Effects of soil mechanical impedance on root and shoot growth of *Lolium perenne* L., *Agrostis capillaris* and *Trifolium repens* L.

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Abstract

A method was used for applying a uniform mechanical impedance to plant roots using sand packed at different bulk densities with depth within each growth cylinder. In a growth experiment, replicate cylinders were packed with sand to give the following mechanical impedances: 0.25 MPa penetration resistance (negligible impedance), 1.40 MPa (moderate impedance) and 2.30 MPa (severe impedance). Seedlings of *Lolium perenne* L., *Trifolium repens* L. and *Agrostis capillaris* were grown for 23 d in each impedance treatment and effects on both roots and shoots were studied. Severe mechanical impedance affected both root and shoot growth rates for all three species resulting in smaller leaves and shorter roots. For the grasses, the root-to-shoot ratio at harvest was the same for all the treatments, but a delay in the initiation of both shoots and roots was observed in the severe mechanical impedance treatment. The results are discussed in relation to the possibility that roots penetrating the impeding treatments may have caused signalling that kept shoot and root growth in synchrony. Differences observed in the response to mechanical impedance of *T. repens* compared to the other two species may be a function of differences in the physiology between mono- and dicotyledonous species.

Key words: Mechanical impedance, *Lolium perenne*, *Trifolium repens*, roots, shoots.

Introduction

Mechanical impedance is ubiquitous within the root environment. Penetration resistances of 0.5–1.0 MPa and greater are commonly experienced in soil and can reduce root elongation rates considerably (Bengough and Mullins, 1990a; Tsegaye and Mullins, 1994). Thus it is likely to be the norm rather than the exception for at least part of the plant root system to experience mechanical impedance which will significantly reduce the rate of growth. Despite this, the great majority of research on relations between the soil physical environment and above-ground growth has focused on effects of soil water deficit. As a consequence of this, there remains a gap in our knowledge of how and under what circumstances mechanical impedance to root growth affects shoot growth.

Part of the reason for this lies in the difficulty of setting up a growth medium in which mechanical impedance is spatially uniform and in which the supply of water, nutrients and aeration are not limiting to growth. A novel technique that satisfies these requirements is described in Cook (1995) in which sand was packed to different bulk densities down the growth cylinder. Uniformly packed sand columns are commonly reported in the literature to provide treatments with controlled mechanical impedance that is assumed to be uniform with depth. However, it has been shown that there can be a large and systematic variation in penetration resistance with depth in such treatments (Cook, 1995). In this paper, the aim was to characterize the response of roots and shoots of individual plants to uniform soil mechanical impedance whilst other soil factors were non-limiting to root growth using the new technique. The species examined were the sown species *Lolium perenne* L. (perennial ryegrass) and *Trifolium repens* L. (white clover), and *Agrostis capillaris*, an indigenous grass species that is widespread in Scottish upland pastures.
Materials and methods

Mechanical impedance treatments
The growth medium used was washed sand, with a particle size distribution of 2.6% >2 mm diameter, 7.8% 2–1 mm, 24.7% 1–0.5 mm, 41.0% 0.5–180 μm, and 23.9% <180 μm. This was packed moist in 20 mm thick layers with different bulk densities at each depth in perspex cylinders in order to obtain a profile with a penetration resistance that was as uniform as possible with depth (Table 1; Fig. 2). This was achieved by trial and error. Three treatments were produced in this way corresponding to the penetration resistances of approximately 0.25, 1.40 and 2.30 MPa (Cook, 1995). These represent negligible, moderate and severe mechanical impedances, respectively.

