Root-Shoot Growth Interactions of Sorghum (*Sorghum Bicolor L. Moench*) in Response to Mechanical Impedance

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Abstract

Soil mechanical impedance has a widespread influence on plant organ expansion, penetration, and growth. Studies on root-shoot interactions in relation to mechanical impedance have only investigated the effect on shoots of mechanical impedance imposed on roots. The aim of the reported study was therefore to fill the identified gap in knowledge, including an investigation into all root-shoot interations in response to mechanical impedance. Individual pregerminated sorghum (Sorghum bicolor L. Moench) seeds cultivar ICSV-112 were grown for 8 days in a growth room in seven replicate cylinders per treatment. Treatments were: (a) impeded root and impeded shoot (II), (b) impeded root and unimpeded shoot (IU), (c) unimpeded root and impeded shoot (UI), and (d) the control, in which both the root and shoot systems were unimpeded (UU). The impeding growth medium was a mixture of sand and vermiculite packed to give a penetration resistance (PR) of 1.18 MPa below the seed and 0.32 MPa above the seed. Control cylinders were completely packed with expanded vermiculite to a bulk density of 0.2 Mg m^{-3} *giving a PR of 0.025 MPa. Matric suction was 5.kPa in both media. Results were that: (i) Impedance to the shoot significantly (*$P < 0.05$*) delayed emergence, more so when the root was also impeded. (ii) Shoots emerging through a mechanically impeding layer, had significantly greater extension rates after emergence than unimpeded ones. (iii) Mesocotyls became significantly thicker only when the root systems were impeded. (iv) Impeding the shoot system, significantly increased root extension rate. (v) The length of the first internode, the number of leaves and the spacing of lateral roots were not changed by any of the treatments. Root-shoot signalling is suggested as one of the factors responsible for these interactions. Generally, our findings indicate that mechanical impedance which may be caused by surface crusting and hardsetting soils and shallow tilth achieved with a hand hoe results in poor crop establishment and probably total crop failure.*

Key words: Root-shoot interactions, mechanical impedance, crop establishment, sorghum

Introduction

The literature on how mechanical impedance affects plant growth falls into three categories namely, work in which (a) both root and shoot systems are impeded simultaneously (e.g. Collis-George and Yoganathan, 1985), (b) only the root system is impeded (e.g. Eavis, 1967; 1972; Greacen *et al.*, 1968; Goss, 1977, Masle and Passioura, 1987), and (c) only the shoot system is impeded (e.g. Arndt, 1965; Sinclair, 1985). Root-shoot communication in response to MI has been suggested and studied (Carmi and Euer, 1981; Dawkins *et al.*, 1983; Masle and Passioura, 1987; Sharp, 1990). The restriction of root growth is usually accompanied by a considerable reduction in shoot growth and an increased root-shoot mass ratio. Possible explanations include, increased demand for photosynthate by roots growing in high strength media and that reduced root proliferation limits the supply of water and nutrients to the plant (Taylor, 1971). Some studies have however demonstrated that, impeding the root system

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would still induce increased root-shoot ratio even when water and energy reserves are not limiting. In wheat for example, Masle (1990) observed a significant increase in root-shoot mass ratio with an increase in MI in seedlings still dependent on the endosperm for their energy requirements. In Masle's study, reduced plant growth and stomatal conductance were observed before there were any detectable shortage of water, carbon or nutrients. A form of hormonal message from the roots to the shoot whenever the former sense mechanical impedance in their path has been suggested. Abscissic acid (ABA) (Moore and Smith, 1984, 1985; Sharp, 1990) and ethylene (Dawkins *et al.*, 1983; Moss *et al.*, 1988) have been identified as growth regulators that may be responsible.

Studies of root-shoot interactions in relation to MI have been one sided. Only the effect on shoots of MI imposed on roots has received attention. The literature reviewed contains no work on how the root system responds to MI imposed on the shoot. There are field situations where only the shoot is impeded. Formation of a surface crust for example, can subject shoots of germinating seeds to MI leaving roots in relatively unimpeding soil. Rapid drying of the surface layer in hardsetting soils can subject emerging shoots to greater MI compared to the roots (Weaich *et al.*, 1991). Research on shoot impedance has been pre-occupied by one theme, the ability of shoots to emerge from high strength layers of soil. How the root system responds to MI imposed on shoots is a subject that has never been studied. The aim of the current study was therefore to fill the gap in knowledge identified above including an investigation into all root-shoot interactions in response to MI.

