

REVIEW PAPER

# Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits

A. Glyn Bengough<sup>1,2,\*</sup>, B. M. McKenzie<sup>1</sup>, P. D. Hallett<sup>1</sup> and T. A. Valentine<sup>1</sup>

<sup>1</sup> Scottish Crop Research Institute, Dundee DD2 5DA, UK

<sup>2</sup> Division of Civil Engineering, University of Dundee, Dundee DD1 4HN, UK

\* To whom correspondence should be addressed. E-mail: Glyn.Bengough@scri.ac.uk

Received 24 August 2010; Revised 4 October 2010; Accepted 5 October 2010

## Abstract

Root elongation in drying soil is generally limited by a combination of mechanical impedance and water stress. Relationships between root elongation rate, water stress (matric potential), and mechanical impedance (penetration resistance) are reviewed, detailing the interactions between these closely related stresses. Root elongation is typically halved in repacked soils with penetrometer resistances >0.8–2 MPa, in the absence of water stress. Root elongation is halved by matric potentials drier than about –0.5 MPa in the absence of mechanical impedance. The likelihood of each stress limiting root elongation is discussed in relation to the soil strength characteristics of arable soils. A survey of 19 soils, with textures ranging from loamy sand to silty clay loam, found that ~10% of penetration resistances were >2 MPa at a matric potential of –10 kPa, rising to nearly 50% >2 MPa at –200 kPa. This suggests that mechanical impedance is often a major limitation to root elongation in these soils even under moderately wet conditions, and is important to consider in breeding programmes for drought-resistant crops. Root tip traits that may improve root penetration are considered with respect to overcoming the external (soil) and internal (cell wall) pressures resisting elongation. The potential role of root hairs in mechanically anchoring root tips is considered theoretically, and is judged particularly relevant to roots growing in biopores or from a loose seed bed into a compacted layer of soil.

**Key words:** Root growth, soil compaction, soil strength, water potential.

## Introduction

The importance of root growth for maintaining crop yields is becoming recognized and of increasing interest to plant breeders (Gewin, 2010). Extensive root systems are vital when plants are grown in soils containing insufficient supplies of water or nutrients. With the demand for food escalating globally, and variable soil water regimes associated with changing weather patterns, it is particularly important that we have a good understanding of the processes affecting root growth.

Root growth in soil can be limited by physical, chemical, and biological properties of the soil. Despite much work on these topics, there is still insufficient basic understanding of what soil factors limit root growth, for what periods, and under what weather and associated soil water conditions. Without this information, it is difficult to manage soil to

maximize crop production. In terms of physical limitations to root growth, water stress (too little water for root growth), hypoxia or anoxia (too little oxygen), and mechanical impedance (soil that is too hard for roots to penetrate rapidly) are the major causes of poor root system growth and development. Of these factors, there is a strong interplay between the strength and water content of soil. As soils dry, capillary forces make matric potential more negative, often causing strength to increase rapidly (Whalley *et al.*, 2005a; Whitmore and Whalley, 2009). Thus mechanical impedance may be a major limitation to root growth in soil as wet as –100 kPa, due to the increase in effective stress between soil particles, resulting from the tension in water films between soil particles (Whalley *et al.*, 2005a). These effects are exacerbated by increased soil

compaction associated with heavier farm machinery in arable systems. This may result in mechanical impedance limiting root growth to a relatively greater extent than water stress *per se*, with a penetrometer resistance of 2 MPa often taken as an indicator of a soil where mechanical impedance will be a major limitation to root elongation, unless a network of channels or fissures exists for roots to exploit (daSilva *et al.*, 1994; Bengough *et al.*, 2006). Even where such channels exist, root growth may become very clustered in these channels that by-pass the hard soil, restricting water and nutrient uptake from any impenetrable areas in between (Passioura, 1991). It should also be noted that leaf expansion is decreased in hard soils, due to direct signalling between root and shoot associated with the mechanical impedance (Masle and Passioura, 1987; Young *et al.*, 1997). Compacted soils are also more susceptible to waterlogging after heavy rain, and hypoxia is likely to limit root growth if there is <10% air-filled pore space (daSilva *et al.*, 1994).

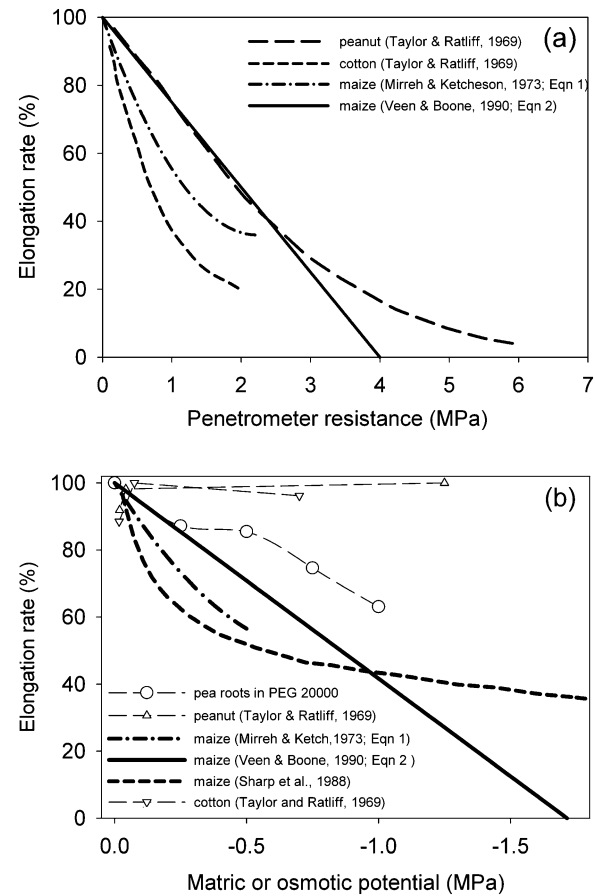
The aim of this paper is to review selectively both old and new literature on root elongation in drying soil to evaluate the importance of water stress and mechanical impedance, and their likely interactions. Penetration resistances measured in a number of Scottish soils are presented to consider physical limitations to root elongation in these soils, and root tip traits beneficial to elongation through hard soils are discussed.