Packing of cylinders
Before packing, the sand was moistened and homogenized with nutrient solution to water contents calculated to lie between 0.2–0.25 m$^3$ m$^{-3}$ after packing, depending on the treatment (Table 1). The volumetric water content was the same in each layer of sand regardless of bulk density, within each treatment. These water contents were chosen to give the sand an air porosity of ≥0.18 m$^3$ m$^{-3}$ to ensure that the oxygen diffusion rate would be more than sufficient to satisfy root respiration (Campbell, 1985) whilst also maintaining a constant and small matric suction of around 3 kPa. Within any given treatment, the air porosity of the layers with the greatest bulk density never exceeded 0.10 m$^3$ m$^{-3}$. The nutrient solution used was modified from Dart and Pate (1959) and comprised (in mmol dm$^{-3}$): 5.58 H$_2$SO$_4$, 5.83 CaCO$_3$, 2.30 K$_2$HPO$_4$, 2.50 NH$_4$NO$_3$, 1.66 MgSO$_4$, and (in μmol dm$^{-3}$): 46.13 H$_2$BO$_3$, 91.03 MnSO$_4$.4H$_2$O, 0.766 ZnSO$_4$.7H$_2$O, 0.103 Na$_2$MoO$_4$.2H$_2$O, 0.320 CuSO$_4$.5H$_2$O, 1.017 CoSO$_4$.7H$_2$O, and 89.54 FeEDTA and was adjusted to pH 6.0 with NaOH. The moist sand was put into 300 mm tall perspex cylinders of 49 mm internal diameter and a rubber plunger of diameter 45 mm was used to pack each layer of sand. The bulk density of the sand in each layer was varied (Table 1) to achieve the desired uniform mechanical impedance obtained from the preliminary experiments.

It was not possible to achieve a sufficiently large penetration resistance within the top 50 mm of the cylinder even with the tightest packing. Therefore, a plastic funnel of length 50 mm was pushed into the top layers of sand in all three treatments until the rim of the funnel was level with the top of the cylinder. In this way, seeds could be planted at the tip of the funnel where they would immediately encounter the desired mechanical impedance whilst the emerging shoot experienced negligible impedance and was quickly exposed to light (Fig. 1).

Seed germination and sowing
Seeds of L. perenne, A. capillaris and T. repens were germinated in darkness on wet filter paper until the radicle had just ruptured the testa. Ten seeds were then transferred to each packed cylinder. To avoid upward heaving of the seed as a result of the radicle pushing against the highly impeding sand each seed was glued to the inner base of the funnel using cowgum (Fig. 1), ensuring that the radicle was not affected. A 10 mm layer of loose sand was placed over the seeds. The cylinders were then transferred to the greenhouse in early July 1994 and arranged in a randomized block design with five blocks. This comprised three plant species in each of the three treatments with five replicates (3 x 3 x 5 cylinders). The seedlings were thinned to one per cylinder approximately 10 d after sowing when most shoots had emerged. Roots were shielded from light by placing a black plastic sleeve around the cylinders and painting the top 3 cm of each cylinder black. It was necessary to repeat the experiment for T. repens because the seedlings became desiccated before the cotyledons emerged. The

Table 1. Soil physical properties in the growth cylinders for the different mechanical impedance treatments

<table>
<thead>
<tr>
<th>Mean penetration resistance (MPa)</th>
<th>Bulk density (Mg m$^{-3}$)</th>
<th>Depth intervals (mm)</th>
<th>Volumetric water content (m$^3$ m$^{-3}$)</th>
<th>Mean air porosity (m$^3$ m$^{-3}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.30</td>
<td>1.80</td>
<td>20–60</td>
<td>0.20</td>
<td>0.179 (0.015)</td>
</tr>
<tr>
<td></td>
<td>1.70</td>
<td>60–100</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.50</td>
<td>100–160</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.48</td>
<td>160–220</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.70</td>
<td>220–240</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.80</td>
<td>240–300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.40</td>
<td>1.70</td>
<td>20–40</td>
<td>0.23</td>
<td>0.182 (0.009)</td>
</tr>
<tr>
<td></td>
<td>1.65</td>
<td>40–60</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.48</td>
<td>80–200</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.55</td>
<td>200–260</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.65</td>
<td>260–300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.25</td>
<td>1.50</td>
<td>20–80</td>
<td>0.25</td>
<td>0.206 (0.005)</td>
</tr>
<tr>
<td></td>
<td>1.40</td>
<td>80–200</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.33</td>
<td>200–280</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.55</td>
<td>280–300</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
seeds were replanted following the procedure used for the grasses, but with the daily addition of three drops of water above the seed until the shoot emerged, to prevent desiccation. Irradiance, soil matric suction and ambient and soil temperatures were measured from both of the sowing times.

Growth conditions
The plants were grown for 23 d until the roots of *L. perenne* in the control treatment had almost reached the bottom of the cylinders. The ambient temperature in the greenhouse was within the range 20–30 °C during the day and 15–18 °C at night. Supplementary irradiance was supplied for 16 h daily. Irradiance at plant height ranged between 400 and 700 μmol m$^{-2}$ s$^{-1}$ on a dull day and between 500 and 900 μmol m$^{-2}$ s$^{-1}$ on a bright day. The cylinders were rearranged twice weekly within their blocks to minimize any positional effects.