Materials and methods

Individual pregerminated sorghum seeds from cultivar ICSV-112 were grown for 8 days in a growth room in seven replicate containers in each of four treatments. Treatments were: (a) impeded root and impeded shoot (II), (b) impeded root and unimpeded shoot (IU), (c) unimpeded root and impeded shoot (UI), and (d) the control, in which both the root and shoot systems were unimpeded (UU).

The growth apparatus was based on the dead load technique (Materechera *et al.*,1991). Since the load is usually placed on top of the growth medium after planting, the technique suffers from a problem of trapping emerging seedling shoots under the weights. Thus, several modifications had to be made to the technique to enable the achievement of the objectives of the current study. Bell (1993) suggested two modifications (a) the use of pregerminated seeds in which the shoot had already emerged and (b) to place a drinking straw above the seed so as to guide the shoot to the surface. Bell's modifications, can not enable a simultaneous imposition of MI to the root and shoot systems. Modifications were therefore made to the dead load technique to enable the investigation of all possible root-shoot interactions as shown in Figures 1 to 4. The basic units were open-ended perspex cylinders of internal diameter 50 mm and height of 300 mm with a removable base. They were each fitted with a removable black plastic sleeve to prevent light entering the side of the cylinders and painted black near their tops to prevent light "piping" down the cylinder wall.

The growth media were, either a 40:1 mixture by weight of dried silica sand 250-500 μm with vermiculite or expanded vermiculite. The sand was supplied by Hepworth Minerals and Chemicals Surrey. The sand-vermiculite mixture was wetted to 20 g/100 g, and vermiculite to 200 g/100 g with a dilute nutrient solution (Hackett, 1968). The matric suction corresponding to the above moisture contents was 5 kPa in both media. Matric suction was estimated using the filter paper technique (Fawcett and Collis-George, 1967).

The constructions made to subject both the root and shoot systems to MI were as shown in Figure 1. Cylinders and funnels were packed separately and later assembled to give a complete growth apparatus. The cylinders were packed in 30 mm layers with moist sand-vermiculite mixture to a dry bulk density of 1.45 Mg/m^3 leaving a 40 mm gap at the top. Plastic funnels cut to just fit in the cylinders were packed with the mixture to a dry bulk density of 1.31 Mg/m3 to give a 30 mm layer of growth medium. The smaller of the two dead loads was fitted at the end of the funnel stem.

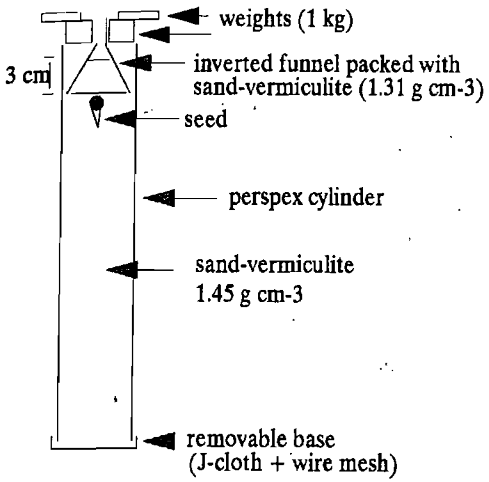

Figure 1: Growth apparatus in which both roots and shoots were impeded (treatment II)

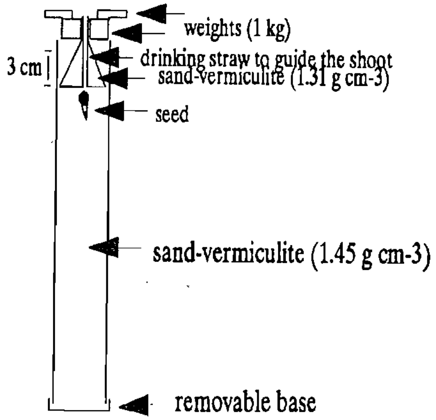

Figure 2: Growth apparatus in which roots were impeded but shoots unimpeded (treatment IU)

