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Morphological Changes in Cotton Roots in Relation to Soil Mechanical Impedance and Matric Potential

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Abstract. Soil mechanical impedance (MI) and matric potential can both cause reduction in the root growth rate, modify rooting pattern and root diameter. Cotton seedlings are sensitive to the soil physical environment, particularly during early stages of growth. Soil matric potential and MI effect on root biomass, axial root length and diameter, and the number and length of lateral roots in soil packed to penetration resistances (PR) of 0.1, 1.0, 1.1 and 1.2 MPa (megaPascal = 10^6 Pascal), each at three matric potentials of −10, −100 and −500 kPa (kiloPascal = 10^3 Pascal), were determined. Total root lengths were reduced by 29, 50 and 53% at impedance of 1.0, 1.1 and 1.2 MPa, respectively, as compared to the control, whereas MI of 1.2 MPa resulted in 60% reduction in axial root length. A similar increase in diameter was caused by increasing mechanical impedance, while decreasing matric potential had little effect. Roots that were water stressed did not change their diameter but had a shorter axis and longer lateral length. In contrast, the impeded roots (PR = 1.0, 1.1 and 1.2 MPa) had both a shorter axis and a smaller total length, but had increased diameter. These results not only illustrate the plasticity of root response to stress but also demonstrate how the response differs between different types of stresses.

Keywords: soil mechanical impedance, soil matric potential, root plasticity, root length, penetration resistance, soil physical environment

Introduction

Plants require networks of roots to absorb water and nutrients from the soil. Soil factors, which influence the distribution of plant root system, often limit plant productivity by modifying the extent of plant root exploration and by reducing the efficiency of water absorption. Soil physical factors, such as soil matric potential and mechanical impedance, affect the root growth. Mechanical impedance is the resisting pressure encountered by growing roots. It is ubiquitous within the root environment. Penetration resistance of 0.5-1.0 MPa (megaPascal = 10^6 Pascal), and greater, are commonly experienced in soils that can reduce root elongation rates considerably (Martino and Shaykewich, 1994). It increases with increase in soil bulk density. It also usually increases as the soil matric potential decreases during soil drying. Unless roots are able to exploit soil structural features to bypass the bulk of soil, their growth rate reduces as mechanical impedance is increased (Bengough and Mullins, 1990). Indeed, drying soils can become strong enough to affect root growth at matric potential as high as – 0.1 MPa (Mullins *et al.*, 1992). Water potential of – 0.1 MPa appears to have little direct effect on root elongation, or root growth pressure (Whalley *et al.*, 1998). Under controlled conditions, root growth rate varies in approximately inverse proportion to mechanical impedance. This is in consequence of both a reduction in the rate of cell division in the meristem and a decrease in the length of fully expanded cells (Smucker and Atwell, 1988; Eavis, 1967). Wilson *et al.* (1977) reported that under impeding conditions, cell length and the volume of inner cortical cells decreased but the diameter and volume of the outer cortical and epidermal cells was considerably increased. The epical meristem and zone of cell expansion of impeded roots is short and the cells on the surface of the tips may slough off (Bengough and McKenzie, 1997). In barley, initiation of lateral roots and growth of root hair took place nearer the tip under impeded conditions (Goss and Russell, 1980). In roots that bent after an encounter with an obstacle, lateral roots predominated on the concave side of the bent while root hairs dominated on the convex side.

Under field conditions, plant root systems encounter considerable spatial variations in mechanical impedance. Even in compact soils, areas of lower mechanical impedance will occur due to shrinkage cracks and channels formed by earthworms or roots of previous crops (Tardieu, 1988). Furthermore, dense compact layers frequently underline the loosened top soil in cultivated soils. Under these conditions, a root system encountering hard compact zones of soils has

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the opportunity to proliferate in zones of looser soil. Such plasticity in root system development, in response to heterogeneous soil conditions, has been reported in both pot (Garcia *et al.*, 1988) and field experiments (Bengough *et al.*, 2006; Pietola, 2005; Clark *et al.*, 2003; Montagu *et al.*, 1998). However, a common consensus on the root morphology changes is lacking.