## Mechanical impedance and matric potential, and their roles in limiting root elongation

### *Mechanical impedance and water stress as independent stresses*

In this first section, the limited evidence for which physical factors most limit root elongation in drying soil is explored, and so the relationships between root elongation, soil matric potential, and soil strength are reviewed. Penetrometer resistance is a common empirical measure of soil strength that is equal to the force required to push a metal cone into the soil divided by its cross-sectional area. Penetrometer resistance is between two and eight times greater than the root penetration resistance, the force exerted by a penetrating root divided by its cross-sectional area (Bengough and Mullins, 1990; Bengough and Mullins, 1991). Several studies showing the relationship between root elongation rate and penetrometer resistance (water stress not limiting elongation), and between root elongation rate and matric potential (mechanical impedance not limiting elongation) are shown in Fig. 1 (detailed in Table 1). For ease of comparison, the root elongation rate is plotted as a proportion of the fastest elongation rate measured in each study, and only studies that include measures of elongation rate under minimal stress (i.e. penetrometer resistance and matric potential approaching zero) are shown. Despite the importance of root elongation for sustaining plant growth in dry soils, it is interesting to note the relative absence of

comment on relationships between root elongation and matric potential from even classical texts on plant water relations. In Fig. 1b, data showing the effect of osmotic



**Fig. 1.** Relationships between root elongation rate and (a) penetrometer resistance or (b) matric or osmotic potential (see Table 1 for details). The elongation rate is expressed as a percentage of that measured for the fastest elongating treatment in each study.

**Table 1.** Details of root elongation studies shown in Fig. 1a and b

Reference	Growth medium	Species and plant age (d, after germination)	Penetrometer details, where given (diameter, cone angle, rate of penetration)
Taylor and Ratliff (1969)	Loamy sand soil	Peanuts, cotton (<6 DAG; 32 °C)	2 mm, 60 °, 4 mm min <sup>-1</sup>
Mirreh and Ketcheson (1973)	Clay loam	Maize (<1.5 DAG, 24 °C)	3.2 mm
Veen and Boone (1990)	Sandy loam	Maize (<9 DAG, 22 °C)	2 mm, 60 °
Sharp <i>et al.</i> (1988)	Vermiculite	Maize (<2 DAG, 29 °C)	N/A
Whalley <i>et al.</i> (1998)	PEG20000	Pea (<2 DAG, 25 °C)	N/A

DAG, days after germination; N/A, not available.

potential induced by PEG20000 on root elongation is included, for comparison. It is important to note that these studies concentrate on root elongation in relatively young seedlings where there is little or no transpiration occurring. Root elongation has been observed in non-transpiring maize seedlings at matric potentials as negative as  $-1.9$  MPa (Sharp *et al.*, 1988), and individual roots of tomato elongate in soil as dry as  $-4$  MPa if the rest of the plant is in wet soil (Portas and Taylor, 1976). However, if a transpiring plant was placed entirely in soil drier than the permanent wilting point ( $-1.5$  MPa), any root elongation would probably be short-lived.

Root elongation rate decreases in response to both increasing penetrometer resistance and decreasing matric potential, but there is considerable variation between individual studies (Fig. 1a, b). Root elongation rates were halved by a penetrometer resistance of between  $0.8$  MPa (cotton) and  $2$  MPa (maize and peanut), and by matric potentials below  $-0.5$  MPa (maize). The data of Taylor and Ratliff for cotton and peanut elongation at matric potentials of  $-0.7$  MPa and  $-1.2$  MPa are distinct in having rapid root elongation in relatively dry soil (Fig. 1b). The reason for this is unclear—their experiments were performed for a period of 110 h, and the elongation rates calculated by observing root elongation between 40 h and 80 h after transplanting; this is not dissimilar to the other studies. There remains the possibility of species differences, as the other studies reported were for maize and peas, or that some other aspect of the experimental design caused the different behaviour. Studies of root elongation versus strength and matric potential have focused predominantly on maize, due to its experimental convenience and importance in world production. It is not obvious whether we can generalize from studies on maize (as a  $C_4$  cereal) to the important  $C_3$  cereals including wheat, rice, and barley. Valuable literature exists concerning the penetration of hard soil layers by rice roots (Price *et al.*, 2000) and wheat root responses to soil compaction (Atwell, 1990), but very few studies have published comparisons between the root responses to soil physical conditions for different crop species (Iijima and Kato, 2007). The comparisons that have been done suggest that thicker roots penetrate hard soil layers more effectively, and better maintain their elongation rate in very hard soils (Materechera *et al.*, 1991, 1992).

The practical difficulty in performing this type of experiment is illustrated in relation to the accurate control of soil matric potential at the root surface. All of the experiments in solid growth media rely on the matric potential at the root surface remaining constant throughout growth, particularly in the soil adjacent to the expanding tissue of the root elongation zone. The water-release characteristic is often relatively steep at matric potentials approaching  $-1$  MPa, and so even a small decrease in water content can result in a large decrease in soil matric potential. For example, a decrease in soil water content from  $0.040$  g g $^{-1}$  to  $0.038$  g g $^{-1}$  decreased the matric potential from  $-0.7$  MPa to  $-1.25$  MPa in the loamy sand

used by Taylor and Ratliff (1969). Thus even condensation at a transparent root observation window may cause significant fluctuations in matric potential, though there is no evidence that this occurred in the experiments of Taylor and Ratliff.

#### *Combinations of mechanical impedance and water stress*

In the field, soil water content increases after rainfall and then decreases as the soil drains under gravity and dries by evapotranspiration, leading to a continual fluctuation in matric potential and soil strength at any given location. There are very few published studies in which both matric potential and soil strength have been varied systematically—two of the most comprehensive, both using maize, are Mirreh and Ketcheson (1973) and Veen and Boone (1990). These authors fitted the following empirical relationships to their data to describe maize root elongation rate ( $E_r$ , mm d $^{-1}$ ) as a function of penetrometer resistance ( $Q_p$ , MPa) and matric potential ( $\psi$ , MPa):

$$E_r = 31.1 - 17.8Q_p + 39.3\psi + 4Q_p^2 + 24.7\psi^2 + 3.3Q_p\psi \quad (1)$$

$$E_r = 48 + 28\psi - 12Q_p \quad (2)$$

For Equation 1, it is important to note that it was developed for penetrometer resistances in the range  $0 < Q_p < 2.4$  MPa (matric potentials greater than  $-0.8$  MPa), and is clearly not valid outside these ranges as parabolic functions are used (Mirreh and Ketcheson, 1973). Equation 2 was developed for penetrometer resistances in the range  $0 < Q_p < 2.9$  MPa (matric potentials greater than  $-0.63$  MPa), with linear extrapolation beyond this range (Veen and Boone, 1990). Figure 2 shows the root elongation rate (relative to a control) as affected by different combinations of soil strength and water stress, as predicted from Equations 1 and 2. It is likely that the maximum strength of soil penetrable by roots decreases with decreasing matric potential (Fig. 2a). For example, rearranging Equation 2 and setting  $E_r = 0$ , gives