Acting as a base, the smaller load enabled the funnels to stay upright unsupported during packing. Funnels were packed by placing them upright at the bottom of an empty open-ended cylinder. The growth medium was introduced from the top of the cylinder, and it was collected in the funnel at the bottom. A rubber bung of diameter equal to the internal diameter of the cylinder and with a recessed metal shaft was used to push (pack) the media to required bulk densities. Pregerminated seeds of sorghum cultivar ICSV-112 were planted one per cylinder. At planting, the radicle had just ruptured the seed coat. The seed was placed in a shallow depression at the centre of the cylinder. To assemble the growth apparatus, both the cylinder and funnel were tilted almost horizontally and the packed funnel carefully inverted over the seed. Thus, the root had to grow in a 1.45, and the shoot in a 1.31 Mg/m^3 bulk density medium, respectively. The funnel cone and stem guided the emerging shoot to the surface. In addition, the funnel stem supported a 1 kg dead load.

In order to subject only the root system to MI, the set up was as in Figure 1 except that the shoot had to grow through a drinking straw passing through the centre of the funnel (Figure 2). The seedling was attached with cow gum at the bottom of the straw and surrounded with moist vermiculite to prevent it from pushing the straw upwards. To subject only the shoot system to MI, the set up was also as in Figure 1, except that cylinders were packed with moist expanded vermiculite (Figure 3). Control plants were grown in cylinders completely packed with moist vermiculite and no dead load was applied (Figure 4). The planting depth was 30 mm in all four constructions. So as to prevent light from interfering with shoot growth, a black polythene circle was placed and maintained on top of each cylinder until emergence. This was crucial especially in the construction

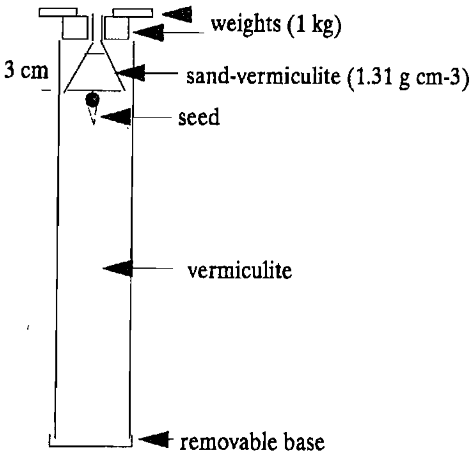

Figure 3: Growth appparatus in which roots were unimpeded but shoots impeded (treatment UI)

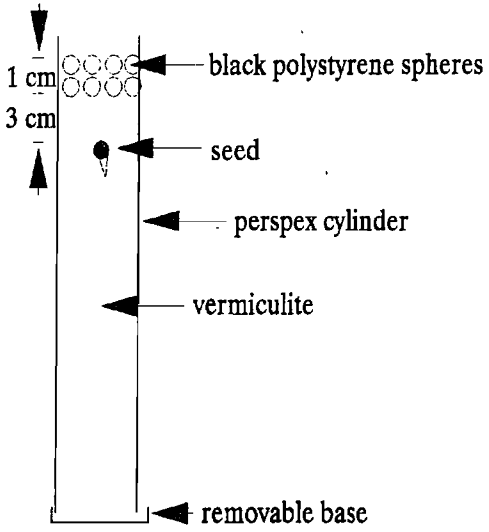

Figure 4: Growth apparatus in which both roots and shoots were unimpeded (treatment UU)

shown in Figure 2 where the shoot had to grow uncovered with any growth medium.

Cylinders were packed at a bulk density of 1.45 Mg m^{-3} giving a mean penetration resistance (PR) of 1.18 ±0.064 MPa below the seed. Funnels were packed at a bulk density of 1.31 Mgm^{-3} giving a PR of 0.32 ± 0.033 above the seed. Control cylinders were completely packed with expanded vermiculite to a bulk density of 0.2 Mg m^{-3} giving a PR of 0.025 MPa.

After planting, growth columns were placed in a growth room and 12 h photo period imposed. Température in the growth media (measured in vermiculite only) at seed depth was measured daily before lights came on and went off using a digital thermocouple sensor (type K). Ambient growth room temperature over the period was monitored by a thermohygrograph. At harvest, moisture contents in sand-vermiculite mixture and in vermiculite were estimated gravimetrically. Separate samples were also taken from the vermiculite with corresponding matric suctions were measured using the filter paper technique.

