The Effect of Soil Strength on the Growth of Young Wheat Plants

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Abstract

Wheat seedlings were grown in soil of various strengths, obtained by changing the bulk density or the water content of the soil. Leaf expansion and transpiration rate were monitored from emergence until the main stem had 5-7 leaves. Leaf area, and shoot and root dry weights, were negatively correlated with soil strength as measured by penetrometer resistance. The growth of roots was less affected than that of shoots. Leaf expansion was reduced before the first leaf was fully expanded. Relative rates of leaf expansion thereafter were consistently lower at high soil strength, although not always significantly. High soil strength also produced substantially smaller stomatal conductances. All effects were the same whether variations of soil strength were brought about by changes in water content or in bulk density.

Three possible causes of reduced shoot growth were examined: (1) a limiting supply of nutrients; or (2) of water, because of a restricted root system; or (3) a reduced carbon supply because of a higher carbon demand from the roots, or because of the low stomatal conductance. We conclude that these are all unlikely explanations for the onset of the effects of soil strength, which were independent of soil phosphorus content, of leaf water potential, and of the amount of carbon reserves in the seed. We suggest that growth of the shoot is primarily reduced in response to some hormonal message induced in the roots when they experience high soil strength.

Introduction

Plants usually grow poorly when their roots are in soils of high strength (Taylor and Ratliff 1969; Eavis 1972; Cornish and Fettell 1978). The reasons for this poor growth, which is of both roots and shoots, are not known. A probable but controversial explanation for the poor root growth is that roots are unable to build up sufficient turgor to push aside the soil (Greacen and Oh 1972; Russell and Goss 1974). One possible explanation for the poor shoot growth is that it results from the restricted root system supplying insufficient water and nutrients to the shoot. Another is that shoot growth may be limited by insufficient carbon supply because more carbon may be required by the roots, for increased osmotic pressure (Greacen and Oh 1972). It is also possible that the shoot growth may be controlled by hormones originating in the roots, as Richards and Rowe (1977) and Carmi and Heuer (1981) have suggested for the bonsai effect — the inhibition of shoot growth that occurs when the roots have only a very small volume of soil in which to grow, and which may be very similar physiologically to the effect of high soil strength.

Most of the information on the effects of high soil strength on shoot growth has come from field experiments on soil compaction (Kubota and Williams 1967; Blackwell \textit{et al}. 1985; Brereton \textit{et al}. 1986), which is a serious and much-studied agronomic problem. But these field experiments are very hard to interpret physiologically. Soil strength depends on the continuously changing water content of the soil as well as on bulk density, and its effect on root growth depends on temperature (Greacen and Hignett
which is also continuously changing. Furthermore, in the field, anaerobic conditions around the roots frequently accompany soil compaction.

Several laboratory studies have explored the effects of soil strength per se on early growth, but they have mainly concerned root growth. Barley (1962), Goss (1977), and Goss and Russell (1980) simulated high soil strength by applying radial pressure to roots growing in soil or glass beads. They showed that the rate of root elongation fell sharply when mechanical resistance was increased, whereas root dry weight was not necessarily affected; they gave no information on shoot growth. Taylor and Ratliff (1969), using soil packed to various bulk densities and at various water contents, also showed that root length responded markedly to soil strength; they noted that shoot growth was also affected, but did not analyse the causes of this.

The aims of the work described here were: (1) to characterise under controlled conditions the responses of wheat plants, especially the growth of the shoot, to high soil strength during early growth; (2) to seek the physiological explanations of these responses, and in particular to see if shoot growth was restricted by an inadequate supply of water, carbohydrate, or phosphorus. We thought that phosphorus was the most likely of the macronutrients to be limiting because it has by far the lowest mobility in soil.

