al. (1969) are much greater than P in completely impeded pea roots, which is about 0.8 MPa (Clark et al., 1996).

Direct measurement of root growth pressure in soil

Measurements of σ_{\max} reflect the most extreme mechanical impedance as the roots are no longer elongating. It is important to be able to measure σ in a more typical situation, where an impeded root is still elongating through strong soil. However, there have been relatively few studies where F has been measured directly as roots grow through soil because of the experimental difficulties (Bengough and Mullins, 1990). Root growth force can be measured directly by growing roots into cores of strong soil on a balance, but F must be measured after the root has penetrated to a depth of several times its diameter but before root hairs can anchor the root (Stolzy and Barley, 1968). Whiteley et al. (1981) used this approach to measure the penetration resistances of pea roots, which were between 0.16 and 0.33 MPa. Similarly, Bengough and Mullins (1991) obtained values for elongating maize roots between 0.26 and 0.47 MPa. Misra et al. (1986b) measured σ of up to 0.31 MPa when roots of pea, cotton and sunflower were allowed to penetrate aggregates on a balance (there was no significant species effect on σ).

Estimating growth pressure using penetrometers

As σ is difficult to measure directly, root penetration resistance is often estimated using penetrometers. Most penetrometers consist of a conical head on a cylindrical shaft, which is pushed through the soil at a slow constant rate. Penetrometer resistance is calculated by dividing the force required for penetration by the cross-sectional area of the cone. Penetrometer tips

commonly have semi-angles of 30° , which generate a spherical expansion front, or 5° , which deform the soil cylindrically, more like a root (Greacen, 1986).

Roots generally experience a much lower resistance to penetration than penetrometers, although relatively few direct comparisons have been made. Whiteley et al. (1981) compared direct measurements of root penetration with penetrometer resistances. They found that penetrometer resistance was 2.6 – 5.3 times greater than pea root penetration pressure. Misra et al. (1986b) reported that penetrometer resistance was 1.8 – 3.8 times greater than root penetration resistance. Similarly, Bengough and Mullins (1991) reported that penetrometer resistance was 4.5 – 7.5 times greater than maize root penetration pressure. These results arise because roots penetrate soil in a different way to penetrometers (Bengough and Mullins, 1990). Root tips are not forced to take a pre-set direction and can capitalise on local weak spots as they grow through the soil. Friction to root growth is much lower both because the root penetrates the soil much more slowly than a penetrometer and because the friction experienced by the advancing root tip is lowered by cells detaching themselves and by the production of mucigel (Bengough and McKenzie, 1997; Iijima et al., 2000). Mechanical impedance also increases the secretory activity of root cap cells (Iijima and Kono, 1992).

Better estimates of the actual growth pressures experienced by roots can be calculated from the resistance to a sharp penetrometer. Root growth pressure can be calculated from the penetrometer resistance, q_p , as the pressure required to expand a cylindrical cavity using the equation:

$$\sigma = q_p / (1 + \mu \cot \alpha), \quad (3)$$

where μ is the coefficient of soil-metal friction and α is the penetrometer cone semi-angle. The coefficient of soil-metal friction is calculated by a separate procedure. Bengough and Mullins (1991) reported that using Equation (3) gave estimates of σ that were similar to their direct measurements obtained by growing roots into cores of soil on a balance.

Summary: root growth pressure

Values of σ_{\max} for pea seedlings reported in the literature vary between 0.5 and 1.3 MPa. Some of these values seem improbably high, given that the reported value of P in completely impeded pea roots is about 0.8 MPa.

Responses of plants to mechanical impedance

Morphological responses

It used to be thought that roots could not penetrate rigid pores that were narrower than their nominal diameter (Wiersum, 1957). However, other workers have since demonstrated that roots can grow into rigid pores smaller than their nominal diameter (Bengough et al., 1997; Scholefield and Hall, 1985). In ryegrass, Scholefield and Hall (1985) found that this ability was limited by the size of the root cap and the stele, but Bengough et al. (1997) reported that the stele of maize did narrow in response to radial constriction. In soil, roots will often exploit cracks, voids and large pores, or enlarge smaller pores by displacing soil particles. On encountering mechanical impedance, root cell division and elongation are decreased (Eavis, 1967). Root diameter just behind the apex increases and the production of lateral roots can be increased and also commences closer to the apex (Atwell, 1988; Goss, 1977). Lateral roots are finer than the parent axis and are therefore capable of penetrating smaller pores. This response presumably optimises the exploratory capabilities of the root system as a whole. The increase in root diameter in response to impedance is caused by cortical cells enlarging radially rather than axially, with a corresponding change in the orientation of the cellulose microfibrils in the cell walls (Veen, 1982).