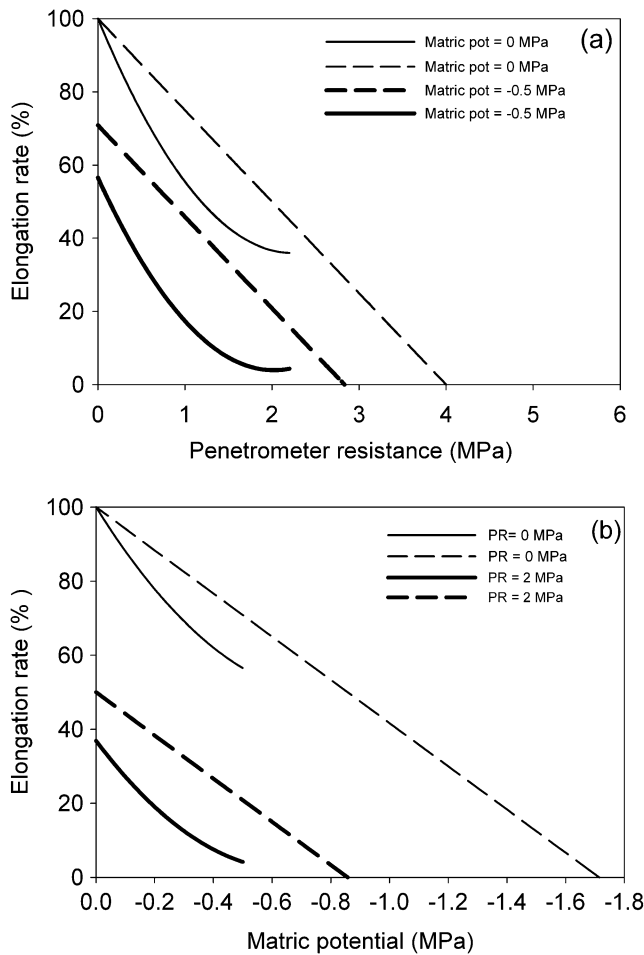
$$Q_{pmax} = 4 + 2.33\psi \quad (3)$$

where,  $Q_{pmax}$  is the penetration resistance of soil sufficient to stop root elongation completely. The maximum growth pressure exerted by a growing root influences the maximum strength of soil that the root will be able to penetrate, and is equal to the force exerted by the root when its elongation is restricted completely, divided by its cross-sectional area. This maximum growth pressure is ultimately limited by the turgor pressure in the expanding cells of the root elongation zone, and is typically up to  $\sim 1$  MPa (Clark *et al.*, 1999). Maximum growth pressure has been calculated from direct measurements of forces exerted by roots and their diameters, using either electronic balances or other force transducers. For pea root tips, maximum axial growth pressure decreased linearly from  $0.66$  MPa to  $0.35$  MPa when the external osmotic potential of a bathing solution decreased

from 0 to  $-0.45$  MPa (Whalley *et al.*, 1998). Maximum growth pressure ( $\sigma_{\max}$ ) for pea roots was found to decrease linearly with decreasing osmotic potential of the external osmotic solution ( $\pi$ ), approximately according to the relationship:

$$\sigma_{\max} = 0.663 + 0.707\pi \quad (4)$$

Thus, in soils with a large negative osmotic potential, water-stressed roots can only exert a fraction of the growth pressure possible in soils where water is freely available. This finding is consistent with the relationship between  $Q_{p\max}$  and  $\psi$  obtained in Equation 3 previously (noting that penetrometer resistances are typically between two and eight times greater than root penetration resistances; Bengough and Mullins, 1990). Here roots subjected to a large negative matric potential were unable to penetrate hard soils. This at least partly explains interactions observed between root elongation rate, matric potential, and mechanical impedance.



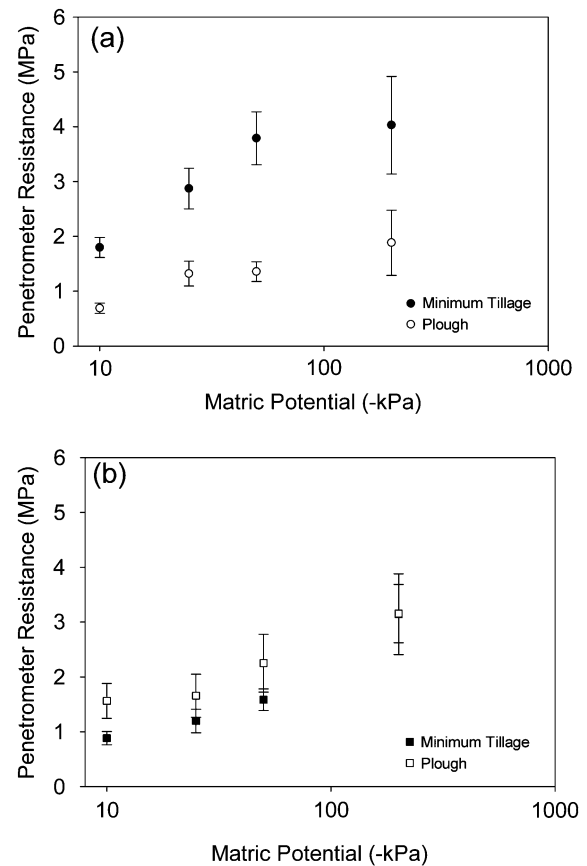
**Fig. 2.** Estimated relative root elongation rate as a function of (a) penetrometer resistance (matric potential either 0 MPa or  $-0.5$  MPa) and (b) matric potential (penetrometer resistance either 0 or 2 MPa); from relationships determined by Veen and Boone (1990; dotted lines) and Mirreh and Ketcheson (1973; continuous lines).