Materials and Methods

Experiment 1

(a) Growth Conditions

Soil strength

Wheat plants (Triticum aestivum L. cv. Egret) were grown in cylindrical p.v.c. pots (190 mm high, 85 mm diameter), in a growth chamber. The variation in soil strength was obtained by varying both the bulk density and the water content of the soil. The soil was a silty loam (5% coarse sand, 40% fine sand, 31% silt, 19% clay), rich in organic matter (4·5%), and poor in phosphorus (1 p.p.m. available phosphorus, test Bray P1). Each pot contained 1100 g of dry soil, which had been passed through a 5 mm sieve and packed, in 10 mm thick layers, to five bulk densities: 1·17, 1·29, 1·37, 1·41 and 1·45 g cm⁻³. The packing was done with a piston of diameter equal to the internal diameter of the pot, mounted in an arbor press and moved vertically within a pot by a torsion wrench set to apply a given pressure to each layer. The standard error of the mean density between layers within a pot was 1·1-1·5%. The packing procedure produced no obvious boundaries between the layers. Variation of bulk density within a treatment was small (s.e. = 0·2-0·3%, i.e. 0·03 to 0·05 g cm⁻³). Before sowing, the water content of the soil (θ) was raised to an initial value of 0·22-0·23, 0·25 or 0·27 (g/g dry soil), and then maintained at that initial value by daily weighing and watering. The soil was covered with 18 mm of black polyethylene beads of 2 mm diameter to reduce evaporation of water from the soil.

Soil strength was measured at sowing using a 60° cone penetrometer of diameter 2·0 mm. The different combinations of water content and bulk density gave a range of penetrometer resistance from 1·5 to 5·5 MPa in the top 3 cm of the soil (Table 1).

Nutrient supply

In a set of pots representing the range of soil strength (Table 1), P was supplied at either 32 or 189 mg P per kg soil, as finely ground superphosphate. Nitrogen was added to all pots at a rate of 125 mg N per kg soil as ammonium nitrate. Both fertilisers were mixed uniformly throughout the soil before packing. A preliminary study had shown that these conditions would allow the plants to grow without any nutritional limitation at low soil strength, except for the low P level, which severely hindered growth.

Water and oxygen supply

Our aim was to vary soil strength without inducing complications arising from having too little water in the soil, or too little air. We determined the moisture characteristic of the soil at each bulk density, using a pressure plate, and from these characteristics calculated that the suctions developed in the soil were within the ranges: 18-30, 35-65, and 70-100 kPa for θ = 0·27, 0·25, and 0·22, respectively. These
are quite low suctions, and would not normally restrict the uptake of water by roots (Gardner 1983) but, to check that water supply to the shoots was adequate we also measured the leaf water potential (see later).

Poor aeration was potentially a more serious problem, for the air-filled porosity at the highest bulk density at the highest water content was less than 10% of the soil volume. Such a low porosity is likely to induce oxygen deficiency (Wesseling and Van Wijk 1957; Grable and Siemer 1968). To check on this possibility we ventilated a set of supplementary pots, in treatments shown in Table 1, by injecting humidified air continuously into the centre of each pot, at a rate of about 2 litres h\(^{-1}\) during the growth of the plants. The distribution of air bubbles emerging at the surface of the soil when this was covered with water was uniform, indicating effective ventilation.

**Temperature and light conditions**

The plants were grown at 15°C day, 13°C night, 10 h photo- and thermoperiod, and photosynthetic photon irradiance 550 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). Leaf temperature measured for two extreme treatments with a

