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Restriction to Root and Shoot Growth Limits Their Growth Rates and Changes the Morphology of Cotton Seedlings During Emergence

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Abstract. Pre-germinated cotton seedlings were grown under laboratory conditions to determine the affect of root and/or shoot impedance on their growth. The treatments studied were: (i) both shoot and root unimpeded, (ii) shoot impeded and root unimpeded, (iii) root impeded and shoot unimpeded, and (iv) both root and shoot impeded. Impeding the root alone, or root and shoot together, significantly ($P < 0.05$) reduced axial root length, total root length, and increased root diameter. The axial root length was reduced by 55%. The number of root laterals was not affected by impedance but lateral spacing was reduced significantly. Root diameter was increased in treatments where only roots had been impeded. Shoot diameter was significantly ($P < 0.05$) greater in the root and shoot impeded treatments. Shoot length was reduced by 15% when only the shoots were impeded, while 38% reduction was noted when both root and shoot were impeded. Shoot impedance did not cause any significant effect on the root growth rate when roots were unimpeded. In terms of shoot length, root impedance had no effect on shoot length, although the combined effect of root and shoot impedance was greater than shoot impedance alone.

Keywords: mechanical impedance, root/shoot length, root/shoot diameter, restricted root elongation, root development

Introduction

The development of a root system capable of anchoring the shoot and the ability to uptake sufficient water and nutrients from the soil is essential for the survival of most terrestrial plants. The root zone soil constraints prevent the development of root system and eventually the crop yield (Rengasamy and Vadakattu, 2002). The growth of roots and shoots are often slower when plants are grown in soil of large bulk density (Voohees, 1992). In such soils, various physical (availability of oxygen and water, and mechanical impedance) and biotic factors may limit root and shoot growth. However, the mechanical impedance (resistance pressure encountered by growing roots) of the soil is often the single most important factor that can limit root and shoot elongation. It increases with the increase in soil dry bulk density (e.g., due to compaction) and also increases as the soil matric potential decreases. Unless roots are able to exploit the soil structural features, their growth rate is reduced as mechanical impedance is increased (Townend *et al.,* 1996). Clark *et al.* (2001) showed that pea roots are capable of sensing a partial increase in mechanical impedance that can increase the turgor of seedlings but there was still some reduction in root growth. In natural conditions, plant roots invariably encounter some degree of mechanical resistance to their penetration through the soil.

It used to be generally believed that roots are unable to penetrate into rigid pores that were narrower than their normal diameter. More recent studies have revealed that roots can grow into rigid pores that are smaller than their diameter (Bengough *et al*., 1997). In soils, roots can often exploit cracks, voids and larger 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 can increase and the production of lateral roots may also be increased, with laterals emerging closer to the apex (Atwell, 1988; Goss, 1977). Restricting the soil volume explored by roots reduces shoot growth (Young, *et al.,* 1997; Passioura, 1991; Carmi and Heuer, 1981). This is often accompanied by an increased root : shoot mass ratio (Cook *et al.,* 1996; Blaikie and Mason, 1993). Slower shoot growth of wheat seedlings was reported in compacted soils while plants were still in the seed reserve-dependent growth stage (Nabi and Mullins, 2001; Masle *et al.,* 1990). Dawkins *et al.* (1983) observed smaller shoot : root ratio in peas when roots were growing in compacted than in loosened soil. Masle and Passioura (1987) grew wheat seedlings for 22 d in small cores of compacted soil and found that shoot growth and development were severely restricted. Andrade *et al.* (1993) also found that strong soil affected shoot growth early in sunflower. Montagu *et al.* (2001) found that soil compaction decreased root growth in broccoli.

Roots experience mechanical impedance as they elongate in the soil and the decrease in their growth rate is due to the force required to displace soil particles. Strong soil can be a

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serious problem in agriculture, as it can restrict access of root system to water and nutrients and can thus decrease crop yields. In the field, topsoil may be strong due to lack of tillage, while tillage operations can compact soil just beneath the plough layer and can lead to the formation of hardpans. Some subsoils are naturally strong due to the presence of gravely horizons (Babalola and Lal, 1997), or clay pans (Clark *et al.,* 1998). Also, under field conditions, emerging shoots may encounter compaction such as that due to raindrop impact and soil crusting. The present study was, therefore, conducted to determine the effect of soil compaction on the growth of shoots as well as roots in cotton during emergence.