Soil strength affects shoot growth as well as root growth. Masle and Passioura (1987) found that high soil strength affected leaf expansion in wheat before the first leaf had reached 20% of its final length. There were differences in stomatal conductance evident when the second leaf was starting to elongate, although there were no differences in leaf water potential. At harvest 22 d after emergence, the strong soil treatment affected shoot dry weight more than root dry weight. Andrade et al. (1993) also found that strong soil affected shoot growth early in sunflower. Montagu et al. (2001) found that the more soil compaction decreased root growth in broccoli, the more shoot growth was decreased. For a review on soil-root-shoot interactions, the reader is referred to Bingham (2001).

The possible role of hormones in mediating plant responses to impedance

Ethylene

When unimpeded roots are treated with ethylene, a decrease in elongation rate and an increase in root diameter are observed (Baluška et al., 1993; Osborne, 1976). Mechanical impedance stimulates ethylene production (Moss et al., 1988; Sarquis et al., 1991), suggesting a role for ethylene in mediating these morphological responses in impeded roots. Sarquis et al. (1991) found that when roots were pre-treated with inhibitors of ethylene biosynthesis before application of impedance, the inhibitors decreased the morphological responses to impedance, suggesting that ethylene production played a key role in mediating responses to impedance. The combination of aminoethoxyvinyl glycine (AVG, which inhibits 1-aminocyclopropane-1-carboxylic acid (ACC) formation) and silver thiosulphate (Ag^+ ions inhibit the formation of a functional ethylene-receptor complex) was most effective in overcoming impedance. This combination was able to maintain the root elongation rate of impeded roots at 90% of the unimpeded value. The effect of impedance without inhibitors was to decrease root extension by 50%, so the inhibitors relieved 80% of the effect of impedance. The increase in ethylene production on impedance also preceded measurable morphological changes by at least 1 h. Moss et al. (1988) reported that inhibitors of ethylene action blocked the morphological response to applied ethylene, while not affecting the response to impedance. This contrasting finding might reflect the lack of a pre-treatment period with inhibitors, similar to that used by Sarquis et al. (1991).

Ethylene production in impeded roots was due partly to increased ACC synthase activity, leading to increased tissue ACC concentrations (Sarquis et al., 1992). However, there was also an increase in the concentration of the conjugated form malonyl-ACC and of the ethylene-forming-enzyme (EFE) complex. This suggests that regulation of ethylene production under mechanical stress involves the coordinated action of ACC synthase, the EFE complex and ACC *N*-malonyltransferase. Mechanical impedance and hypoxia led to synergistic effects on ACC synthase activity and ethylene evolution, suggesting that the mechanism of action of these stresses to promote ethylene biosynthesis was different (He et al., 1996).

Absciscic acid

Lachno et al. (1982) and Moss et al. (1988) did not find an increase in the abscisic acid (ABA) content of mechanically impeded maize roots. However, Tardieu et al. (1991) did find that a compacted treatment increased ABA concentration in xylem sap in the field, but concluded that this was a response to decreased water availability, rather than a direct response to mechanical impedance. The compacted treatment altered the spatial arrangement of the root system, and tended to clump the roots into cracks and voids, so increasing the tendency of the roots to dry out their immediate environment. In young maize seedlings, soil compaction caused transient increases in xylem sap ABA concentration, but this response appeared to be related to changes in water relations (Hartung et al., 1994). In young barley seedlings, Mulholland et al. (1996a) observed that soil compaction caused a transient increase in xylem sap ABA concentration, although there were no changes in leaf water potential. The xylem sap ABA concentration appeared to control stomatal conductance in response to compaction. Stomatal conductance decreased when roots encountered compacted soil but this response was not seen in ABA-deficient mutants (see also Hussain et al., 1999). The ABA signal seems to maintain leaf growth at moderate levels of compaction (Mulholland et al., 1996b). In tomato, ethylene production in response to compaction led to an inhibition of shoot growth, but ABA limited ethylene production, and so maintained leaf growth at moderate levels of compaction (Hussain et al., 2000). It remains to be elucidated to what extent these signalling responses reflect changes in mechanical impedance or changes in aeration of the soil (Roberts et al., 2002). In response to water stress, ABA functions to maintain root elongation by restricting ethylene production (Sharp, 2002). It is possible that a similar antagonistic relationship between ABA and ethylene may control root growth of mechanically impeded roots but this is yet to be shown.