<table>
<thead>
<tr>
<th>Treatment No.</th>
<th>Soil water content (g g(^{-1}) dry soil)</th>
<th>Soil bulk density (g cm(^{-3}))</th>
<th>Soil ventilation (+/-)</th>
<th>Phosphorus level (mg kg(^{-1}))</th>
<th>Soil penetrometer resistance (MPa)(^{\ast})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.22</td>
<td>1.37</td>
<td>-</td>
<td>189</td>
<td>5.5 ± 0.04</td>
</tr>
<tr>
<td>2</td>
<td>0.23</td>
<td>1.41</td>
<td>-</td>
<td>189</td>
<td>5.4 ± 0.20</td>
</tr>
<tr>
<td>3</td>
<td>0.25</td>
<td>1.17</td>
<td>-</td>
<td>189</td>
<td>1.5 ± 0.04</td>
</tr>
<tr>
<td>4</td>
<td>0.25</td>
<td>1.29</td>
<td>-</td>
<td>189</td>
<td>2.0 ± 0.07</td>
</tr>
<tr>
<td>5</td>
<td>0.25</td>
<td>1.29</td>
<td>-</td>
<td>32</td>
<td>1.8 ± 0.04</td>
</tr>
<tr>
<td>6</td>
<td>0.25</td>
<td>1.37</td>
<td>-</td>
<td>189</td>
<td>3.5 ± 0.09</td>
</tr>
<tr>
<td>7</td>
<td>0.25</td>
<td>1.37</td>
<td>-</td>
<td>32</td>
<td>3.6 ± 0.09</td>
</tr>
<tr>
<td>8</td>
<td>0.25</td>
<td>1.41</td>
<td>+</td>
<td>189</td>
<td>5.2 ± 0.12</td>
</tr>
<tr>
<td>9</td>
<td>0.25</td>
<td>1.41</td>
<td>+</td>
<td>32</td>
<td>5.0 ± 0.12</td>
</tr>
<tr>
<td>10</td>
<td>0.25</td>
<td>1.41</td>
<td>-</td>
<td>189</td>
<td>5.0 ± 0.24</td>
</tr>
<tr>
<td>11</td>
<td>0.25</td>
<td>1.45</td>
<td>+</td>
<td>189</td>
<td>4.0 ± 0.12</td>
</tr>
<tr>
<td>12</td>
<td>0.25</td>
<td>1.45</td>
<td>-</td>
<td>189</td>
<td>4.1 ± 0.20</td>
</tr>
<tr>
<td>13</td>
<td>0.27</td>
<td>1.37</td>
<td>-</td>
<td>189</td>
<td>3.2 ± 0.12</td>
</tr>
<tr>
<td>14</td>
<td>0.27</td>
<td>1.41</td>
<td>+</td>
<td>189</td>
<td>5.0 ± 0.20</td>
</tr>
<tr>
<td>15</td>
<td>0.27</td>
<td>1.41</td>
<td>-</td>
<td>189</td>
<td>4.6 ± 0.13</td>
</tr>
<tr>
<td>16</td>
<td>0.27</td>
<td>1.45</td>
<td>+</td>
<td>189</td>
<td>3.2 ± 0.14</td>
</tr>
<tr>
<td>17</td>
<td>0.27</td>
<td>1.45</td>
<td>-</td>
<td>189</td>
<td>3.4 ± 0.15</td>
</tr>
</tbody>
</table>

\(\ast\)Values are means ± s.e.

thermocouple (No. 40 Brown and Sharp gauge, Evanohm/constantan) was 15·6 ± 0·6 (values averaged over five leaves, for 1 h). From this value and the dew point in the chamber (measured at the same time as the leaf temperature), we estimated the leaf-to-air vapour pressure difference to be 0·50 kPa, with a likely uncertainty of 5–10%.

Soil temperature was measured for three treatments (bulk density = 1·17, 1·37, 1·45 g cm\(^{-3}\); \(\theta = 0·25\)) at the surface of the soil, below the layer of beads, and at depths of 5 cm and 15 cm (copper/constantan thermocouples; four replicates per treatment at each depth). Temperature was similar for all treatments, being 23°C below the beads, 19°C at 5 cm, and 17°C at 15 cm during the day, and 13°C at all depths during the night.

**Establishment of the plants**

There were three pots per treatment. Four seeds were sown in each pot, 30 mm apart, 17 mm deep, in conical depressions, and covered with loose soil so that the growth of the coleoptile would not be
limited directly by any mechanical resistance. The plants were thinned to three on day 8 after emergence, and to two on day 15, when they had 1–2, and 3 visible leaves, respectively. The final harvest (two plants per pot) was made on day 22 at the 5 leaf stage, when the second tiller was appearing. The pots were widely separated. Mutual shading was negligible throughout the experiment.

(b) Plant Measurements

Growth

Non-destructive measurements: The length of the coleoptile and of the first leaf was measured daily from the time of emergence. After the second leaf had appeared, the length ($L$) and breadth ($B$) of each leaf was measured with a ruler. Leaf area was estimated as $0.84LB$, the value and constancy of this factor $0.84$ having been established in a preliminary experiment. From these data the elongation rate and relative leaf expansion rate (RLER) between successive measurements were calculated, RLER being the natural logarithm of the ratio of the successive measurements of total area divided by the time interval between the measurements. The phyllochron, the period of time elapsed between the appearance of two successive leaves on the main shoot, was estimated from the slope of the curve relating the number of leaves, described in decimal notation (Haun 1973), to time.