The cylinders were inspected regularly to record emerged seedlings and the time taken to emerge. In treatment IU where the shoot had to grow through a drinking straw and therefore in an empty space, shoot were considered to have emerged when they attained a length of 30 mm (*i.e.* including the mesocotyl), the planting depth. A calibrated "deep stick" cut out of white polystyrene packaging material was used to detect for emerged seedlings in the funnel stem. Emerged seedlings could also be seen by looking into the funnel stem under a bank of tube lights. Harvesting was 8 days after planting. Plants were harvested by removing the bottom from the cylinders and carefully removing the growth medium to free the root system. True shoot length was measured from the first internode to the tip of longest leaf. The length of the first internode was also measured. Each shoot was weighed to obtain its fresh mass. Shoot extension rate (mm h-1) was calculated by dividing the mean final shoot length to the number of hours in 8 d less the time to emergence. Root length was measured from the seed to the root tip. Root extension rate (mmh^{-1}) was calculated by dividing the final main axis length to the number of hours in 8 days. The diameter of the main root was measured just behind the root tip and that of the mesocotyl in the middle of the internode using a travelling microscope. Roots were washed in water then dried with soft paper towels before weighing and counting lateral roots.

Results

Average temperature in the growth media (vermiculite only) at seed depth was 26.6o C over the 8 day growth period. Ambient growth room temperature over the period, was 26.5o C and 24.2° C on the average during the day and night time respectively. At harvest, moisture contents in sand-vermiculite mixture and in vermiculite were 18.9 g/100 g and 190 g/100 g respectively. Matric suctions corresponding to these moisture contents measured using the filter paper technique, were 8.5 and 20 kPa.

The time to seedling emergence as affected by different treatments is given in Table 1. Emergence was significantly ($P < 0.05$) delayed in treatments II and UI where shoots were impeded compared to the control. Seedlings emerged 45 h after planting in the control. The time to emergence was 1.33 times greater when only the shoot was impeded. By impeding both the root and shoot systems, the time to emer-

Table 1: Time (h) to seedling emergence for sorghum cv ICSV-112 as affected by root-shoot interactions with and without mechanical impedance. Values are: Mean ± se (CV %), n=7.

Treatment	Time to seedling emergence (h)	Time relative to the control (UU) (%)
Root and shoot impeded (II)	73.14 ± 5.4 (19)c	163
Root impeded, shoot unimpeded (IU)	42.71 ± 2.4 (15)a	95
Root unimpeded, shoot impeded (UI)	59.86 ± 4.8 (21)b	133
Root unimpeded, shoot unimpeded (UU)	45.0 ± 0.5 (3)a	_
LSD (P < 0.05)	**11.08**	
LSD (P < 0.01)	**15.01**	

Values sharing the same letter are not significantly different at P < 0.05.

gence was increased to 1.63 times that of the control. Thus, impeding both the root and shoot further delayed emergence. The one day delay in emergence in II compared to UI was significant at P < 0.05.

Root growth parameters as affected by the treatments are shown in Figure 5. Root length was significantly (P < 0.05) reduced to 44-48 % of the control in seedlings whose root systems were subjected to MI (IU and II) Respective root extension rates were 0.46 and 0.50 mm h-1, almost 50 % of the rate in the control. However, impeding the shoot but not the root (UI), resulted in a significant (P < 0.05) 22 % increase in root length compared to the control. The root extension rate was 1.27 mmh^{-1} in UI, which was more than double the rate in IU and II.

Root diameter was significantly (P < 0.05) increased compared to control seedlings only in treatments where the root system was impeded (IU and II). The increase was 1.67 times when only the root system was impeded (IU) and 1.85 times when both the root and shoot systems were impeded (II). Seedlings had significantly (P < 0.05) thicker roots especially when both the root and shoot were impeded compared to when only the root system was impeded.