### Soil strength characteristics

So far the detail of the relationship between soil strength and matric potential has not been considered. The increase in soil strength with drying is primarily a physical phenomenon associated with the increase in effective stress ( $\sigma'$ ) between soil particles,

$$\sigma' = \sigma - \chi \cdot \psi \quad (5)$$

where,  $\sigma$  is any externally applied stress, and  $\chi$  is the degree of saturation of the soil. Effective stress is stress that is generated by the tension in the water films between particles, and so the more negative that  $\psi$  is, the greater the effective stress at a given saturation (Mullins and Panayiotopoulos, 1984). Penetrometer resistance typically increases in a power-law relationship with decreasing soil matric potential, and is related linearly to the effective stress (Mullins *et al.*, 1987; Weaich *et al.*, 1992; Whalley *et al.*, 2005a). The relationships between penetrometer resistance and matric potential are shown in Fig. 3 for soil cores extracted from an arable soil with a sandy loam texture at 5–10 cm and 25–30 cm depths under two management regimes. Penetrometer resistance increased rapidly

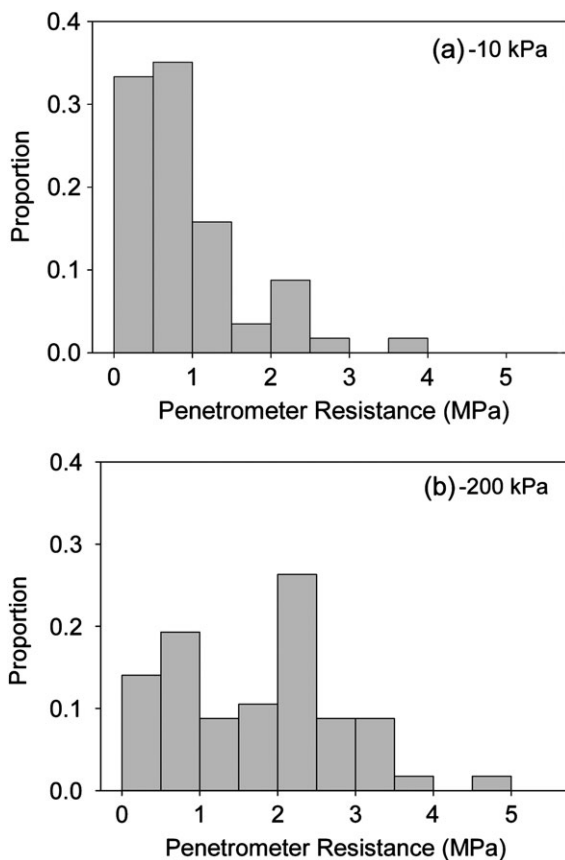


**Fig. 3.** Penetrometer resistance as a function of matric potential for a sandy loam at depths of (a) 5–10 cm or (b) 25–30 cm, either ploughed or minimally tilled. Measurements were made on 55 mm diameter soil cores equilibrated on a tension table or pressure plate apparatus, using a 1 mm diameter  $30^\circ$  angle cone at a constant penetration rate of  $4 \text{ mm min}^{-1}$ .



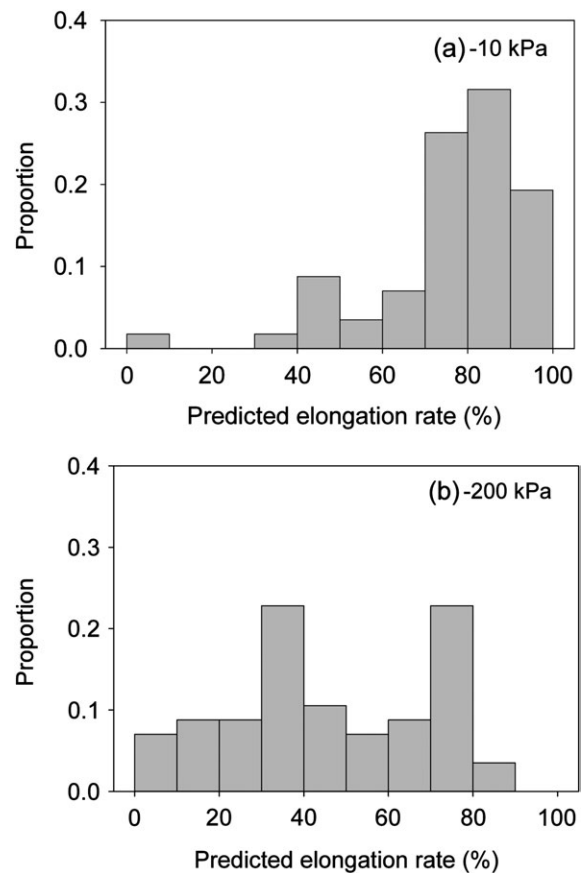
to  $>2$  MPa as the soil dried to  $-100$  kPa, except for the softer ploughed topsoil. The location of a compacted zone can be seen clearly in the strength characteristics, with penetrometer resistance  $>3$  MPa associated with the compacted zone beneath the tilled surface layer (Fig. 3a), and also a slightly increased penetrometer resistance below the plough depth (Fig. 3b).

Given that soil with a penetrometer resistance of 2 MPa may restrict root elongation substantially (e.g. Equation 3 predicts it will halt elongation if  $\psi$  is less than  $-0.86$  MPa), it is interesting to determine the range in soil strengths present in a wider range of soils. Figure 4 shows the distribution of penetrometer resistances measured in 57 individual soil cores taken from the A horizon of 19 different Scottish soils, with textures ranging from loamy sand to silty clay loam. The effect of decreasing matric potential from  $-10$  kPa to  $-200$  kPa is shown on the distribution of penetrometer resistances for these soils in Fig. 4a and b. The proportion of soil cores for which penetrometer resistance  $>2$  MPa increased from 12% to 47%, suggesting that mechanical impedance may well pose a significant limitation to root elongation even in many relatively wet soils.



**Fig. 4.** Frequency distribution of penetrometer resistances measured for 19 Scottish soils at either (a)  $-10$  kPa or (b)  $-200$  kPa. Measurements were made on 55 mm diameter soil cores equilibrated on a tension table or pressure plate apparatus, using a 1 mm diameter  $30^\circ$  angle cone at a constant penetration rate of  $4 \text{ mm min}^{-1}$ .