Increased mechanical impedance has been associated with decreased root elongation rates in many plant species including maize (Veen, 1982), cotton (Nabi *et al*., 2001; Taylor and Ratiliff, 1969), wheat (Nabi and Mullins, 2001; Masle, 1992), peas (Tsegaye and Mullins, 1994), grasses (Cook *et al*., 1996), and radiata pine (Zou *et al*., 2001). With increased mechanical impedance, the above-ground plant growth is also affected. Reduced root growth has often been associated with reduced shoot growth (Kirby and Bengough, 2002; Cook *et al*., 1996; Blaikie and Mason, 1993). Young *et al*. (1997) observed 36.2% and 22.6% reduced leaf elongation rates in barley and wheat, respectively. Reduced transpiration rates (Masle, 1992) and stomatal conductance (Masle, 1998) have also been associated with increased mechanical impedance sensed by plant roots. Decreased nutrient uptake (total P and N) has been reported with increased soil mechanical impedance (Pietola and Tanni, 2003; Chassot and Richner, 2002; Habib, 2002).

The present study was conducted to determine the effect of mechanical impedance and matric potential on morphology of cotton roots and to demonstrate how the root growth responses differ between different types of stresses.

Materials and Methods

Experimental work was conducted during 1998 at the Department of Plant and Soil Science, University of Aberdeen, UK, in a growth cabinet in packed soil wetted to three matric potentials, i.e., –10, –100 and –500 kPa (kiloPascal = 10^3 Pascal). The soil was packed in perplex cylinders (300 mm long, with 50 mm internal dia) to dry bulk density equivalent to the mechanical impedance of 0.1, 1.0, 1.1 and 1.2 MPa. Pregerminated seedlings of cotton (variety MNH 147) were grown for 72 h at 32 °C in the dark. Each treatment had three replications with two seedlings in each of the cylinders.

A sandy clay loam (Carpow Series) topsoil (0-10 cm) was sieved and aggregates between 1 and 3.35 mm dia were retained. The prepared soil contained 0.21% organic matter with particle size distribution of 20.6% clay, 18.0% silt and 61.4% sand. Water retention curve of the soil was developed following standard procedures of tension table and pressure plate apparatus (Klute, 1986). According to the water retention curve, the soil was wetted to the required matric potentials and packed into cylinders in layers of 20 mm increments up to 200 mm depths, separately, at different bulk densities. The packed cylinders were then incubated at 32 °C for 24 h. The incubation was intended to attain a homogeneous temperature and consequently moisture distribution inside the cylinders, and to avoid heat shock of seedlings at transplanting. After incubation, two germinated seedlings of 5 mm length were transplanted, 5 mm apart, in each cylinder and rest of the packing was completed with more soil accordingly. Finally, the cylinders were shifted inside the phytotron cabinet maintained at 32 °C in the dark. Temperature within cylinders was recorded hourly with a bead thermistor attached to a data logger (Skye Instruments Data Hog, Skye Ltd., Ddole Industrial State, Llandrindod, Wells, UK).

After 72 h of transplanting, the cylinders were removed from the phytotron. The seedlings were excavated from the cylinders alongwith the soil, and soil was separated from the seedlings with gentle washing. After washing and blotting, the root weight, root length, root diameter and the number of root laterals were recorded. The roots were then dried in an oven at 80 °C for 72 h to record their dry weights. Total root length was measured using DIAS image analyzer with the root measurement system software (Root Measurement System Software, version 1.6, Delta-T Devices Ltd., Burwell, Cambridge, UK). High quality photocopies of the stained roots were used for length measurement. Each image was measured three times to check for reproducibility and mean of these was used for further data analyses.

Analysis of variance (ANOVA) was computed for each parameter using four mechanical impedance and three matric potentials with four replications in a 4 x 3 factorial design using Minitab Statistical Software, Minitab for windows version 10.5 (Minitab Corporation, Inc., USA). Least significant difference (LSD) test was used to compare the treatment means.