The number of lateral roots produced was significantly (P < 0.05) reduced compared to control seedlings only in treatments where the root system was impeded (IU and II). The number of lateral roots was only 57 and 41 % of the control respectively when only the root system was impeded and when both the root and shoot systems were impeded. When only the shoot system was impeded (UI), there was an insignificant 22 % increase in the number of laterals. The mean distance between any two consecutive lateral roots did not vary significantly between treatments. Overall, lateral spacing varied within a narrow range of 2.5 to 3.0 mm.

Impeding both the root and shoot systems significantly (P < 0.05) increased root mass 1.41 times compared to control. Root mass was not significantly affected by impeding either the root or shoot system.

The effects of the treatments on shoot growth parameters are shown in Figure 6. Seedlings in treatment II had significantly (P <

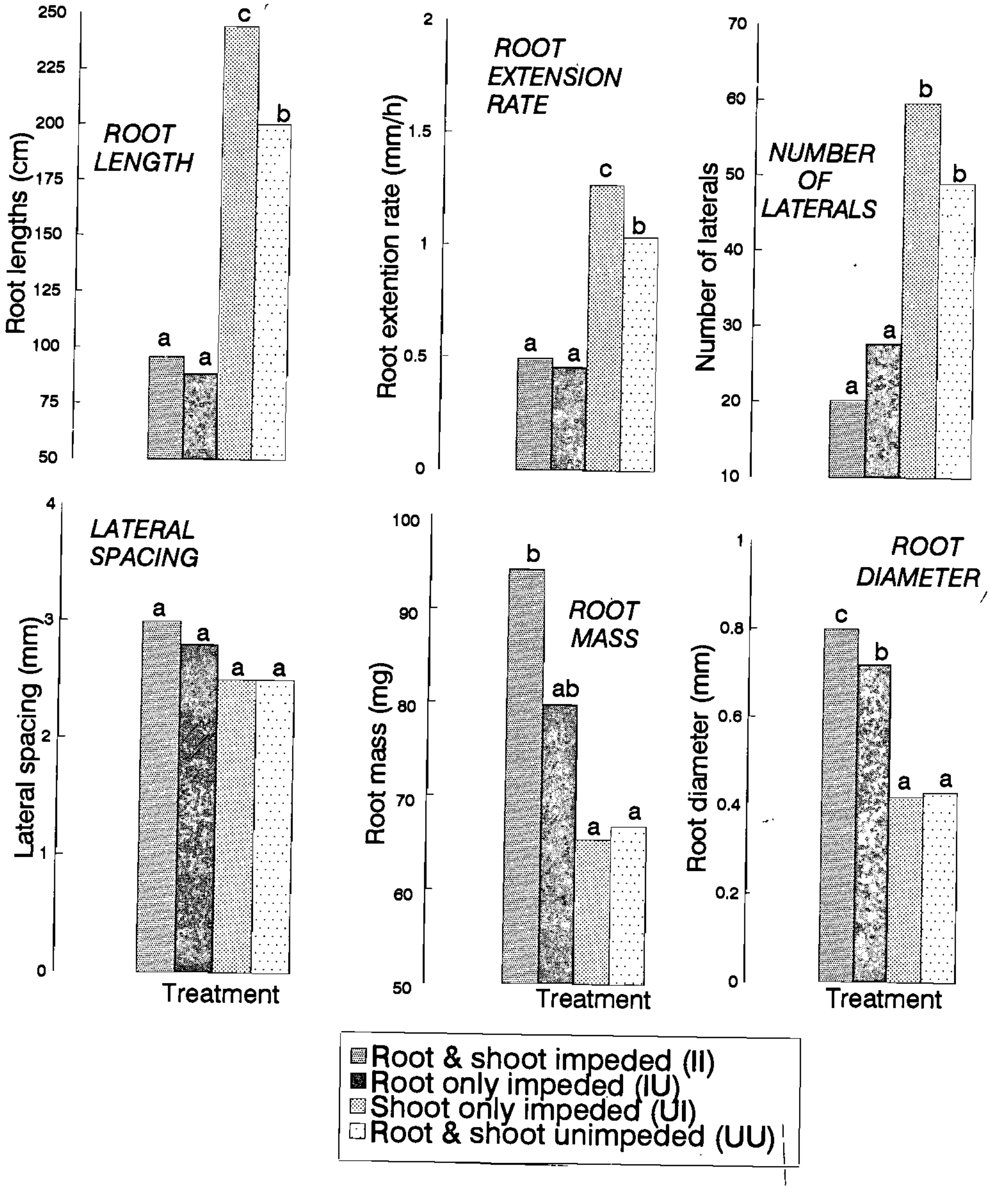

Figure 5: Root growth parameter as affected by root-shoot interactions with and without mechanical impendence. Values that differ significantly ($p < 0.05$) are indicated by different letters