Summary: hormones

The balance of evidence suggests a role for ethylene in mediating root morphological responses to impedance but a role for ABA has yet to be demonstrated. However, both ABA and ethylene play important roles in mediating shoot responses to compaction, although some of the observed responses might not be due to direct effects of impedance.

Osmotic potential and turgor pressure

Partially impeded roots

In some studies, indirect evidence from measurements of sap osmotic potential suggests that impedance increases P . Greacen and Oh (1972) reported that at a soil water potential of -0.4 MPa, an increase in mechanical impedance (estimated using Equation (3)) caused a decrease in osmotic potential. They suggested that this decrease in osmotic potential would allow greater P to be generated by impeded roots. Atwell (1988) also reported that soil compaction decreased osmotic potential. The sap K^+ /sugar ratio was relatively constant when impedance was increased and the decrease in osmotic potential could be accounted for by the decreased rate of volume expansion of the root. Atwell (1988) suggested that the decrease in osmotic potential was caused by a decreased dilution of solutes by growth rather than an increased local deposition of solutes.

The first direct measurements of P in impeded roots were reported by Atwell and Newsome (1990). They grew lupin in soil with two levels of compaction, removed the roots from the soil and then measured P with a pressure probe. Compaction decreased sap osmotic potential from -1.06 to -1.28 MPa, but did not increase P in the zone of elongation, which was about 0.35 MPa. As these authors acknowledged, interpretation of this data is difficult due to the large discrepancy between osmotic potential and P . They suggested that this may have been due to a decrease in P when the roots were removed from the soil, although subsequent experiments in pea showed that P did not decrease rapidly on removal of impedance (Clark et al., 1996). In wheat, however, Atwell and Newsome (unpublished data, cited in Atwell, 1990) found that soil compaction increased P from 0.52 to 0.73 MPa.

Croser et al. (2000b) also found differences between P and osmotic potential in their responses to compaction. In pea roots, they found that compaction did not affect P (measured with a pressure probe), but decreased osmotic potential (measured with a nanolitre osmometer) by 0.2 MPa. Clark et al. (2001) found that a high impedance treatment that decreased root elongation rate by 50% did increase P in the apex of pea roots. The effect was very small in roots that had been impeded for 1 day, but the mean increase after a 2-day impedance treatment was 0.18 MPa. In contrast to other studies on the turgor relations of impeded roots, Clark et al. (2001) varied mechanical impedance independently of aeration and bulk density using

a sand core system. This avoids the possibility that the roots were responding to changes in aeration and root-soil contact as well as to the change in mechanical impedance.

Completely impeded roots

Clark et al. (1996) developed an approach that allowed P in impeded roots to be measured without the need to remove the root from the impeding environment. Roots were impeded using the shear beam apparatus (Figure 1), which makes it possible to gain access to the impeded root with the microcapillary tube of a pressure probe, and so make direct measurements of P *in situ*. Mechanical impedance increased P in the apex of pea roots from 0.55 to 0.78 MPa, which corresponded to a decrease in W from 0.55 to 0.26 MPa at the measured σ_{\max} of 0.52 MPa. These values of P and σ_{\max} are consistent with each other, in that $P > \sigma_{\max}$. Perhaps surprisingly, when roots were removed from the apparatus and bathed in 0.5 mM CaSO_4 , there was no decrease in P measured with the pressure probe over the next 90 min. This suggests that the approach of measuring P in partly impeded roots by removing the root from the high impedance environment and then measuring P appears to be sound. There do not appear to be any other *in situ* measurements of P in impeded roots in the literature to-date.

Summary: turgor pressure

No clear picture emerges of how P in roots responds to partial mechanical impedance. While mechanical impedance can increase P , mechanical impedance caused by compaction does not necessarily lead to an increase in P . This might indicate that changes in P are not central to the response of roots to impedance.