To attempt semi-quantitative estimates of the likely effect of soil strength and matric potential on root elongation rate, the expected distributions of relative root elongation rates were calculated using Equation 2 and the data in Fig. 4 (Fig. 5). Equation 2 was chosen because it estimates root elongation rate for maize for a wide range of matric potentials and penetrometer resistances, and also is not untypical of the relationships plotted in Fig. 1. The distribution of estimated elongation rates showed that root elongation would be limited substantially in many of the soils, even when the soil was still relatively moist at a matric potential of  $-200$  kPa. Equation 2 from Veen and Boone (1990) was obtained for repacked cores, and may not apply for field conditions where continuous cracks and pores provide many pathways for relatively unimpeded root elongation. However, even when such channels are present, regions of soil with these physical conditions are likely to remain poorly explored by roots and so the resources will be less accessible due to root clustering (Passioura, 1991). Direct assays of seedling root growth in a range of soils are currently being used to determine whether the degree of soil physical limitation is as predicted here. In the next section how different characteristics of the root tip may influence penetration of soil by roots is considered briefly, with particular attention to root growth in hard soils.



**Fig. 5.** Frequencies for estimated root elongation rates for soils at (a)  $-10$  kPa or (b)  $-200$  kPa, calculated by applying Equation 2 to the data in Fig. 4.

## Traits of the root tip that influence soil penetration

The pressure required for an object (root or probe) to penetrate the soil can be thought of as the sum of the pressure required to expand a cavity in the soil and the pressure required to overcome the frictional resistance between the object and the soil. In the case of roots, the turgor within the expanding cells of the elongation zone must also overcome the tension in their own cell walls. Thus, three sources of mechanical resistance oppose root penetration of soil—in the following section root traits that influence these pressures are considered in turn. It remains a significant research challenge to investigate the way in which these root traits interact with soil physical properties, largely due to the difficulty in visualizing roots *in situ* and quantifying their interaction with the soil at the scale of micrometres. Recently, however, promising image analysis techniques have become available for determining both rhizosphere deformations and cell expansion rates at transparent interfaces (Bengough *et al.*, 2010; Vollsnes *et al.*, 2010), and in visualizing roots and the rhizosphere in 3D using X-ray and neutron tomography (Carminati *et al.*, 2010). These techniques will enable quantification of soil displacements to investigate mechanisms of soil displacements around growing roots, and to assess what differences exist between genotypes in soils of different strengths and matric potentials. For example, particle image velocimetry (White *et al.*, 2003) of maize roots growing in sand showed that displacements (resolved down to 0.5  $\mu\text{m}$ ) extended up to eight times the root diameter into the sand, and resulted in localized compression of sand in front of the tip of decapped mutants that did not exude mucilage or release border cells (Vollsnes *et al.*, 2010). Mechanistic and soil mechanical models of root growth and soil deformation can then be tested properly and improved as appropriate (Faure, 1994; Kirby and Bengough, 2002).

### *Cavity expansion pressure*

This is determined largely by the shape of the object, its rate of penetration, and the soil mechanical properties. In the case of the root tip, the shape of the root tip may influence root penetration—more narrowly pointed root tips favour the more efficient cylindrical deformation of soil, whereas blunter shapes may give rise to the less efficient spherical-like mode of soil deformation (Greacen *et al.*, 1968; Vesic, 1972; Bengough *et al.*, 1997). Theoretically, root mucilage and other rhizodeposits may change the mechanical properties of the rhizosphere soil immediately around the root tip. This may occur either by changes in the hydraulic or water release properties of the rhizosphere (Read *et al.*, 2003; Whalley *et al.*, 2005b; Carminati *et al.*, 2010), or by rhizodeposits interacting particularly with the charged clay particles in the soil to change mechanical properties including viscosity (Barré and Hallett, 2009). The importance of these latter factors remains largely untested, and requires better understanding of mucilage and exudate interaction

with the soil immediately around the growing root tip. Studying changes in bulk mechanical properties of soil samples containing components of root exudates is one way to clarify this, although it is possible that mechanics at the root tip scale may differ from mechanical properties measured at much larger scales. Again, organ-scale imaging is a promising approach and has been used to study the mechanically efficient process of crack propagation in the burrowing of worms through gelatin analogues of marine sediments (Dorgan *et al.*, 2005).

### *Frictional resistance*

Frictional resistance between a penetrating object and the soil may account for up to 80% of the total penetration resistance (Greacen *et al.*, 1968; Bengough *et al.*, 1997). This important observation largely explains why penetrometer resistance is typically between two and eight times greater than root penetration resistance (Bengough and Mullins, 1990). The frictional resistance between roots and soil is likely to be relatively small, due to the lubricating action of border cells and mucilage (Bengough and McKenzie, 1997; Iijima *et al.*, 2003). For example, the coefficient of friction between the root cap and a rough ground glass surface has been measured to be between 0.02 and 0.04 under saturated conditions (Bengough and Kirby, 1999). Although this figure is sufficiently small to leave little scope to be decreased, it is possible (and perhaps likely) that under drier conditions friction may be substantially greater. Increasing rates of border cell and mucilage production are possible ways that roots could further decrease root–soil friction and, indeed, rates of border cell production and mucilage production both increase with increasing mechanical impedance in granular media (Barber and Gunn, 1974; Boeuf-Tremblay *et al.*, 1995; Iijima *et al.*, 2000). Recent imaging of particle movement around elongating maize roots has shown that root cap lubrication enables sand particles to slide more easily alongside the epidermis of the elongation zone than is the case for decapped mutants (Vollsnes *et al.*, 2010).