0.05) longer shoots (x1.22) compared to the control in which the mean shoot length was 124.4 mm. Impeding either the root (IU) or the shoot (UI) had no significant effect on shoot length. The extension rate of the shoot after it had emerged was also greatest when both the root and shoot were impeded (II) but was also significantly greater than the control when only the shoot had been impeded before emergence.

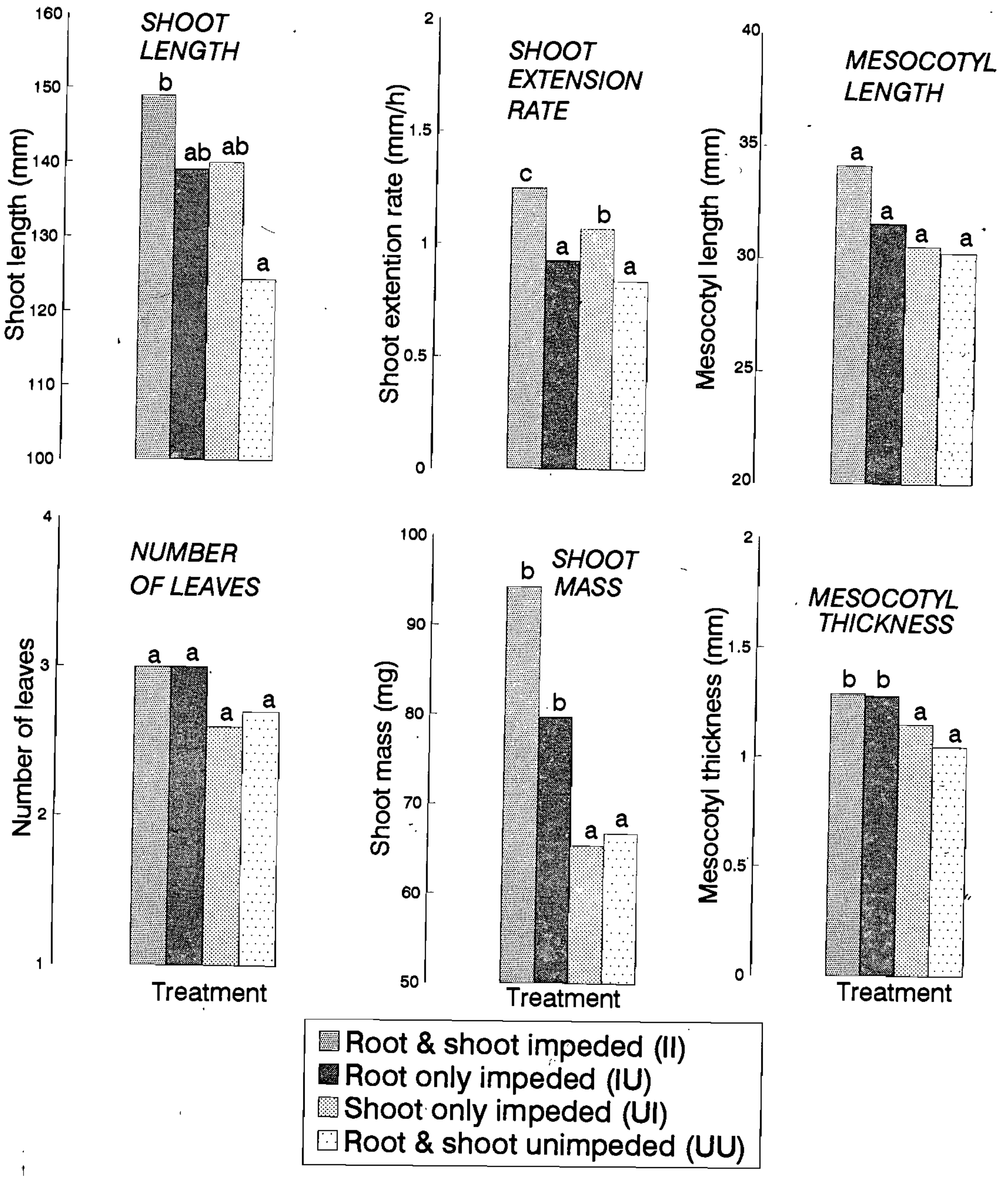

Figure 6: Shoot growth parameters as affected by root-shoot interactions with and without mechanical impendence. Values that differ significantly ($p < 0.05$) are indicated by different letters