Root responses to changes in mechanical impedance

There is good evidence that the effects of impedance on roots persist for some time after roots are removed from a high impedance environment. Goss and Scott Russell (1980) used a ballotini bead system to impose mechanical impedance on barley roots. They found that when the roots were relieved of impedance, it took 3 d for the rate of elongation to return to that of the low impedance controls. Bengough and Young (1993) grew pea roots in layered soil of different penetrometer resistances. When roots grew down out of a layer of strong soil into a layer of weak soil, the effect of impedance on root elongation rate persisted for at least 2 d. Similarly, Croser et al. (2000a) found that when

impeded pea roots were transferred to hydroponic culture, it took 60 h for root elongation rate to reach that of the previously unimpeded roots. The lack of change in P when completely impeded pea roots were removed from the impeding environment (Clark et al., 1996) is consistent with these observations. Pritchard et al. (1990) observed a similar lag after the relief of chilling in maize roots. They found that expansion of cells arrested by chilling did not resume after re-warming, but that root elongation recovered by the expansion of cells newly produced by the meristem. Croser et al. (2000a) similarly suggested that the lag after removal of mechanical impedance was due to the slower expansion of cells formed during impedance in the transition zone of the meristem. Once these cells had expanded, the elongation rate would increase to unimpeded rates.

Implications for models of root growth

Greacen and Oh (1972) reported that the elongation rate of roots was proportional to effective cell wall stress ($W - W_c$), according to the model of Equation (2). They were able to describe the response of roots to mechanical impedance and soil drying with a simple model that used a single value for each of the parameters m and W_c . However, the responses of roots to changes in mechanical impedance show that the elongation rates of roots cannot be explained only by the mechanical response of wall material to the balance of pressures at the apex. Instead, elongation rate also depends on stress history and the role of ethylene. In terms of the Lockhart model, the parameters m and/or W_c must change in response to changes in impedance (Bengough et al., 1997).

Summary: responses to changes in impedance and implications for root growth models

A simple mechanical model of cell expansion cannot generally be applied successfully to mechanically impeded roots. The responses of roots to impedance do not simply depend on the balance of pressures at the apex but also on their stress history.

Effects of impedance on the whole root system and on crop productivity

Effects on crop productivity

Adverse effects

The effects of mechanical impedance depend on the

extent to which water and nutrients are limiting and how impedance affects the crop's ability to gain access to water and nutrients. Barraclough and Weir (1988) found that deep rooting of wheat was improved when a subsoil pan was destroyed by double-digging. However, when water was not limiting, grain yield was improved by just 1%. In previous drier years at the same site, the average yield response to double digging was 20% (McEwen and Johnston, 1979). Schmidt and Belford (1994) found that wheat yields increased by up to 60% as the depth of tillage of a sandplain soil prone to compaction was increased.

In irrigated lowland rice, Kundu et al. (1996) found that increasing the depth of primary tillage from 15 to 40 cm increased root proliferation at depth. Deep tillage also increased the mineral N availability, and there was a mean grain yield increase of 17% across three growing seasons. In rainfed lowland rice, disruption of a shallow (10 cm depth) ploughpan by deep tillage also increased rooting below 10 cm and led to a 15% increase in grain yield (Wade, 1996).

Beneficial effects

Despite the adverse effects of high impedance, it should be remembered that soils can be too loose and weak as well as too compacted and strong. In rainfed lowland rice grown in coarse-textured soils, deliberate subsoil compaction can decrease water percolation and increase the duration of ponded water on the soil surface (Wade, 1996). In two growing seasons in a loamy sand, subsoil compaction increased grain yield by 70% (Sharma et al., 1995). In seedbeds, a certain consolidation of the tilth decreases drying out of the surface layers, leading to better germination and emergence.

Different types of impedance: spatial heterogeneity in soil strength

In the field, root systems rarely encounter uniform mechanical impedance, and this has important implications for how plants deal with impedance in the real world. When there is a subsoil pan that decreases rooting at depth, there is often increased rooting in the topsoil (e.g. Barraclough and Weir, 1988). This is probably due both to the decreased penetration of deeper soil layers, so that roots are kept in the surface layers, and to increased lateral root formation by those roots experiencing impedance at the apex. In pot experiments, Misra and Gibbons (1996) found that lateral roots of eucalypt were less sensitive to uniform

high bulk density that the main root axis. Montagu et al. (2001) found that compensatory growth (increased lateral root formation) occurred when roots encountered horizontally-compacted layers, but not when they encountered vertically-compacted layers.

Where cracks exist in compacted soil in the field due to drying, then the roots can be clumped together (Tardieu, 1988; Tardieu et al., 1991). This leads to less uniform exploration of the soil beneath the compacted layer. Such effects mean that some roots in compacted soil may experience very low impedance.

In agricultural soils, re-colonisation of root channels made by previous crops may be important. In doing this, roots are exploiting a low impedance pathway. Rasse and Smucker (1998) reported that for maize grown after alfalfa, 41% of the maize roots were found in root-induced macropores made by the alfalfa. When maize followed maize, the figure was only 18%.