Soil matric suction and soil temperature
Soil matric suction and soil temperature were monitored throughout the experiment. Tensiometers (Webster, 1966) were installed into four additional replicate cylinders from each of the treatments at a depth of 120 mm from the surface of the sand. Seeds of the three plant species were grown in these cylinders without funnels, because the spout could not accommodate the width of the tensiometers. Instead, a 10 mm layer of black polythene beads was used to cover the surface of the sand to reduce evaporation in a similar way to the effect of the funnels in the main experiment. None of the cylinders were watered during the experiment.

Soil temperature at 140 mm depth was measured every 30 min using thermistors (four in each treatment) connected to a data logger (Data Hog, Skye Ltd., Llandrindod Wells, UK).

Shoot measurements
Daily measurements (±0.01 mm) of the length and central width of each leaf were taken using vernier callipers. Measurements ceased when no increase was detected for 2 d. Leaf area was calculated by multiplying leaf length by leaf width. Leaf relative expansion rate (RER) was calculated using the formula (Hunt, 1982):

$$RER = \frac{\log(n_{L2}) - \log(n_{L1})}{T}$$

where $A_{L1}$ and $A_{L2}$ are leaf area on day $n$ and $n-1$, respectively, and $T$ is the time between successive measurements (1 d). The time of leaf appearance and rate of tillering was also recorded. Shoot fresh and oven dry (80 °C for 48 h) weights were determined after harvesting.

Root measurements
After 23 d the plants were harvested and the roots were carefully washed free of sand. The roots were separated from the shoots and stained by placing in a 0.001% methyl violet solution overnight in order to facilitate image analysis. The roots were then stored in a preservative solution of 40% methanol, 5% formaldehyde and 5% glacial acetic acid in distilled water. No noticeable shrinkage of roots was detected during storage.

Vernier callipers were used to measure the length and diameter of all root axes. Lateral length and spacing was measured by subsampling along selected axes taking five laterals from the top, middle and bottom of these axes. For the grass species, two axes were chosen for lateral measurements because some axes had noticeably more laterals than others. To ensure a more representative subsample of the entire root system, the first axis was chosen as representative of those with more laterals and the second as representative of others with fewer. Lateral counts were taken from each of the subsampled axes.

Total root length was measured using an image analyser with the Root Measurement System software, version 1.6 (Skye Ltd., Llandrindod Wells, UK). High quality photocopies of the stained root systems were used to avoid drying of the roots during measurement. Each image was measured five times to check for reproducibility (coefficient of variation <0.01%) and the mean of these was used. Fresh and dry weights of the whole root system were also determined.

Statistical analyses
Analysis of variance (ANOVA) was computed for each variable using Minitab Statistical Software, release 9.1. A separate analysis was performed for the data of each species. Bartlett's test was used to check for homogeneity of variance required for ANOVA. Where this was not met, square root or log transformed data was used in the analyses. The Bonferroni multi-comparison significance test was used to calculate least significant differences between treatment means for each species.

Results
Soil water status, penetration resistance and temperature
Matric suction increased steadily from 2.4±0.1 kPa 5 d after sowing (DAS) to 5.1±0.4 kPa 23 DAS (data not shown). Matric suction did not differ significantly ($P < 0.05$) between the treatments. Even at 23 DAS, these suctions corresponded to large volumetric water contents at rooting depth. Consequently, the sand should have retained a high unsaturated hydraulic conductivity and thus there should have been no significant limitation on water availability to any part of the root system.

Measurements made on replicate packed columns, each with a funnel inserted, showed that the penetration resistance was comparatively uniform throughout the whole rooting depth although it was slightly less than the nominal values for the 1.40 and 2.30 MPa treatments within the first few centimetres of rooting depth (Fig. 2).

The temperatures in the sand columns all followed very similar diurnal patterns with average daily temperatures of around 21.8±0.33 °C in each of the treatments. There was no obvious treatment or block effect (data not shown).

There were no significant differences in the monitored growth conditions between the sowing dates of the grasses and the later re-sowing of *T. repens*. Any differences that did occur would not have affected the response of the individual species to the treatments.