At 1.25 mmh^{-1}, shoot extension rate in treatment II was 1.56 times that of control. The length of the first internode (mesocotyl) was not affected by any of the treatments . Overall, mesocotyl lengths varied within a narrow range of 30 to 34 mm. On the other hand, mesocotyls were significantly ($P < 0.05$) thicker than in the control seedlings only in treatments where the root system was impeded (IU and II). The increase in mesocotyl thickness was 1.21 and 1.22 times the control respectively when only the root system and when both the root and shoot systems were impeded. The number of leaves produced by seedlings was not affected by any of the treatments. At harvest, seedlings in all treatments had three leaves on the average.

Fresh shoot mass was increased significantly ($P < 0.05$) compared to the control but only in seedlings in which the root system was impeded (IU and II). The increase was 1.41 times when only the root system was impeded and 1.46 times when both the root and shoot systems were impeded. Shoot mass was unaffected when only the shoot system was impeded (UI).

Discussion

Emergence was significantly delayed in seedlings whose shoots were impeded. Similar findings have been reported for seedlings emerging from surface crusts (Glass, 1980), and through hardsetting soils (Weaich *et al.*, 1991). Emergence was delayed even more when the root system was also impeded. In hardsetting soils and especially under fast drying conditions common in the SAT, seedling emergence is a race against time (Weaich, 1993). Thus, the delay in emergence caused by impeding both the root and shoot systems can drastically reduce or completely prevent emergence. In the current study however, shoot emergence was not delayed when only the root system was impeded. Masle and Passioura (1987) also observed that time to emergence of wheat seedlings was not affected when root systems were subjected to MI ranging from 1.5 to 5.5 MPa.

Although seedling emergence was significantly delayed by subjecting shoots to MI, subsequent shoot extension rate was significantly greater in seedlings emerging under MI than in unimpeded ones. Thus, at harvest, impeded shoots were comparable to or significantly longer than IU or the control. This implies either that mechanical impedance to the shoot, may have induced the plant to produce a "growth promoter" which enhanced growth after emergence or that a growth promoting substance was accumulating (or a growth inhibitor depleting) with time before the shoot was exposed to light. The above observations contradict those by Masle and Passioura (1987) where the extension rates of emerged shoots were significantly reduced when only root systems were impeded. There are several possible explanations. One, the MI used by Masle and Passioura was extremely high. Penetration resistance (PR) in their control treatment was 1.5 MPa against 0.025 MPa in the current study. In other treatments, Masle and Passioura used PR varying from 2 to 5.5 MPa. Impeded conditions in the current study had a PR of merely 0.86 ± 0.073 MPa which was only 60 % of the PR in their control treatment. Thus, high MI might have confined the root system in a small soil volume where water and nutrients became limiting resulting in reduced shoot growth. Second, with an initial matric suction of 5 kPa and a final of 8 to 20 kPa, the current study used relatively low matric suctions compared to 18 to 100 kPa as the initial values in the quoted study. Matric suctions lower than those quoted above (Rwehumbiza, 1994) have been shown to negatively affect seedling growth. Thus, the influence of water stress on seedling growth in Masle and Passiouras' study can not be ruled out.