Species and cultivar differences in root penetration of strong soil

Evidence for species differences

There is evidence for species differences in the ability of roots to grow through strong soil. Iijima et al. (1991) found that maize roots were better able to penetrate a compacted soil layer in root boxes than rice roots. Materechera et al. (1991) found that the root elongation of dicotyledons (dicots) was generally less affected than monocotyledons (monocots) in high impedance sand. Sand cores were used for these experiments so that impedance could be controlled independently of aeration and water status. They also found a positive correlation between root diameter and elongation rate in impeded conditions among different species. This is consistent with the work of Abdalla et al. (1969), which suggested radial expansion might relieve the constraint at the root tip by weakening the soil ahead of the advancing tip.

Dicot roots have also been observed to penetrate compacted subsoil in the field better than monocot roots (Materechera et al., 1992). In both pea and lupin, 59% of the roots that reached the compacted layer were able to penetrate it, whereas in wheat and barley the root penetration was only 33% and 36%, respectively. They found that species with thicker roots had better penetration of the subsoil, and particularly that the extent of thickening in the high impedance treatment relative to the control was important. It was also

suggested that thicker roots gave better penetration because they would be more resistant to buckling (Barley and Greacen, 1967). Where there is a sudden increase in soil strength with depth, such as a plough pan, the root must avoid deflecting sideways in order to grow downwards through the strong soil. Dexter and Hewitt (1978) showed that this deflection behaviour depends strongly on the geometrical and mechanical properties of the soil and that buckling in air gaps may limit penetration. Differences in resistance to buckling may be more important than any differences in root elongation rate once a root reaches the strong soil. Whiteley et al. (1982) found that thicker roots tended to have greater buckling stress, although measured buckling stress did not simply depend on root diameter. An interesting question is whether roots physically buckle when they encounter strong layers, or whether cellular changes following elastic bending induce a new orientation of growth.

Species differences in root penetration ability have been exploited by including thick-rooted dicot crops in the rotation. Henderson (1989) demonstrated beneficial effects on a wheat crop following lupin in a rotation. This 'biological plough' effect has also been demonstrated in the Barind tract of north-western Bangladesh, where shallow hardpans are common (Wade, 1996). A pre-rice *Sesbania aculeata* crop was used to perforate the hardpan, which increased rooting in the subsequent rice crop and gave a 15% increase in rice grain yield.

Could differences in root penetration ability also be due to differences in friction at the advancing root tip? There are few data available but Bengough and Kirby (1999) found that the tips of pea and maize roots had similar frictional properties.

The role of σ_{\max} in species differences

It was suggested that differences in σ_{\max} might be responsible for differences in root penetration between species (Materechera et al., 1991, 1992). This followed the work of Misra et al. (1986a), who reported that σ_{\max} increased with root diameter, based on measurements in pea, cotton and sunflower roots. Clark and Barraclough (1999) measured σ_{\max} in young seedlings of lupin, pea, sunflower, rice, barley, wheat and maize. In this sample of crop species, there was no significant difference in σ_{\max} between monocots and dicots (Table 1). Dicots had thicker roots than monocots (except for maize), but there was no trend for σ_{\max} to increase with root diameter. Interestingly, σ_{\max} in

Table 1. Comparison of the maximum axial root growth pressure (σ_{\max}) of monocotyledons (monocots) and dicotyledons (dicots), modified from Clark and Barraclough (1999)

Species	Monocot/dicot	σ_{\max} (MPa)
Pea (<i>Pisum sativum</i> L.)	dicot	0.58
Wheat (<i>Triticum aestivum</i> L.)	monocot	0.49
Barley (<i>Hordeum vulgare</i> L.)	monocot	0.49
Maize (<i>Zea mays</i> L.)	monocot	0.43
Lupin (<i>Lupinus albus</i> L.)	dicot	0.41
Rice (<i>Oryza sativa</i> L.)	monocot	0.34
Sunflower (<i>Helianthus annuus</i> L.)	dicot	0.24
Mean for monocot species		0.44
Mean for dicot species		0.41

rice and maize is lower than P in cells of unimpeded roots of these species, which is about 0.6 MPa. While P might increase in impeded roots of these species, an increase does not seem to be necessary to account for the measured values of σ_{\max} . While these results suggest that differences in root penetration ability between dicots and monocots are not due to differences in σ_{\max} , it would be interesting to measure σ_{\max} in roots of older plants, and in nodal as well as seminal axes of cereals.