Destructive measurements: The thinned plants were used for destructive measurements on days 8 and 15 after emergence, and the two remaining plants per pot were harvested on day 22. The shoots were cut at the level of the ligule of the first leaf, then at the level of the soil. The fresh weights of the two fractions, blades and sheaths, were immediately measured. The areas of blades and sheaths were measured by planimetry. The dry weight was measured after oven-drying for 48 h at 70°C. At the final harvest, the roots were also collected and their dry weights determined before and after ashing for 6 h at 600°C.

Chemical analyses of the plants

The shoots harvested on days 15 and 22 were analysed for total nitrogen, total phosphorus, and soluble carbohydrates (although not for starch because this usually occurs in only very small amounts in wheat leaves (e.g. Fischer and Stockman 1980)). Nitrogen was determined by the Kjeldahl method, and phosphorus by nitric–sulfuric acid digestion, according to Williams and Twine (1967) and Twine and Williams (1967). Soluble carbohydrates in the shoot were measured by extracting 15 mg of finely ground material in $2\text{ ml}$ of water at 60°C (two extractions for 1 h). The extract was then hydrolysed by adding $0.6\text{ ml }2\text{ N HCl}$ ($2\text{ h at }70^\circ\text{C}$). The concentrations of glucose and fructose were measured spectrophotometrically at 340 nm, after successive additions of a formulation of hexokinase and glucose-6-P dehydrogenase (Worthington Flozyme glucose reagent) and phosphoglucose-isomerase (Sigma P5381).

Measurements of leaf water potential

Leaf water potential was measured on days 8, 15, and 22 after emergence, with a pressure chamber, following the recommendations of Turner and Long (1980). The measurements were made just before harvesting the plants, around midday, on the last fully expanded blade and, when the plants had very different numbers of leaves, on the last two expanded blades.

Estimation of transpiration and leaf conductance to water vapour

The amount of water transpired by a plant was estimated gravimetrically. Six pots without plants, representing the range of bulk density, were used to estimate the loss from the soil, which was $1.2\text{ g}$ of water per pot per day for all pots whatever their water content, their bulk density, or the frequency with which they were watered. We assumed that this value applied to the pots with plants, i.e. that soil shading by the leaves was negligible. Thus the water transpired by a plant each day was calculated as the amount of water lost by the pot less $1.2\text{ g}$. On average, 88% of the water transpired over a 24 h period was lost during the light period, regardless of the soil bulk density or water content.

The average leaf conductance, $g$, mol m$^{-2}$ s$^{-1}$, during the light period was calculated from the water transpired as follows: $g = Ep/\Delta e$, where $E$, mol m$^{-2}$ s$^{-1}$, is the transpiration rate averaged over all leaves for the light period, $p$ is the local atmospheric pressure (95 kPa), and $\Delta e$ is the difference in vapour pressure between leaf and air (0.50 kPa). This estimate was checked on several treatments with a porometer (Automatic Porometer MK3, Delta-T Devices), the measurements being made on the last fully expanded leaves.
Experiment 2

For two treatments differing in penetrometer resistance (1.0 and 3.0 MPa), a supplementary set of pots was established to see if carbon limitation was responsible for the extremely early effect of soil strength on leaf expansion (see below, results of experiment 1). For each treatment, three pots (nine plants) were sown with an intact seed, three others with seeds which had half of the endosperm cut off; i.e. half of the starch reserves, which are a major source of carbon for the expansion of the first leaf, had been removed. All seeds originally had the same weight. Sowing, growth conditions and measurements of growth were as described for experiment 1.

Fig. 1. Relationships between shoot size and soil penetrometer resistance (R, MPa). (a) Length of leaf 1 (l, mm) on day 2 after seedling emergence, (b) and (c) Leaf areas (s, cm²) on day 9 and day 21, respectively. Bars show the standard error of the mean. Regression lines for (a), (b) and (c), respectively, are: l = -4.09R + 52.5, r = -0.90, P < 0.001; s = -1.19R + 9.4, r = -0.95, P < 0.001; s = -8.98R + 65.4, r = -0.96, P < 0.001. Symbols are as follows: shape refers to soil bulk density (g cm⁻³): ○ 1.17; △ 1.29; □ 1.37; ▽ 1.41; ▽ 1.45; shade refers to soil water content (g g⁻¹ dry soil): open symbols 0.22 or 0.23; half-shaded 0.25; closed 0.27. All data are for high P level.