Root and shoot dry weight
The treatments significantly affected the dry weights of roots of all three species (Fig. 3). The root dry weight of both *A. capillaris* and *T. repens* was significantly lower in both the 2.30 MPa and the 1.40 MPa treatments compared to the 0.25 MPa (control) treatment. Significant treatment effects were also observed for the
Fig. 2. The three mechanical impedance treatments used in which bulk density was varied with depth (see Table 1); 2.30 MPa (○), 1.40 MPa (■), 0.25 MPa (▲). Measurements were taken with funnels inserted at the top of the cylinder and start 1 cm below the tip of the funnel, n=4. Bars represent typical values for ±SE.

The logarithms of fresh weight of roots and fresh weight of shoots after 23 d of growth were significantly linearly related (P<0.001) for both grass species, but not for T. repens (Fig. 4). All three species showed a linear relationship between the logarithms of dry weight of roots and dry weight of shoots (Fig. 4). The fresh weights of roots and shoots of A. capillaris had a 1:1 relationship. A. capillaris plants had approximately two to four times as much shoot as root dry weight whereas shoot dry weight was usually less than twice root dry weight for L. perenne.

Both root and shoot dry weight decreased as mechanical impedance increased. The results also show that the allometric ratio between roots and shoots at final harvest remained constant as impedance increased. For A. capillaris under 1.40 MPa and 2.30 MPa mechanical impedance, there was a large variation in root and shoot weights between replicates which suggests that any interpretation of these results should be viewed with caution. The variation may be partly a result of the greater inherent variability in a natural seedlot. In contrast, the variability seen for root and shoot weight of L. perenne and T. repens was still high (coefficient of variation approximately 50%), but this was often due to a single outlying value. At any given depth, the coefficient of variation in penetration resistance in the mechanical impedance treatments were <18% which suggests that most of this variability was due to inherent differences between different plants, which may be due both to difference in seed vigour and in genotype.

**Root length and morphology**

The total root length of both L. perenne and A. capillaris in the 2.30 MPa treatment was only 23% of the control whereas T. repens was reduced to 54% of the control (Fig. 5). There was no significant difference between treatments in the number of seminal axes for either grass, but there were significantly less nodal axes present for L. perenne in the 2.30 MPa treatment, only 29% of the number of nodal roots in the control (Table 2). The mean lengths of both seminal and nodal axes were significantly reduced to approximately 23% of the control for L. perenne in the 2.30 MPa treatment, but only the mean length of seminal roots was significantly reduced for A. capillaris in the 2.30 MPa treatment. For T. repens, the mean length of the axis was significantly reduced in the 2.30 MPa treatment to 42% of the control (Table 3).

The number of laterals per axis was significantly less in the 2.30 MPa treatment compared to the control for all three species due to the shorter axis length in this treatment. No consistent significant effects on mean lateral length or lateral spacing were observed for the grasses (Table 2). For T. repens, lateral spacing was only slightly, but significantly, greater than the control in the 2.30 MPa.
Impedance to roots affects shoots

Fig. 4. Allometric relationship between shoot and root fresh and dry weights of plants grown in sand at three different penetration resistances; (O) 2.30 MPa, (O) 1.40 MPa, and (●) 0.25 MPa for L. perenne, A. capillaris and T. repens. R² values for these respective species are 55.9%**, 70.4%** and 0.4% (fresh weight) and 65.2%***, 74.7%*** and 52.1%** (dry weight), where ** = P<0.01 and *** = P<0.001. On each figure the line represents the function, root weight = shoot weight. Each point represents a paired root and shoot value for one plant.

Fig. 5. Total root length of the three species after 23 d of growth in sand at three different penetration resistances; (O) 2.30 MPa, (●) 1.40 MPa and (●) 0.25 MPa; n = 5. The left scale refers to results for L. perenne and the right scale for the other two species. Means that do not differ significantly (P>0.05) share the same letter.

treatment and there was no significant effect of impedance on the mean length of laterals (Table 3).

For all three species, the dominant factor responsible for the reduced total root length in the impeded treatment(s) was the reduction in mean axis length (in the case of the grasses, seminal axes). In L. perenne, however, the reduction in the number and mean length of the nodal axes (Table 2) indicates that over a longer period of time, the behaviour of the nodal roots could also have been strongly affected by mechanical impedance. It is not clear from the results whether mechanical impedance had either a direct effect on the number of nodal axes produced or delayed their emergence.