Results and Discussion

The mechanical impedance and matric potential were noted to reduce significantly the axial and total root length ($p < 0.05$). Interactions between matric potential and mechanical impedance were also significant. Axial root length decreased with increasing mechanical impedance (Fig. 1). A reduction of 52% and 56% was observed at mechanical impedance of 1.2 MPa as compared to control (0.10 MPa) in seedlings grown at –10 and –500 kPa, respectively. With a decrease of matric potential from –10 kPa to –100 and –500 kPa, the axial lengths were also reduced significantly. At the three matric potentials studied, significant higher reductions were observed in the impeded treatments of penetration resistance 1.0, 1.1 and 1.2 MPa. These results were expected, as the mechanical impedance has been reported to reduce elongation of roots (Nabi and Mullins, 2001; Bennie, 1996; Verpraskas, 1994). However, a single line drawn through all the points (to within the limits of experimental error) indicated a unique relationship between penetration resistance and root growth rate, independent of matric potentials down to –500 kPa (Fig. 2). This line suggested that any apparent effect of matric potentials on the rate of root growth was no longer significant if the undesirable effects of matric potential on penetration resistance were taken into account.

Total root lengths were also decreased with increased mechanical impedance (Fig. 3). A reduction of about 50% was observed at all the matric potentials at 1.2 MPa relative to the control. In contrast to the reduction in axial root lengths with decrease in matric potential, total root lengths tended to increase with decreasing matric potential. In 1.0 and 1.1 MPa treatment, 25% and 3% longer roots were recorded at –500 kPa than at –10 kPa matric potential. These longer roots at the lower matric potential may either be due to increase in the number of root laterals or lengths of individual laterals in response to decreased matric potential.

The number of root laterals was reduced by impedance, but the overall effect of matric potential on the lateral root number was non-significant (Table 1). The interactions between matric potential and mechanical impedance were also non-significant. Only in the 0.1 MPa treatments, the number of root laterals decreased significantly with decrease in matric potential. A reduction of 20, 39 and 54% was noted when mechanical impedance increased to 1.0, 1.1 and 1.2 MPa, respectively, over the unimpeded treatment. This was in line with the earlier findings that root branching of plants grown in mechanically impeded soil is restricted but does not necessarily mean that spacing of laterals has changed (Misra and Gibbons, 1996; Boone and Veen, 1982).

Total length of root laterals was reduced significantly ($p < 0.05$) by increased mechanical impedance (Table 1). On the average, a reduction of 29, 50 and 53% was observed at impedance of 1.0, 1.1 and 1.2 MPa, respectively, as compared to the control. Matric potential also reduced the length of laterals, though it was statistically non-significant. In treatments with higher mechanical impedance, longer laterals were observed in response to a decrease in matric potential. This was in contrast to the control treatment where laterals were shorter at –500 kPa than at –10 and –100 kPa. Neither matric potential, nor mechanical impedance, affected lateral spacing at all impedance levels.

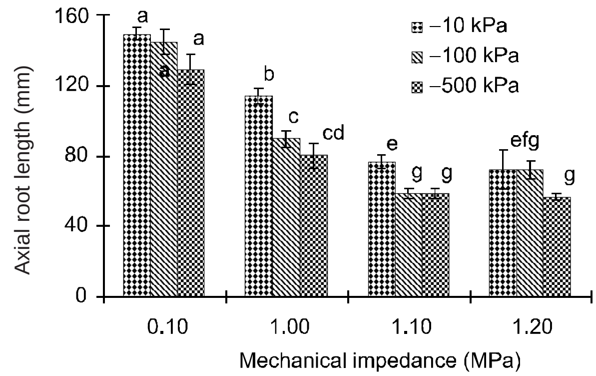

Fig. 1. Effect of mechanical impedance and matric potentials on axial root length of cotton seedlings (values are mean ±SE; single SED value computed from ANOVA = 5.77; bars with similar letters do not differ significantly at $p > 0.05$).