Results

Experiment 1

Seedling emergence

Seedlings emerged uniformly across treatments, within 95–100 degree days (2 days) after sowing, which is a typical value for wheat in the absence of water stress during germination. Seven per cent of the grains failed to germinate, but their distribution among treatments was random.

Development of leaf area

Fig. 1 shows shoot size at different times in relation to soil penetrometer resistance. The treatments for which there were ventilated and non-ventilated pots are combined, because similar growth was observed for the two sets of pots over the whole experiment (see Table 2). At all times, even as early as 2 days after emergence, leaf length and area were negatively correlated with soil strength. The equations for the regression lines are given in Fig. 1. Inspection of Fig. 1 shows that similar relations were obtained whether
soil strength was changed by varying soil water content or density. This observation is confirmed by statistical analysis: the distribution of residuals of the linear regressions (Fig. 1) are independent of soil water content and bulk density, all tests of analysis of variance being non-significant. We may therefore conclude that variations in soil strength account for the highly significant effects of bulk density and of soil water content on shoot growth that are shown in Table 2.

<table>
<thead>
<tr>
<th>Day</th>
<th>Soil water content (g g⁻¹ dry soil)</th>
<th>Soil bulk density (g cm⁻¹)</th>
<th>Mean length of leaf 1 (mm)</th>
<th>Mean plant leaf area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>0·22–0·23</td>
<td>1·17</td>
<td>30c</td>
<td>3.0f</td>
</tr>
<tr>
<td></td>
<td>0·25</td>
<td></td>
<td>45a</td>
<td>7.9a</td>
</tr>
<tr>
<td></td>
<td>0·27</td>
<td></td>
<td>43ab</td>
<td>6.1bc</td>
</tr>
<tr>
<td>9</td>
<td>0·22–0·23</td>
<td>1·29</td>
<td>35bc</td>
<td>6.7de</td>
</tr>
<tr>
<td></td>
<td>0·25</td>
<td></td>
<td>43ab</td>
<td>3·7bc</td>
</tr>
<tr>
<td></td>
<td>0·27</td>
<td></td>
<td>32c</td>
<td>3·7de</td>
</tr>
<tr>
<td>21</td>
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<td>1·37</td>
<td>42ab</td>
<td>4·7de</td>
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<td>40ab</td>
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</tr>
<tr>
<td></td>
<td>0·27</td>
<td></td>
<td>32c</td>
<td>5·7bc</td>
</tr>
</tbody>
</table>

Leaf expansion was affected by soil strength remarkably early. Significant differences were evident by day 2 (Fig. 1a), when the first leaf had not even reached 20% of its final length. Differences in relative rate of leaf expansion (RLER) among treatments varied from one day to the next, depending on what phase of their ontogeny the expanding leaves were at. However, over a period of several days, covering at least one phyllochron, the overall response was as shown in Fig. 2: RLER decreased with increas-
Soil Strength and Growth in Wheat Seedlings

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Fig. 3 shows leaf area as a function of time and of amount of phosphorus in the soil, for the extreme bulk densities at which phosphorus treatments were compared. It is notable that the reduction of leaf expansion with the higher bulk density occurred much earlier than any effect of low phosphorus level. A significant difference in leaf area between the two phosphorus levels was first observed on days 16 and 14 for densities 1.41 and 1.37 g cm$^{-3}$, respectively (the latter is not shown in Fig. 3), but was not observed until day 21 at the lowest density (1.29 g cm$^{-3}$). And the higher the bulk density the greater was the reduction in leaf area at low phosphorus level (8, 15, and 20% at final harvest for the bulk densities 1.29, 1.37 and 1.41 g cm$^{-3}$, respectively). However, the interaction between bulk density and phosphorus level was never significant.

**Fig. 3.** Response of leaf area to phosphorus level through time measured from seedling emergence, for two bulk densities: (a) 1.29 g cm$^{-3}$; (b) 1.41 g cm$^{-3}$. Solid line is for high P, broken line for low P.

**Rate of leaf appearance and individual rate of leaf elongation**

The leaf area of a plant is the product of two components — the number of leaves, and the average area per leaf — which depend on somewhat different processes and which have different responses to most environmental variables. To understand growth it is important to consider these components separately.