Materials and Methods

Pre-germinated seedlings of cotton, MNH-147, were grown for 72 h in 300 mm long cylinders having 75 mm internal dia in a growth cabinet maintained at 32 °C. Long cylinders (150 mm) were packed with soil, either at a bulk density of 0.88 Mg m^{-3} (mega gram per cubic meter) to represent unimpeded soil, or 1.25 Mg m^{-3} to represent an impeding soil. Two cylinders, either of the same, and/or different bulk densities (as required by the treatment), were joined one above the other to make a 300 mm length. The four treatments, three replicates each, were: (i) both shoots and roots unimpeded (RuSu), (ii) roots unimpeded and shoots impeded (RuSi), (iii) roots impeded and shoots unimpeded (RiSu), and (iv) both roots and shoots impeded (RiSi).

A sandy clay-loam (Carpow Series) topsoil (0-10 cm) was used as the growth medium. The air-dried soil was sieved and aggregates between 1 and 3.35 mm diameter were retained. The prepared soil contained 0.21% organic matter and its particle size distribution was 20.6% clay, 18.0% silt (2-60 mm) and 61.4% sand. Water retention curve of the soil was determined following standard procedures using a tension table and pressure plate apparatus (Townend *et al.*, 2001). Based on this curve, the soil was wetted with nutrient solution to a matric potential of -10 kPa (kilo Pascal) before packing. The cylinders were packed at bulk densities of 0.88 and/or 1.25 Mg m^{-3}. They were packed in layers, in 20 mm increments, to the required bulk density. After packing, two pre-germinated seedlings of cotton (5 mm long radicle) were transplanted at the juncture of the two cylinders, before joining them. Bead thermistors were placed inside the cylinders, and attached to a data logger (Skye Data Hog) to log temperature at 5 min intervals and record hourly averages. The cylinders were kept in a growth cabinet maintained at 32 °C. After 72 h, the cylinders along with intact seedlings were removed from the cabinet and penetration resistance (PR) in each cylinder was recorded with a portable cone pentetrometer (300 mm long recessed shaft, steel cone of 3 mm dia and 15° semi-angle). Two trials were run for each treatment in duplicate cylinders and mean values were computed. After the penetration resistance measurements, the contents of each cylinder along with seedlings were removed carefully and the soil was gently separated from the seedlings. The soil was then placed in jars to determine its gravimetric water content and matric potential by the filter paper method (Deka *et al*., 1996). The roots were separated from the shoots. The shoot length, diameter, fresh weight, axial root length, number of root laterals, root dia, and fresh weight of roots were recorded.

The roots were stained in a 0.01% methyl violet solution and used for measuring the total root length using a DIAS image analyser with the root measurement system software, Version 1.6 (Skye Ltd., Llandrinod, Wells, UK). High quality photocopies of the stained roots were used for measurement. After root length measurements, the roots were dried at 80 °C to determine their dry weight.

The data obtained were statistically analysed for the four treatments and three replications with completely randomised design in statistical software Minitab for Windows version 10.5 (Minitab Corporation Inc., USA). Treatment means were compared, using the least significant difference test. Where this was not met, standard error of means and coefficient of variation were computed to compare the treatment means.

Results and Discussion

Growth conditions. Average soil temperature, near the seedlings, during the 72 h growth period was ~31.8±1 °C. Temperature remained fairly constant during the growth period. The soil moisture content at the start of the experiment was 26.82 g/100 g that corresponded to matric potential of -12.87 kPa. At harvest time, the moisture content was 22.1 g/100 g that corresponded to - 45 kPa. Since the moisture content changed only slightly and the matric potential remained in a range in which water was readily available, it can be assumed that it had negligible effect on growth. Penetration resistance in the cylinders, with intact seedlings, was measured before harvesting (i.e., after 72 h). Resistance in the unimpeded sections of cylinders was ~0.02±0.01 MPa (mega Pascal), while in the impeded sections it was ~1±0.2 MPa.

Effect on root growth. The axial root length was significantly ($P < 0.05$) reduced when root systems were mechanically impeded (RiSu and RiSi; Table 1a). A reduction of about 55% in the axial root length of RiSu, relative to the control (RuSu) was observed, which corresponded to a reduction in growth rate from 2.11 to 0.96 mm/h. Impeding the shoot alone (RuSi) did not affect root length. However, impeding the root with or without shoot significantly ($P < 0.05$) reduced the total root length. The total root length was reduced by 37% in seedlings whose root system was impeded (RiSu) and (RiSi), as compared to the control (RuSu). Impeding the shoot but not the root (RuSi) also resulted in a significant reduction (17%) in the total root length, as compared to the control (RuSu). Late-ral spacing was significantly reduced, but the number of late-ral roots was not reduced by mechanical impedance compared to the control.