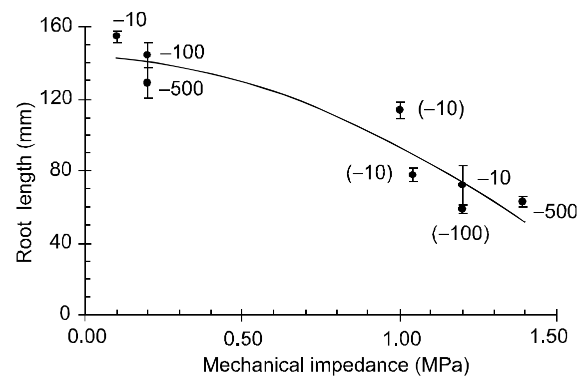

Fig. 2. Effect of mechanical impedance and matric potentials on root length of cotton; a single penetration resistance value at any matric potential of –10 kPa, for which data at –100 and –500 kPa at respective mechanical impedance was not available appear in parenthesis.

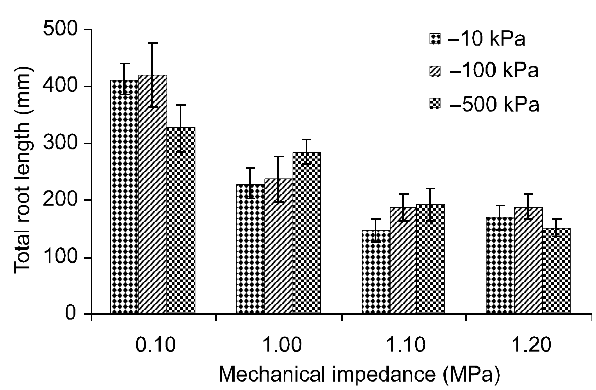

Fig. 3. Effect of mechanical impedance and matric potentials on total root length of cotton seedlings (values are mean ±SE; single SED value computed from ANOVA = 43.7).

Table 1. Effect of mechanical impedance and matric potentials on the number and length of root laterals of cotton seedlings

Mechanical impedance	Number of root laterals*			Length of root laterals (mm)**		
(MPa)	–10 kPa	–100 kPa	–500 kPa	–10 kPa	–100 kPa	–500 kPa
0.1	34	32	28	265	273	192
1.0	24	26	27	113	148	205
1.1	20	20	19	70	130	134
1.2	14	17	12	104	118	95

* = for comparison of number of root laterals: LSD ($p < 0.05$) for mechanical impedence 3.21, LSD ($p < 0.05$) for matric potential 2.76, penetration resistance-mehanical impedance: non-significant; ** = for comparison of length of root taterals: LSD ($p < 0.05$) for mechanical impedance 49, LSD ($p < 0.05$) for matric potential 43, penetration resistance-mechanical impedance: non-significant

Root diameter was significantly increased with increase in soil mechanical impedance (Table 2), but did not change significantly with matric potential. Higher mechanical impedance have been reported to result in thicker roots of maize (Shierlaw and Alston, 1984; Boone and Veen, 1982), wheat (Collis-George and Yoganathan, 1985; Bennie, 1979), Cotton (Bennie, 1979), and potatoes (Boone *et al.*, 1985).

Mechanical impedance and matric potential significantly affected ($p < 0.05$) dry root biomass (Fig. 4). However, their interactions were non-significant. The root biomass was decreased with increase in mechanical impedance. Fresh weights were reduced in the order of 19, 42 and 49% at penetration resistance of 1.0, 1.1 and 1.2 MPa, respectively. Higher fresh weights were observed at –100 kPa matric potential than at –10 or at –500 kPa.

The number of root laterals and the total length of root laterals was reduced with increase in mechanical impedance, while spacing of root laterals was not affected, as was also observed by Tsegaye and Mullins (1994) for peas, indicating some kind of overall plant control to maintain lateral spacing. Reduction in number of root laterals with increased soil compaction has been observed in maize by Sauerbeck and Helal (1986). Stress in soil physical environment imposes contrasting effects on the root system, some of which the plants were able to compensate for, for example, through increase in lateral lengths in cotton with decrease in matric potential. But other stresses imposed constraints which the plants were unable to compensate for, for example, reduced root length with increased mechanical impedance.