The effects of shoot impedance to the root system is best looked at by comparing treatment UI (unimpeded root and impeded shoot) with the control (UU). The root length and hence its extension rate were increased significantly by subjecting the shoot system to MI. There is nothing in the literature to support or contradict these findings. However, MI to the root system either reduces shoot growth according to some studies (Dawkin *et al.*, 1983; Masle, 1990; Sharp, 1990) or has no effect at all (Russell and Goss, 1974). Sharp suggests an increased demand of photosynthates to support a preferential growth of roots and, therefore, a continued exploration of the soil for water as the cause of increased root:shoot ratio with increased MI to the root. In this study therefore, impeding the shoot system produced an opposite effect to that which impeding the root reportedly does to the shoot. Since plant growth can be affected by MI to the root before water and nutrients become limiting, the involvement of growth promoters and inhibitors has been suggested and established (Goss and Russell, 1980; Carmi and Heuer, 1981; Masle, 1990). In the current study, growth substances were possibly involved in promoting root growth when shoots were impeded, for the supply of water and nutrients was not limiting. Since an extensive and deep root system is important for plant survival in the SAT, some degree of MI to the shoot may be desirable to encourage root growth, so long as it does not reduce or prevent emergence altogether. Firming after sowing, is thus bound to promote early root growth where environmental conditions permit.

Comparing IU (impeded root and unimpeded shoot) with the control, shows the effect of root impedance to the shoot system. Fresh shoot mass and the thickness of the first internode (mesocotyl), were increased significantly by impeding the root system. Increased shoot mass when the root was impeded, contradicts findings from other studies (Masle and Passioura, 1987). Masle and Passioura observed a progressive reduction in shoot mass of 22 day old wheat seedlings when root systems were subjected to MI ranging from 1.5 to 5.5 MPa. Thus, how the extra shoot mass was generated in the current study, lacks explanation especially when significantly more shoot mass was accumulated even when both root and shoot systems were impeded. Usually, the interpretation of results from soil strength-plant growth studies in terms of MI alone is valid only if sub optimal levels of other growth factors are shown to be absent in all treatments. Whatever the cause of the above observations, it was linked to the growth media. More shoot mass was obtained when roots were impeded (in sand-vermiculite mixture) and less when they were unimpeded (in vermiculite). Recent work by Tsegaye and Mullins (1994) indicates that loose soil or sand is a better control growth media in regard to seedling growth than vermiculite. The limitations of using vermiculite include the fact that it dries out very fast and that being coarse it offers relatively poor contact with roots compared to soil. Thus, water absorption is likely to lag behind that in sand or soil and this may be reflected in seedling growth. The question thus remains whether if a different control medium had been used, the results from the current study would have been different. The above could be easily tested by using say compacted soil for the impeded treatment and loose soil for the control.

There was a significant thickening of the first internode only in treatments where root impedance was involved. The thickening of the first internode seems therefore, to have been controlled by a factor from impeded roots. When only the shoot system was impeded, the diameter of the first internode was unaffected.

Roots growing under MI were thicker than those in UI or in the control. Work by Eavis (1967) has shown that when apical extension is restricted, more cells become deposited per unit root length and individual cells become shorter but expand laterally resulting in increased root diameter. When only the shoot was impeded, root diameter was similar to that in the control. This was a further indication that growth regulators responsible for mesocotyl thickening originated from the root and not the shoot.

Spacing of lateral roots and the number of leaves produced were unaffected by any of the treatments. Similar observations have been reported by Mullins (1994). This suggests that these two parameters are genetically controlled and insensitive to changes in mechanical impedance. Thus, the longer the main axis, the greater the number of lateral roots.

Conclusion

The following conclusions can be drawn from this study: (i) Impedance to the shoot significantly delayed emergence, more so when the root was also impeded. (ii) Shoots emerging under MI, had significantly greater extension rates after emergence than unimpeded ones. (iii) Mesocotyls became significantly thicker only when the root systems were impeded. (iv) Impeding the shoot system, significantly increased the root extension rate. (v) The length of the first internode, the number of leaves and the spacing of lateral roots were not affected by any of the treatments.(vi) The involvement of growth regulators in: (a) delaying emergence when the shoot is impeded and especially when the root is also impeded; (b) promoting greater extension rates in shoots after emergence under MI; (c) increasing mesocotyl thickness when the root system is impeded and (d) increasing root extension rate when the shoot is impeded is suggested. The general implication of our findings given the agricultural practices and environmental conditions common in the SAT, that is: (i) use of low vigour seeds which are slow to germinate, (ii) surface crusting and hardsetting soils which impede shoot growth and (ii) shallow tilth achieved with a hand hoe which restricts root growth, is that of poor crop establishment or total crop failure.

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