Effect on shoot growth. Impeding the shoot (RuSi and RiSi) significantly ($P < 0.05$) reduced the shoot length (Table 1b). Seedlings in unimpeded treatment (RuSu) had 1.6 times longer shoots than in the impeded (RiSi) treatment. When only the shoot was impeded (RuSi), a reduction of 15% was observed in its length. However, when both root and shoot were impeded, it resulted in a 38% reduction. Fresh shoot mass was significantly ($P < 0.05$) decreased, as compared to the control, only in those treatments in which the root system was impeded (RiSi and RiSu; Table 1b). A reduction of 18% was observed when the root and shoot systems were impeded (RiSi), but only 13% when only the root system was impeded (RiSu). Shoot mass was less affected when only the shoot system was impeded (RuSi). Shoot diameter was significantly ($P < 0.05$) greater in the root and shoot impeded (RiSi) seedlings than where only the root system had been impeded (RiSu). However, when the root system alone was impeded, shoot

Table 1. Root Growth **(a)** and shoot growth **(b)** of cotton seedings, as affected by root-shoot interactions, with and without mechanical impedance

a. Root growth

Treatments	Axial root length (mm)	Root growth rate (mm/h)	Total root length (mm)	Length of root laterals (mm)	Spacing of laterals (mm)	Root diameter	
						Dia (mm)	Performance relative to control
RuSu (control)	$152^{a} \pm 7$ (11)	2.11 ± 0.01 (11)	$370^{a} \pm 18$ (11)	$245^{a} \pm 16$ (16)	2.53^{a}	0.94^{c}	control
RuSi	$146^{a} \pm 7$ (12)	2.03 ± 0.01 (12)	$330^{b} \pm 18$ (13)	$183^{b} \pm 21$ (28)	2.67^{a}	0.97^{c}	103
RiSu	$69^{b} \pm 12$ (41)	0.96 ± 0.16 (41)	$237^{c} \pm 26$ (27)	$168^{b} \pm 16$ (24)	1.57^{b}	1.11^{b}	118
RiSi	$69^{b} \pm 5$ (18)	0.95 ± 0.07 (18)	$229^{c} \pm 10$ (10)	$161^{b} \pm 14$ (21)	2.17^{a}	1.23^{a}	131
LSD ($P < 0.05$)	24	-	**	**	**	0.12	-
LSD ($P < 0.01$)	32	0.16	-	-			

b. Shoot growth

Treatments	Shoot length (mm)	Shoot growth rate (mm/h)	Fresh shoot mass (mg)	Dry shoot mass (mg)	Shoot diameter	
					Dia (mm)	Performance relative to control
RuSu (control)	$50^{a} \pm 1.2$ (5)	$0.69^{a} \pm 0.02$ (7)	391 ± 24^{a} (15)	21 ± 1 (6)	3.08 ± 0.04^{b} (3.4)	control
RuSi	$42^{b} \pm 1.76$ (10)	$0.59^{b} \pm 0.04$ (15)	358 ± 28^{a} (20)	19 ± 2 (28)	3.24 ± 0.12^{ab} (8.6)	106.2
RiSu	$50^{a} \pm 1.76$ (8)	$0.68^{a} \pm 0.04$ (16)	340 ± 14^{b} (10)	21 ± 2 (23)	3.02 ± 0.06^{b} (4.6)	98
RiSi	$31^{c} \pm 2.26$ (17)	$0.44^{c} \pm 0.03$ (18)	321 ± 15^{b} (12)	20 ± 1 (8)	3.54 ± 0.16^{a} (0.11)	114.9
LSD ($P < 0.05$)	7.29	0.10	*	NS	3.08 ± 0.04^{b} (3.4)	control
LSD ($P < 0.01$)	9.90	0.14				

RuSu = both root and shoot unimpeded; RuSi = root unimpeded and shoot impeded; RiSu = root impeded and shoot unimpeded; RiSi = both root and shoot impeded; LSD = least significant difference, values are mean ±1 standard error, se (coefficient of variation, CV%), n = b; values sharing the same letter in each column do not differ significantly at $P < 0.05$; NS = non-significant diameter was not reduced substantially. Root diameter was significantly ($P < 0.05$) increased in root impeded treatments, as compared to the control, while shoot diameter was significantly ($P < 0.05$) increased in the shoot impeded treatments (RuSi and RiSi), as compared to the control seedlings.

Impeding the root alone or root and shoot together, significantly reduced the axial root length and total root length, and increased the root diameter. Impeding the shoot alone reduced total shoot length, but did not significantly affect axial root length, the number of root laterals, or the shoot diameter. The only major effect was reduction in the length of laterals, which was quite substantial.