Evidence for cultivar differences

There is evidence for cultivar differences in root penetration of compacted soil in cotton (May and Kasperbauer, 1999) and maize and soybean (Bushamuka and Zobel, 1998). Bushamuka and Zobel (1998) also found that different root types (their nomenclature is used below) had different sensitivity to soil compaction in different cultivars. In one maize cultivar, SA-3, taproot penetration of a compacted soil layer was > 90%, but basal root penetration was < 20%, whereas in cv. La Posta taproot penetration was < 25% but basal root penetration was 70%. Similar differences were noted between soybean cultivars. These findings have implications for the selection of particular cultivars for adverse soil conditions or for use in breeding programmes.

In rice, wax layers have been used as a test system to screen cultivars for root penetration ability in the laboratory (Yu et al., 1995). Hard paraffin wax is mixed with white soft paraffin to make wax layers of the desired mechanical strength, which is then installed in a low impedance growing-medium (Figure 2). The number of roots that have penetrated the wax

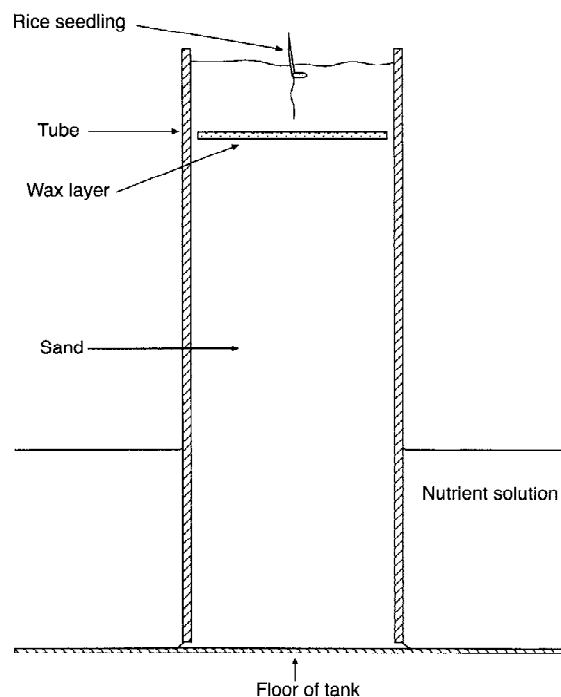


Figure 2. Wax layer growth system for assessing root penetration ability of rice cultivars, showing arrangement of the wax layer in the sand core (Clark et al., 2000).

layer is counted when the plants are harvested. During assessment and further development of the wax layer method, we found that rankings between cultivars could be very sensitive to screening conditions and criteria (Clark et al., 2000). It was important to use a wax layer that was sufficiently strong relative to a low impedance control and to avoid assessing cultivars by the ratio of penetrated roots to total roots. When an 80% wax layer (20% white soft paraffin) was used as the high impedance treatment, there were large differences in root penetration ability between cultivars. For example, the root penetration of Moroberekan was more than 20-fold better than that of Bala. This was true whether root penetration was assessed as number of roots penetrating the strong layer, or as a proportion of the roots that penetrated a low impedance (3% wax, 97% white soft paraffin) control.

In contrast, when rice cultivars were exposed to uniform high mechanical impedance in sand cores, there was little difference between cultivars in their response to impedance (Clark et al., 2002). The ability of roots to penetrate strong layers is therefore not necessarily related to their ability to elongate rapidly through strong media. However, the cultivars with better penetration of wax layers had thicker roots when

grown in high impedance sand. This is consistent with good wax layer penetration resulting from the ability of roots to resist buckling or deflecting when they encounter the strong layer. Some quantitative trait loci (QTLs) for good root penetration are also close to QTLs for root thickness (Price et al., 2000).

Summary: differences in root penetration between species and cultivars

Although roots need to generate sufficient growth pressure to grow through strong soil, differences between species and cultivars in root penetration ability appear not to be related to differences in σ_{\max} . Instead, the role of root thickness in resisting buckling or deflecting when roots encounter strong layers appears to be important.

Conclusions

The physiological responses of roots to changes in mechanical impedance in time are very complex and cannot be explained by a simple mechanical model of root elongation. However, differences between cultivars or species when roots encounter strong layers might be easier to explain, as these differences are related to root diameter. It appears that wider roots are less likely to deflect or buckle when strong layers are encountered. The extent to which this does explain differences in behaviour requires further investigation.

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