It is interesting to note that the overall root biomass was affected very little, implying that seedlings tended to unload/release metabolites at a rate which is not strongly dependent on soil physical conditions. However, there was a clear and interesting contrast between root response to

Table 2. Effect of mechanical impedance and matric potentials on the number of root laterals, spacing of root laterals, length and root diameter (values in parenthesis indicate percentage reduction over control)

Mechanical impedance (MPa)	Number of root laterals	Length of root laterals (mm)	Spacing of root laterals (mm)	Root diameter (mm)
0.1	31[a] (-)	244[a] (-)	2.64[a]	0.93[c]
1.0	26[ab] (16)	155[b] (36)	2.29[a]	0.95[b]
1.1	19[b] (39)	111[b] (53)	2.42[a]	1.10[a]
1.2	14[c] (54)	106[b] (56)	3.46[a]	1.00[a]
LSD ($p < 0.05$)	3.21	49	ns*	0.15

ns* = non-significant; values in columns with similar letters do not differ significantly ($p > 0.05$)

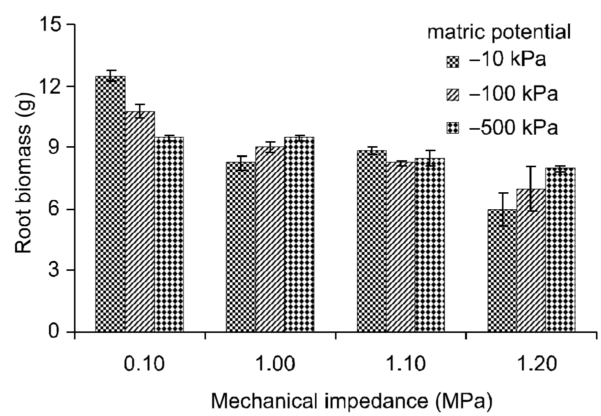

Fig. 4. Effect of mechanical impedance and matric potential on root biomass of cotton seedlings (values are mean ±SE; single SED value computed from ANOVA = 2.74).

water stress (decreasing matric potential) and to mechanical impedance. Roots that were water stressed did not change their diameter but had a shorter axis and longer total lateral length. In contrast, the mechanically impeded roots had both a shorter axis and a smaller total root length but increased root diameter.

Since decreasing matric potential resulted in shorter axis with same lateral spacing but with greater total lateral length, the smaller number of laterals must have been considerably longer. Increasing mechanical impedance also resulted in a shorter axis, with the same lateral spacing, giving ultimately less number of laterals, but also decreased total lateral lengths. Visual observations of roots supported the conclusion that average lateral lengths were greater in water stressed plants. This suggested the plastic behaviour of the root system to cope with stressed conditions.

A contrasting behaviour of the cotton lateral roots in response to water stress was observed. Roots that were water stressed did not change their diameter but had a shorter axis and longer laterals. In contrast, mechanically impeded roots had both a shorter axis and a smaller total root length, but increased root diameter. A plastic nature of the root system to cope with stressed environment has been thus indicated.

Changes of water content in the soil immediately surrounding a root causes changes in the root cell osmotic and turgor pressures. A decline in soil water content, and associated decrease in soil matric potential, results in a reduction in water uptake, a decrease in root cell osmotic potential, a reduction in cell wall extension and decrease in the ability of roots to overcome the mechanical constraints of the soil (Taylor, 1983). The osmotic adjustment will allow growth to continue as if sufficient water were available, but the other changes tended to reduce growth rates. The above explanation emphasizes the hydraulic response of the roots to water shortage. However, chemical changes occur too. Increasing evidence suggests that abscisic acid has a particularly important role in regulating many of these responses (Hartung and Davies, 1991). Root growth at low water potentials appears to be dependent upon abscisic acid accumulation

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