Since factors like temperature, nutrients and water availability remained unchanged and were not limiting during the experiment, it is clear that these responses were directly related to the increased mechanical impedance experienced by the roots and shoots, in agreement with earlier studies which reported that the growth rates were reduced when plants were grown in compacted soils (Young *et al.,* 1997; Bennie, 1996; Cook *et al.,* 1996; Kirkegaard *et al.,* 1992). However, when plants were grown in compact soil it was difficult to rule out completely, the transient shortage in water or nutrients, due to reduced root extension. Such shortages could cause a down regulation of shoot growth resulting in the shoot maintaining critical nutrients and water status. Since in this experiment the soil matric potential ranged between ~ -13 to - 45 kPa, and the soil used was wetted with nutrients solution and further the growth was monitored only for 72 h, for which seed reserves can provide essentially required nutrients for growth, it can be confidently ruled out that decreased supply of water or nutrients to the root system had caused reduced growth and their elongation. Further, the study indicated that the root growth reduction due to impedance was independent of shoot growth. These observations do not agree with those of Rwehumbiza (1994), who found that in 8-d old sorghum plants, shoot impedance increased root elongation rate and number of root laterals. Masle and Passioura (1987) observed in 22-d old wheat plants that the extension rate in emerged shoots was significantly reduced when only the root systems were impeded. However, these studies do not mention about the effect of root and shoot impedance on pre-emerged seedlings. In this study, plants were harvested after a 72 h of growth period. Since it is likely that plant growth will differ at different growth stages, depending upon such factors as the availability of water, nutrients and soil aeration, the growth response of any plant part to mechanical impedance may not be the same during the whole of its life-time. The plant response in later stages, furthermore, may be quantitatively different when factors like a greater demand for water and nutrients arises for growth and maintenance of the seedling. Additionally, in the seedlings in which growth is totally or mainly dependent on the release of seed reserves, the mechanism which operates during the later growth stages to maintain a given allometry may be inactive.

Root lengths were significantly reduced when roots alone (RiSu), or roots and shoots (RiSi) were both impeded. Similarly, shoot lengths were both reduced when shoot (RuSi), or root and shoot (RiSi), were impeded. These results are in agreement with those of Russell and Goss (1974). Sharp (1990) suggested an increased demand for photosynthate to support a preferential growth of roots and, therefore, a continued exploration of the soil for water with increased mechanical impedance to roots. Although these plants were pre-emergent, the roots and shoots are still competing for a limited supply of reserves. Comparing the unimpeded root and the impeded shoot (RuSi), and the impeded root and shoot (RiSi) treatment, it is possible that in the RuSi treatment the shoots were experiencing a low impedance zone before growing into the impeding soil. This means that the extra reduction in shoot growth, which is apparently due to root impedance, could be an experimental artefact.

Mechanical impedance is known to reduce root elongation rates, thus reducing the volume of soil that the root system can exploit (Veen, 1982; Russel and Goss, 1974). Reduced shoot growth of impeded plants has, therefore, often been associated with a restricted root volume and an inadequacy in supplying water and nutrients to the plant (Rahman *et al.,* 1999; Oussible *et al.,* 1992; Atwell, 1990; Boone and Veen, 1982). The studies on the effect of restricted root volume on shoots under the conditions of no water or nutrients stress have shown that reductions in shoot growth still occur (Krizeck *et al.,* 1985; Peterson *et al.,* 1984), and the reduction of certain regulatory substances has been suggested to be responsible for restricting shoot growth.

Other growth characteristics, like the number of root laterals, and fresh and dry root biomass were not significantly affected either in the root or in the root and shoot impeded treatments. Similar observations have been reported by Tsegaye and Mullins (1994). This suggested that these parameters are insensitive to mechanical impedance. However, root diameter was significantly increased in response to mechanical impedance. The increase in root diameter was in line with the results of Young *et al.* (1997) and Wilson *et al.* (1977). When apical extension of the root is restricted, there are more cells per unit root length and individual cells become shorter, but may expand laterally resulting in increased diameter. There was a significant increase in the shoot diameter in response to mechanical impedance. Shoot diameter was increased when shoot alone (RuSi) or shoot and root (RiSi) were impeded. When only the root system was impeded, shoot diameter was not affected significantly. The explanations given above for increase in root diameter hold true for shoot diameter as well. The length of root laterals decreased when the shoot was impeded. However, there was no evidence of a "root signalling" response resulting in reduced shoot growth in response to high soil strength.

Conclusion

Roots that were impeded had the axial growth rate reduced by 55%, irrespective of whether or not shoots were impeded. With unimpeded roots, shoot impedance did not cause any significant effect on the root growth rate. In terms of shoot length, the root impedance alone had no effect, although the combined effect of root and shoot impedance on the shoot length was greater than the shoot impedance alone. Similarly, in terms of the length of the root axis, shoot impedance had no effect, although there was a considerable reduction in the length of the laterals.

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