Shoot size, morphology and development

L. perenne showed a significant reduction in both the length and area of the second and third fully grown (mature) leaves in the 2.30 MPa treatment compared to the control (Fig. 6). The length of these mature leaves was reduced to approximately 65% of the control and leaf area was reduced to 34% and 43% of the control for leaves 2 and 3, respectively, in the 2.30 MPa treatment. The time of leaf appearance was delayed by 1–2 d for all three leaves in the 2.30 MPa treatment, but there was no consistent effect on the growth period defined here as the time taken for a leaf to expand fully (Fig. 6). For the first trifoliate leaf of T. repens, the impedance treatments significantly (P<0.05) reduced mature leaf area (1.4 MPa treatment) and leaf growth period (2.30 MPa treatment) compared with the control (Fig. 6). No significant treatment effects were observed on any of the measured parameters for the unifoliate leaves of T. repens (data not shown).
There were two distinct effects of impedance on the root of barley and wheat: more affected by impedance. Effects of mechanical impedance on roots and shoots. Masle (1992) also found that faster growing genotypes of barley and wheat were more affected by impedance. There were two distinct effects of impedance on the root growth of *L. perenne*. Firstly, it reduced the growth rate and, therefore, the final length of root axes. Secondly, mechanical impedance reduced the number and/or delayed the production of nodal axes. Shoots of *L. perenne* were affected by a reduction of the initial RER of the second and third leaves thus producing smaller leaves, and also by a delay in leaf emergence of up to 2 d. Similar but less pronounced effects were seen for *A. capillaris*. In contrast, although mechanical impedance also reduced root growth rate and initial relative growth rate of *T. repens* (and therefore the size of the shoots), the timing of leaf emergence remained unaffected. The differences in growth seen between the species may have been influenced by the variation in both irradiance and air temperature experienced throughout the experiment. Fluctuations in air temperature may have caused variations in temperature at apical meristems and in the upper sand layers of the columns. Reductions in apical meristem temperature has been shown to reduce leaf extension rates especially for grasses (Peacock, 1975a, b; Stoddart *et al.*, 1986) thus the differences in leaf growth rate between the species in this study may be due to differences in response to temperature fluctuations. Leaf appearance rates of *T. repens* are closely related to mean air temperature (Davies and Jones, 1992), but even more closely related to upper soil temperature (Glendining and

### Table 2. Root length and morphology data for *L. perenne* and *A. capillaris* after 23 d of growth

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seminal axes</th>
<th>Nodal axes</th>
<th>All axes</th>
<th>Laterals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Mean length (cm)</td>
<td>No. Mean length (cm)</td>
<td>Total no. Mean length (cm)</td>
<td>No. per axis Mean length (cm)</td>
</tr>
<tr>
<td><em>L. perenne</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.30 MPa</td>
<td>4.4 a 4.4 a</td>
<td>1.6 a 1.4 a</td>
<td>6.0 a 174.3 a</td>
<td>31.7 a 1.073 a</td>
</tr>
<tr>
<td>1.40 MPa</td>
<td>6.8 a 9.0 ab</td>
<td>4.4 b 3.0 a</td>
<td>11.2 b 567.5 b</td>
<td>65.7 ab 1.816 b</td>
</tr>
<tr>
<td>0.25 MPa</td>
<td>5.6 a 18.8 b</td>
<td>5.6 b 6.4 b</td>
<td>11.2 b 710.5 c</td>
<td>98.3 b 1.635 ab</td>
</tr>
<tr>
<td><strong>Significance level (P ≤)</strong></td>
<td>NS 0.001</td>
<td>0.01</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td><em>A. capillaris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.30 MPa</td>
<td>3.0 a 3.3 a</td>
<td>1.0 a 1.3 a</td>
<td>4.0 a 10.0 a</td>
<td>20.1 a 0.281 a</td>
</tr>
<tr>
<td>1.40 MPa</td>
<td>5.0 a 5.2 ab</td>
<td>1.6 a 1.1 a</td>
<td>6.6 b 15.3 ab</td>
<td>23.4 ab 0.234 a</td>
</tr>
<tr>
<td>0.25 MPa</td>
<td>5.2 a 10.8 b</td>
<td>1.4 a 2.5 a</td>
<td>6.6 b 39.0 b</td>
<td>44.6 b 0.363 a</td>
</tr>
<tr>
<td><strong>Significance level (P ≤)</strong></td>
<td>NS 0.01</td>
<td>NS</td>
<td>0.10</td>
<td>0.10</td>
</tr>
</tbody>
</table>

* Two seminal axes were subsampled for both species in which subsample 1 had more laterals than subsample 2.