### *Cell wall tension*

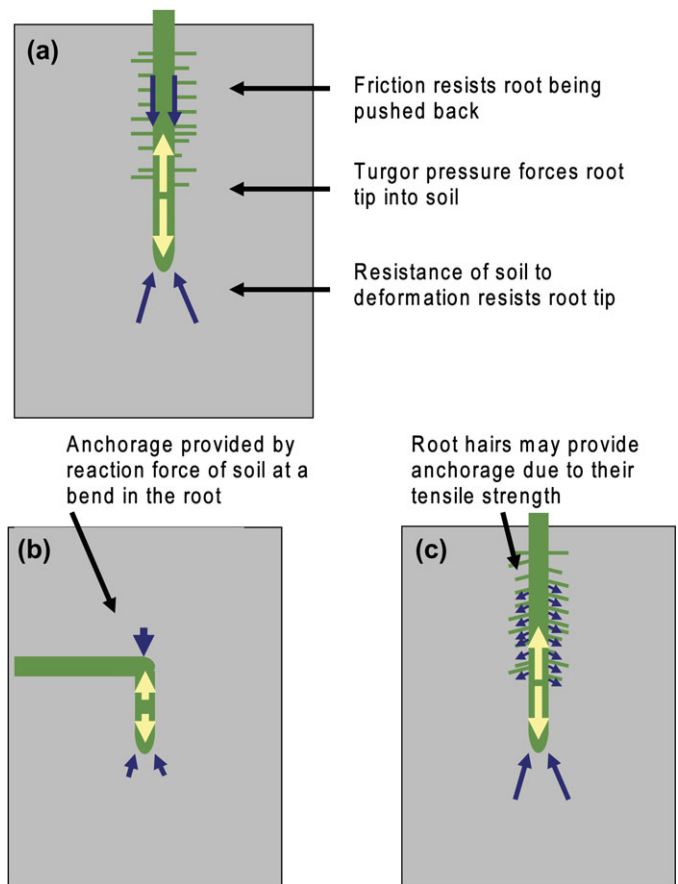
Cell wall tension in the axial direction opposes root elongation. Stiffening of the cell walls in the axial direction of the elongation zone increases this tension, with a corresponding shortening of the elongation zone, in response to mechanical impedance (Bengough *et al.*, 2006). Shortening of the elongation zone also occurs for water-stressed maize roots, though local growth rate (strain rate,  $\text{mm mm}^{-1} \text{h}^{-1}$ ) is maintained at potentials as negative as  $-1.6 \text{ MPa}$  in the apical 3 mm at the front of the elongation zone (Sharp *et al.*, 2004). This is presumably due to softening of the cell walls in the axial direction, and the local growth rate is also maintained at the apical end of the elongation zone in roots that have been subjected to mechanical impedance (Bengough *et al.*, 2006). In the case of mechanical impedance, root diameter is increased by up to 2-fold as cortical

cells expand radially due to microfibril reorientation in the primary cell wall, whereas water-stressed roots may become up to 10% thinner (Veen, 1982; Iijima and Kato, 2007). The detailed physiology and biochemistry of the apical portion of the elongation zone have recently been the subject of transcriptomic and proteomic analysis in water-stressed roots, with the ultimate objective of improving drought tolerance by genetic and metabolic engineering of root function (Yamaguchi and Sharp, 2010). Rapid elongation rates associated with relatively long root elongation zones may be a good strategy for an annual crop to stay ahead of the drying front in a drying soil profile, and also well suited to the unploughed soils associated with zero and minimum tillage regimes (Monteith, 1986; Bengough, 1997; Watt *et al.*, 2005).

In many soils, roots encounter series of cracks and biopores, or grow between regions of soil of contrasting strength. An example of one such agricultural soil is the dense massive subsoil investigated by White and Kirekgaard (2010), where >85% of roots were clumped within biopores and channels. In soils containing many such channels, additional root-tip parameters may also be important. Traits that decrease the likelihood of roots buckling, that give root tips better anchorage so that they can push forward, or that better seek out cracks and pores in the soil (or that exploit resources more efficiently) may prove advantageous (Whiteley *et al.*, 1982). For example, thicker roots are less likely to buckle when penetrating a hard layer of soil, and quantitative trait loci (QTLs) for this property have been demonstrated successfully in rice roots using wax layer tests and are associated with improved root penetration (Clark *et al.*, 2008).

One potentially relevant trait, seldom considered in relation to root penetration, is the anchorage of the root tip, so that expanding tissues can advance into new soil (Fig. 6). This anchorage is achieved by cumulative friction between the soil particles and maturing tissues behind the elongation zone, by production of root hairs close to the root tip, and, perhaps, by major changes in root trajectory that sometimes occur in compacted soils (enabling the reaction force to be transferred to the soil matrix at the bend in the root; Fig. 6b). This may also make it easier for roots to re-enter the bulk soil from a macropore (Hirth *et al.*, 2005), or enter a compacted layer under a loose seedbed. Indeed, root hairs proliferated closer to the tip of barley roots that had been mechanically impeded (Goss and Russell, 1980) and, at least in *Arabidopsis*, appear to elongate only when the epidermal cell extension has ceased (Bengough *et al.*, 2010). The degree of mechanical anchorage provided by root hairs has been seldom investigated; a study of anchorage in *Arabidopsis* mutants found that root hairs did not contribute significantly to pullout resistance at the whole root system scale (Bailey *et al.*, 2002), but it was hypothesized in a much earlier study that root hairs may contribute to anchorage for the penetration of individual root tips (Stolzy and Barley, 1968).

It is interesting to consider theoretically whether root hairs are likely to have sufficient tensile strength to anchor



**Fig. 6.** Schematic diagram illustrating (a) forces exerted by a penetrating root tip on the soil, (b) reaction force of soil at a bend in the root tip, and (c) anchorage of the root tip by root hairs.

the root tip in hard soil. The force required to break a single root hair is equal to the cross-sectional area of the root hair, multiplied by the tensile strength (stress required to break the tissue). Although there do not appear to be any available data on the tensile strength of root hairs, a first approximation may be to assume that it would be similar to the tensile strength of very fine roots, which is ~30 MPa for fine barley roots (Loades *et al.*, 2010). A single cylindrical root hair may therefore provide an anchorage force of up to 0.0024 N, suggesting that 165 root hairs may be sufficient to anchor a 1 mm diameter cylindrical root tip exerting a growth pressure of 0.5 MPa in soil. Given that root hair densities may exceed  $100 \text{ mm}^{-1}$  of root length in the *Gramineae* (Drew and Nye, 1970), this suggests that root hairs may serve a useful anchorage function. Preliminary data concerning direct measurements of root hair anchorage forces suggest that root hairs can indeed exert significant anchorage forces, and there is published evidence that maize root hairs contribute significantly to root-soil adhesion (Czarnes *et al.*, 1999).

The ability of roots to locate cracks and channels in the soil is a characteristic potentially very relevant to the penetration of structured subsoils, and is one where there has been substantial progress in terms of developing a field screening technique (McKenzie *et al.*, 2009). Again, this is

a relatively under-researched area, where there is emerging evidence of varietal differences for potentially heritable traits, and also developing research into processes such as thigmotropism that influence the direction of root growth (Massa and Gilroy, 2003) and enable roots preferentially to locate channels in the soil (Stirzaker *et al.*, 1996). Novel screening methods such as these will be required to assist in the development of varieties that can better utilize pre-existing channels.