For any treatment the rate of leaf appearance was constant through time, but the average phyllochron ($\phi$) was longer the greater was the soil strength. It increased from 5 to 7 days between extreme treatments. For penetrometer resistances ranging from 1.5 to 5.5 MPa, the regression line for $\phi$ (day) as a function of soil penetrometer resistance, $R$ (MPa) was $\phi = 0.68R + 3.9$; $r = 0.90$, $P<0.001$. As in Fig. 1, variations of $\phi$ with soil strength were similar whether soil strength was varied by varying soil water content or density.

In each treatment the rate of elongation for a particular leaf (after its emergence from the enclosing sheath) was constant in all but the last few days of development, when growth abruptly ceased. The effect of treatment on the average rate of elongation of leaf 2 during the constant period of growth is shown in Fig. 4. Other leaves behaved similarly. The slower rate of elongation with increasing soil strength was not compen-
sated for by a longer duration of growth; final leaf area was therefore smaller (Table 3). Soil strength thus markedly affected leaf development throughout, from the primordial stage to full expansion. The size of this effect was similar for successive leaves (Table 3).

**Dry weight**

Fig. 5 shows the dry weights of roots and shoots at the final harvest. They were markedly affected by soil strength, the shoot rather more than the roots. The ratio of root to shoot increased by about 25% from low strengths (2·0-3·2 MPa) to high (4·8-5·5 MPa). As with leaf area, the important independent variable was penetrometer resistance rather than bulk density or soil water content per se.

Leaf weight and leaf area were reduced in similar proportions in response to high soil strength, i.e. specific leaf weight was constant. However, for penetrometer resistances greater than 3 MPa, the ratio of leaf area to total plant weight (leaf area ratio) at final harvest decreased with increasing soil strength, being 132±3 cm² g⁻¹ for R ≤ 3 MPa, and 114±2 cm² g⁻¹ for R = 5·5 MPa. Thus when growth of the whole plant is cont-

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**Table 3. Effect of soil strength on the dimensions of the successive leaves and on the number of visible leaves on the main shoot**

Dimensions are expressed as percentage of the control (i.e. treatment 3 as defined in Table 1)

<table>
<thead>
<tr>
<th>Leaf No</th>
<th>Final dimensions</th>
<th>Treatment No. Penetrometer resistance (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tr. 3 1.5 MPa</td>
</tr>
<tr>
<td>1</td>
<td>Area</td>
<td>100 (4.5 cm²)</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>100 (123 mm)</td>
</tr>
<tr>
<td>2</td>
<td>Area</td>
<td>100 (7.6 cm²)</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>100 (197 mm)</td>
</tr>
<tr>
<td>3</td>
<td>Area</td>
<td>100 (11.7 cm²)</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>100 (237 mm)</td>
</tr>
<tr>
<td>Number of visible leaves on day 21</td>
<td>4.1</td>
<td>3.7</td>
</tr>
</tbody>
</table>
sidered, the accumulation of dry weight was less sensitive to soil strength than was leaf expansion.

Net assimilation rate on a shoot basis was calculated over two periods between the different harvests (days 9–13 and days 15–21) according to Evans (1972). It was similar for all plants, regardless of soil strength (7·2 ± 0·2 and 5·9 ± 0·8 g m⁻² day⁻¹, for the first and second periods, respectively, at high P level; 6·6 ± 0·1 and 4·4 ± 0·4 g m⁻² day⁻¹, for the same two periods, at low P level). Therefore, total net assimilation rate (i.e. allowing for the dry weight accumulated in roots) must have been higher for plants grown at high soil strength, which had higher root to shoot ratios.

Concentrations of nitrogen, phosphorus, and soluble carbohydrates in the shoot

The concentrations of nitrogen and phosphorus (g per 100 g dry weight) measured in the shoot on day 15 were independent of soil strength (5·7 ± 0·2 and 5·0 ± 0·2 for N, 0·53 ± 0·1 and 0·27 ± 0·01 for P, at high and low phosphorus level, respectively). The concentrations measured a week later were still independent of soil strength at high phosphorus level (5·2 ± 0·1 for N; 0·43 ± 0·02 for P); at low phosphorus level, phosphorus concentrations were somewhat lower for the plants grown at the highest soil strength (0·17 against 0·20 at low strength for P; 4·1 against 4·4 for N), although we do not know if these differences are significant. The concentrations of soluble carbohydrates were more variable across treatments, but bore no relation to soil strength. Their only significant variation was in relation to phosphorus level: 24 g per 100 g dry weight and 10–16 g per 100 g dry weight at the low and high phosphorus levels, respectively.