### Table 3. *T. repens* root length and morphology data

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Length of axis (cm)</th>
<th>Laterals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. per axis Mean length (cm) Total length (cm) Spacing on axis (cm)</td>
<td></td>
</tr>
<tr>
<td>2.30 MPa</td>
<td>8.9 a 28.2 a 1.3 a 40.8 a 0.31 a</td>
<td></td>
</tr>
<tr>
<td>1.40 MPa</td>
<td>11.8 ab 32.6 ab 1.2 a 41.6 ab 0.28 a</td>
<td></td>
</tr>
<tr>
<td>0.25 MPa</td>
<td>21.3 b 69.2 b 1.3 a 70.3 b 0.25 b</td>
<td></td>
</tr>
<tr>
<td><strong>Significance level (P ≤)</strong></td>
<td>0.001 0.01 NS 0.01 0.05</td>
<td></td>
</tr>
</tbody>
</table>

Discussion

**Effects of mechanical impedance on roots and shoots**

Effects of mechanical impedance were most apparent in *L. perenne* primarily because of its faster growth rate. Masle (1992) also found that faster growing genotypes of barley and wheat were more affected by impedance. There were two distinct effects of impedance on the root
Impedance to roots affects shoots

Mytton, 1989; Davies and Jones, 1992). Thus the unchanged leaf appearance rate observed for *T. repens* suggests that, at least for this species, temperature variation did not greatly influence plant growth in this experiment. However, different temperatures experienced by the grasses and the clover due to the different sowing times may have had an effect.

The contrasting responses of the species to mechanical impedance treatments may relate to differences between mono- and dicotyledonous species. Klepper *et al.* (1984) observed that the development of the roots of winter wheat (*Triticum aestivum* L.) was very much related to the developmental stage of the shoots; all roots were associated with nodes either in the seed (seminal roots) or in the crown just above the seed (nodal roots). The seminal root system services the shoots until the nodal roots develop in response to the sequential development of tillers (Klepper *et al.*, 1982). Only when a tiller has developed from a node and produced three leaves will the nodal root associated with that tiller begin to elongate (Klepper *et al.*, 1984). This may also be the case with *L. perenne* where, on average, only two nodal roots for the 2.30 MPa treatment were observed compared to six for the control on plants with one or two tillers for the 2.30 MPa treatment compared to three or four tillers for the control (data not shown). In wheat, the number of roots produced per node is usually between two to four, and new nodal roots occur usually when the tiller from the preceding node has three leaves (Klepper *et al.*, 1984; Klepper, 1991). The delay in leaf appearance observed for *L. perenne* under high mechanical impedance may thus account for the limited number of nodal roots. It is suggested that the reduction in the growth rate of seminal axes due to mechanical impedance reduced the initial growth rate of the leaves on the main stem, and increased the length of time between the appearance of subsequent leaves (perhaps due to some form of root-to-shoot signaling) and hence, the production of the nodal root system was delayed.

In contrast, the root systems of dicotyledonous species like *T. repens* comprise one taproot originating from the radicle which is the sole axis supporting the shoots. The mechanically impeded *T. repens* seedlings experienced no significant delay in leaf appearance compared to the control yet a reduction in final leaf area did occur for the first trifoliate leaf. Both the initial relative growth rate and growth period of this leaf were reduced in the 2.30 MPa treatment compared to the control. This suggests that *T. repens* may adjust the growth period of the leaf to avoid the delay in shoot development. Blaikie and
Mason (1993) grew *T. repens* stolon cuttings in cores of field soil at various penetration resistances and found that after 38 d of growth, plants in the soils with high penetration resistance produced significantly fewer and smaller leaves. This implies that a delay in leaf development occurred due to mechanical impedance at the roots. Although stolon cuttings differ from seedlings in terms of root initiation, they are more representative of older plants which suggests that the seedlings were experiencing only the beginning of a response to mechanical impedance which might alter with time.

Masle (1992) observed that genotypes of wheat and barley all showed reduced growth in response to soil mechanical impedance, but the effects varied with genotype in terms of both the mechanism and time-course of response. In general, landrace genotypes were found to be less sensitive to soil mechanical impedance than modern cultivars most probably because they had evolved on shallow soil of high strength. In this study, *A. capillaris* showed less pronounced and non-significant responses to mechanical impedance than the cultivars of *L. perenne* and *T. repens* which may be because it is a native unimproved grassland species. The implication of this is that, in selecting for faster growth rates, improved species may also have lost some of the ability to cope with high mechanical impedance.