## Conclusions

Adequate root elongation is important for plant growth, especially in soil where resources of water and nutrients are scarce. Roots elongate more slowly in drying soil due to a combination of water stress and mechanical impedance. Recent evidence shows that penetrometer resistances in excess of 2 MPa occur even in many relatively moist soils (e.g. matric potentials of  $-100$  kPa to  $-200$  kPa), and that this is sufficient to slow root elongation to less than half of its unimpeded rate. Root tip traits beneficial to root penetration include traits that decrease cavity expansion pressure, frictional resistance, or axial cell wall tension. In soil containing macropores and channels, the ability of roots to exploit such channels may also be of significant benefit, and root hairs are probably sufficiently strong to aid root tip anchorage significantly. It is essential to consider root responses to soil strength when developing strategies to breed drought-resistant crops and, to address this adequately, may require the development of some novel screening approaches.

## Acknowledgements

Thanks to the Scottish Soil Survey of the Macaulay Institute for supplying soil cores for the study of penetrometer resistance. The SCRI receives grant-in-aid from the Scottish Executive Research Environment and Rural Affairs Department (REERAD).

## References

**Atwell BJ.** 1990. The effect of soil compaction on wheat during early tillering. I. Growth, development and root structure. *New Phytologist* **115**, 29–35.

**Bailey PHJ, Currey JD, Fitter AH.** 2002. The role of root system architecture and root hairs in promoting anchorage against uprooting forces in *Allium cepa* and root mutants of *Arabidopsis thaliana*. *Journal of Experimental Botany* **53**, 333–340.

**Barber DA, Gunn KB.** 1974. The effect of mechanical forces on the exudation of organic substances by the roots of cereal plants. *New Phytologist* **73**, 39–45.

**Barre P, Hallett PD.** 2009. Rheological stabilization of wet soils by model root and fungal exudates depends on clay mineralogy. *European Journal of Soil Science* **60**, 525–538.

**Bengough AG.** 1997. Modelling rooting depth and soil strength in a drying soil profile. *Journal of Theoretical Biology* **186**, 327–338.

**Bengough AG, Bransby MF, Hans J, McKenna SJ, Roberts TJ, Valentine TA.** 2006. Root responses to soil physical conditions: growth dynamics from field to cell. *Journal of Experimental Botany* **57**, 437–447.

**Bengough AG, Hans J, Bransby MF, Valentine TA.** 2010. PIV as a method for quantifying root cell growth and particle displacement in confocal images. *Microscopy Research and Technique* **73**, 27–36.

**Bengough AG, Kirby JM.** 1999. Tribology of the root cap in maize (*Zea mays*) and peas (*Pisum sativum*). *New Phytologist* **142**, 421–425.

**Bengough AG, McKenzie BM.** 1997. Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L) root growth. *Journal of Experimental Botany* **48**, 885–893.

**Bengough AG, Mullins CE.** 1990. Mechanical impedance to root growth—a review of experimental techniques and root growth responses. *Journal of Soil Science* **41**, 341–358.

**Bengough AG, Mullins CE.** 1991. Penetrometer resistance, root penetration resistance and root elongation rate in 2 sandy loam soils. *Plant and Soil* **131**, 59–66.

**Bengough AG, Mullins CE, Wilson G.** 1997. Estimating soil frictional resistance to metal probes and its relevance to the penetration of soil by roots. *European Journal of Soil Science* **48**, 603–612.

**Boeuf-Tremblay V, Plantureux S, Guckert A.** 1995. Influence of mechanical impedance on root exudation of maize seedlings at two development stages. *Plant and Soil* **172**, 279–287.

**Carminati A, Moradi A, Vetterlein D, Vontobel B, Lehmann E, Weller U, Vogel H, Oswald S.** 2010. Dynamics of soil water content in the rhizosphere. *Plant and Soil* **332**, 163–176.

**Clark LJ, Bengough AG, Whalley WR, Dexter AR, Barraclough PB.** 1999. Maximum axial root growth pressure in pea seedlings: effects of measurement techniques and cultivars. *Plant and Soil* **209**, 101–109.

**Clark LJ, Price AH, Steele KA, Whalley WR.** 2008. Evidence from near-isogenic lines that root penetration increases with root diameter and bending stiffness in rice. *Functional Plant Biology* **35**, 1163–1171.

**Czarnes S, Hiller S, Dexter AR, Hallett PD, Bartoli F.** 1999. Root:soil adhesion in the maize rhizosphere: the rheological approach. *Plant and Soil* **211**, 69–86.

**daSilva AP, Kay BD, Perfect E.** 1994. Characterization of the least limiting water range of soils. *Soil Science Society of America Journal* **58**, 1775–1781.

**Dorgan KM, Jumars PA, Johnson B, Boudreau BP, Landis E.** 2005. Burrow extension by crack propagation. *Nature* **433**, 475.

**Drew M, Nye P.** 1970. The supply of nutrient ions by diffusion to plant roots in soil. *Plant and Soil* **33**, 545–563.

**Faure AG.** 1994. Stress field developed by root growth: theoretical approach. *Journal of Agricultural Engineering Research* **58**, 53–67.

**Gewin V.** 2010. Food: an underground revolution. *Nature* **466**, 552–553.

**Goss MJ, Russell RS.** 1980. Effects of mechanical impedance on root growth in barley (*Hordeum vulgare* L.). III. Observation on the mechanism of response. *Journal of Experimental Botany* **31**, 577–588.



- Greacen EL, Farrell DA, Cockroft B.** 1968. Soil resistance to metal probes and plant roots. *Transactions of the 9th Congress of the International Society of Soil Science* **1**, 769–779.
- Hirth JR, McKenzie BM, Tisdall JM.** 2005. Ability of seedling roots of *Lolium perenne* L. to penetrate soil from artificial biopores is modified by soil bulk density, biopore angle and biopore relief. *Plant and Soil* **272**, 327–336.
- Iijima M, Griffiths B, Bengough AG.** 2000. Sloughing of cap cells and carbon exudation from maize seedling roots in compacted sand. *New Phytologist* **145**, 477–482.
- Iijima M, Higuchi T, Barlow PW, Bengough AG.** 2003. Root cap removal increases root penetration resistance in maize (*Zea mays* L.). *Journal of Experimental Botany* **54**, 2105–2109.
- Iijima M, Kato J.** 2007. Combined soil physical stress of soil drying, anaerobiosis and mechanical impedance to seedling root growth of four crop species. *Plant Production Science* **10**, 451–459.
- Kirby JM, Bengough AG.** 2002. Influence of soil strength on root growth: experiments and analysis using a critical-state model. *European Journal of Soil Science* **53**, 119–127.
- Loades KW, Bengough AG, Bransby MF, Hallett PD.** 2010. Planting density influence on fibrous root reinforcement of soils. *Ecological Engineering* **36**, 276–284.
- Masle J, Passioura JB.** 1987. The effect of soil strength on the growth of young wheat plants. *Australian Journal of Plant Physiology* **14**, 643–656.
- Massa GD, Gilroy S.** 2003. Touch modulates gravity sensing to regulate the growth of primary roots of *Arabidopsis thaliana*. *The Plant Journal* **33**, 435–445.
- Materechera SA, Alston AM, Kirby JM, Dexter AR.** 1992. Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil* **144**, 297–303.
- Materechera SA, Dexter AR, Alston AM.** 1991. Penetration of very strong soils by seedling roots of different plant-species. *Plant and Soil* **135**, 31–41.
- McKenzie BM, Bengough AG, Hallett PD, Thomas WTB, Forster B, McNicol JW.** 2009. Deep rooting and drought screening of cereal crops: a novel field-based method and its application. *Field Crops Research* **112**, 165–171.
- Mirreh HF, Ketcheson JW.** 1973. Influence of soil water matric potential and resistance to penetration on corn root elongation. *Canadian Journal of Soil Science* **53**, 383–388.
- Monteith JL.** 1986. How do crops manipulate water supply and demand? *Philosophical Transactions of the Royal Society A: Mathematical and Physical Sciences* **316**, 245–259.
- Mullins CE, Panayiotopoulos KP.** 1984. The strength of unsaturated mixtures of sand and kaolin and the concept of effective stress. *Journal of Soil Science* **35**, 459–468.
- Mullins CE, Young IM, Bengough AG, Ley GJ.** 1987. Hard-setting soils. *Soil Use and Management* **3**, 79–83.
- Passioura JB.** 1991. Soil structure and plant-growth. *Australian Journal of Soil Research* **29**, 717–728.
- Portas CAM, Taylor HM.** 1976. Growth and survival of young plant roots in dry soil. *Soil Science* **121**, 170–175.
- Price AH, Steele KA, Moore BJ, Barraclough PB, Clark LJ.** 2000. A combined RFLP and AFLP linkage map of upland rice (*Oryza sativa* L.) used to identify QTLs for root-penetration ability. *Theoretical and Applied Genetics* **100**, 49–56.
- Read DB, Bengough AG, Gregory PJ, Crawford JW, Robinson D, Scrimgeour CM, Young IM, Zhang K, Zhang X.** 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phytologist* **157**, 315–326.
- Sharp RE, Poroyko V, Hejlek LG, Spollen WG, Springer GK, Bohnert HJ, Nguyen HT.** 2004. Root growth maintenance during water deficits: physiology to functional genomics. *Journal of Experimental Botany* **55**, 2343–2351.
- Sharp RE, Silk WK, Hsiao TC.** 1988. Growth of the primary maize root at low water potentials. I. Spatial distribution of expansive growth. *Plant Physiology* **87**, 50–57.
- Stirzaker RJ, Passioura JB, Wilms Y.** 1996. Soil structure and plant growth: impact of bulk density and biopores. *Plant and Soil* **185**, 151–162.
- Stolzy LH, Barley KP.** 1968. Mechanical resistance encountered by roots entering compact soils. *Soil Science* **105**, 297–301.
- Taylor HM, Ratliff LH.** 1969. Root elongation rates of cotton and peanuts as a function of soil strength and water content. *Soil Science* **108**, 113–119.
- Veen BW.** 1982. The influence of mechanical impedance on the growth of maize roots. *Plant and Soil* **66**, 101–109.
- Veen BW, Boone FR.** 1990. The influence of mechanical resistance and soil-water on the growth of seminal roots of maize. *Soil and Tillage Research* **16**, 219–226.
- Vesic AS.** 1972. Expansion of cavities in infinite soil mass. *Journal of the Soil Mechanics and Foundations Division* **98**, 265–290.
- Vollsnes AV, Futsaether C, Bengough AG.** 2010. Quantifying rhizosphere particle movement around mutant maize roots using timelapse imaging and particle image velocimetry. *European Journal of Soil Science* **48**, 926–939.
- Watt M, Kirkegaard JA, Rebetzke GJ.** 2005. A wheat genotype developed for rapid leaf growth copes well with the physical and biological constraints of unploughed soil. *Functional Plant Biology* **32**, 695–706.
- Weaich K, Cass A, Bristow KL.** 1992. Use of a penetration resistance characteristic to predict soil strength development during drying. *Soil and Tillage Research* **25**, 149–166.
- Whalley WR, Bengough AG, Dexter AR.** 1998. Water stress induced by PEG decreases the maximum growth pressure of the roots of pea seedlings. *Journal of Experimental Botany* **49**, 1689–1694.
- Whalley WR, Leeds-Harrison PB, Clark LJ, Gowing DJG.** 2005a. Use of effective stress to predict the penetrometer resistance of unsaturated agricultural soils. *Soil and Tillage Research* **84**, 18–27.
- Whalley WR, Riseley B, Leeds-Harrison PB, Bird NRA, Leech PK, Adderley WP.** 2005b. Structural differences between bulk and rhizosphere soil. *European Journal of Soil Science* **56**, 353–360.
- White DJ, Take WA, Bolton MD.** 2003. Soil deformation measurement using particle image velocimetry (PIV) and photogrammetry. *Geotechnique* **53**, 619–631.

**White RG, Kirkegaard JA.** 2010. The distribution and abundance of wheat roots in a dense, structured subsoil—implications for water uptake. *Plant, Cell and Environment* **33**, 133–148.

**Whiteley GM, Hewitt JS, Dexter AR.** 1982. The buckling of plant roots. *Physiologia Plantarum* **54**, 333–342.

**Whitmore AP, Whalley WR.** 2009. Physical effects of soil drying on roots and crop growth. *Journal of Experimental Botany* **60**, 2845–2857.

**Yamaguchi M, Sharp RE.** 2010. Complexity and coordination of root growth at low water potentials: recent advances from transcriptomic and proteomic analyses. *Plant, Cell and Environment* **33**, 590–603.

**Young IM, Montagu K, Conroy J, Bengough AG.** 1997. Mechanical impedance of root growth directly reduces leaf elongation rates of cereals. *New Phytologist* **135**, 613–619.