### Root-to-shoot communication

The reduction in root growth in response to mechanical impedance has been widely documented (Bengough and Mullins, 1990), but rarely has mechanical impedance been recognized as an important factor controlling shoot growth independently of the effects of water and nutrient deficiency. Masle and Passioura (1987) found that shoot as well as root growth rate of young wheat seedlings were
Reduced in response to soil mechanical impedance implying some form of root-to-shoot signalling. Subsequent longer-term experiments showed that this response was biphasic. Root dry weight accumulation was initially reduced more than that of the shoot up until 9 d after sowing (DAS) with the reverse applying progressively from 10–16 DAS (Masle et al., 1990). This was in contrast to the unimpeded wheat plants for which the root-to-shoot ratio decreased with ontogeny. The actual dry weight accumulation of the impeded roots was greater than for the unimpeded ones in the second phase of response even though root elongation remained restricted by high mechanical impedance (Masle et al., 1990). Thickening of impeded roots was also observed in the present study (data not shown), however, at final harvest, no evidence of preferential C allocation to the roots was seen for the impeded plants compared to those of the control. The root-to-shoot ratio was only determined at one time in this experiment and no measurements to determine the time-course of change in this ratio were taken. It may be that the root-to-shoot ratio of the plants in this study had followed similar patterns of change to those of wheat reported by Masle et al. (1990) and the similarity of this ratio at the time of harvest, may have been coincidental.

Mechanical impedance is known to reduce root elongation rates thus reducing the volume of soil that the root system can exploit (Russell and Goss, 1974; Veen, 1982). 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 (Boone and Veen, 1982; Castillo et al., 1982; Atwell, 1990; Oussible et al., 1992). However, studies on the effects of restricted root volume on shoots under conditions with no water or nutrient stress have shown that reductions in shoot growth still occur (Carmi and Heuer, 1981; Carmi and Shalhevet, 1983; Peterson et al., 1984; Krizeck et al., 1985) and the reduction of certain growth regulatory substances has been suggested to be directly responsible for restricting shoot growth (Carmi and Heuer, 1981). Similar effects may also be due to mechanical impedance. Masle and Passioura (1987) grew wheat seedlings in soil cores at different mechanical impedances and noted that a delay in the appearance of leaves occurred as well as an overall reduction in shoot production when water and nutrient supplies were adequate. This agrees with the results here, yet no such effect is reported from the restricted root volume experiments mentioned previously. This suggests that these responses may be direct effects of mechanical impedance, at least for monocotyledonous species. Although the clover seedlings used here did not show any significant signs of delayed leaf emergence under mechanical impedance, it may be that this response is seen only in more mature plants.

The RER of leaves of both _L. perenne_ and _T. repens_ was significantly reduced by high mechanical impedance in this study, but only for the first 1–2 d after emergence. Reduced mean relative leaf expansion rates in response to increasing soil mechanical impedance was also observed for wheat (Masle and Passioura, 1987) and barley (Masle, 1992). However, no information on the effects of mechanical impedance on the RER of individual leaves and the time-course of these effects is available to serve as a comparison. Whether the reduced RER was a result of reduced cell production or expansion remains to be clarified. Moreover, the reason why mechanical impedance affects RER only between days 1–2 after appearance is also unclear. In this experiment, reduced RER results in smaller, lighter leaves on the impeded plants thus allowing the root-to-shoot ratio to remain relatively unaffected.

**Conclusions**

Unlike many previous studies on the effects of mechanical impedance on plant growth, the treatments used here had penetration resistances that were uniform spatially and with depth. At no time were the plants deficient of nutrient solution in the sand columns and it can be assumed that the response of the plant to impedance was not due to lack of nutrients, water or oxygen. The results showed a clear relationship (especially for the grasses) between root and shoot production, on both a fresh and a dry weight basis. The root-to-shoot ratio remained constant across the treatments at final harvest even though the control treatment plants were much larger than the impeded plants. This control of the shoots was a direct consequence of mechanical impedance encountered by the roots. The results imply that roots penetrating the impeding treatments were responsible for some sort of signalling that kept shoot and root growth in synchrony. There was a reduction in shoot relative growth rate for all three species, but a delay in shoot development was only evident in the grasses. This may be a function of the differences in the physiology between mono- and dicotyledonous species.

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**References**


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