Transpiration rate, leaf water potential, and leaf conductance to water vapour

There were large differences in the average transpiration rates across the range of soil strength. The transpiration rate fell sharply with increasing penetrometer resistance (Fig. 6). For penetrometer resistances lower than 3·5 MPa, this effect seemed especially large before day 13. For the periods considered in Fig. 6 (2 and 3 leaf stage) we estimated the leaf conductance to water vapour to be 0·47 mol m⁻² s⁻¹ at low soil strength, falling to 0·25 mol m⁻² s⁻¹ at high soil strength. Porometer measurements of the stomatal conductance at these stages gave a similar range of values, and showed that
differences in conductance already existed when the second leaf was just starting to elongate.

This fall in conductance was not associated with a change in leaf water potential ($\Psi$). $\Psi$ was high in all plants, ranging from $-0.65$ to $-0.5$ MPa, at all times. In the first two harvests it was not correlated with penetrometer resistance, but in the last harvest the two were positively correlated, i.e. the water potential rose with increasing penetrometer resistance (regression line: $\Psi = 0.0195R - 0.66$ MPa; $r = 0.71$, $P<0.05$).

![Fig. 6. Relationship between transpiration rate per unit leaf area ($g H_2O m^{-2} day^{-1}$) and soil penetrometer resistance over two periods: (a) day 9 to day 13; (b) day 16 to day 22 (days counted from emergence). Curves fitted by eye; symbols as in Fig. 1.]

**Table 4. Effect of the size of the seed endosperm and of soil penetrometer resistance on expansion of leaf 1**

<table>
<thead>
<tr>
<th>Soil penetrometer resistance (MPa)</th>
<th>Seed size</th>
<th>% emergence Day 7 after sowing</th>
<th>% emergence Day 8 after sowing</th>
<th>Rate of elongation of leaf 1 (mm day$^{-1}$)</th>
<th>Final length of leaf 1 (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>Half-seed</td>
<td>32</td>
<td>100</td>
<td>14.9a</td>
<td>83a</td>
</tr>
<tr>
<td></td>
<td>Whole-seed</td>
<td>9</td>
<td>90</td>
<td>19.2b</td>
<td>98b</td>
</tr>
<tr>
<td>3.0</td>
<td>Half-seed</td>
<td>60</td>
<td>100</td>
<td>15.3a</td>
<td>84a</td>
</tr>
<tr>
<td></td>
<td>Whole-seed</td>
<td>0</td>
<td>81</td>
<td>15.8a</td>
<td>79a</td>
</tr>
</tbody>
</table>
Experiment 2

Growth as influenced by soil strength and carbon reserves of the seed

Seedlings emerged earlier for the half seeds (Table 4), presumably because the cut seed imbied faster.

When the seed had been left intact, high soil strength reduced shoot growth, again well before the first leaf was fully expanded (Table 4). However, only at low soil strength did removal of half the endosperm reduce leaf elongation rate and final leaf size.

Discussion

Several things stand out in our results.

1. High soil strength markedly reduced the growth of the shoot, whether this was measured as leaf area or dry matter (Figs 1, 5). The roots were less affected.

2. The correlation between growth and soil strength (measured as penetrometer resistance) was similar whether the variation in strength was brought about by variation in bulk density or in water content, as was previously shown by Taylor and Ratliff (1969) for root growth. It was not affected by ventilation of the soil. These two observations together are good evidence that the effects of soil strength reported here were not confounded by the roots being anaerobic. The reduction of shoot growth by high soil strength was independent of phosphorus level for at least the first 11 days after emergence, by which time the second leaf was fully developed. During the same period, shoot growth at high strength was not further reduced by smaller carbon reserves in the seed.

3. The effects of soil strength on shoot growth occurred very soon after germination, although there was no mechanical resistance to the elongation of the coleoptile because the seed was covered with loose soil (see Methods). The effects were discernible even when the first leaf was only a few millimetres long, and they persisted, for the relative leaf expansion rate was also reduced by high soil strength.

4. The effect on leaf area was due partly to the leaves being smaller when fully expanded, and partly to a slower rate of appearance of the leaves.

5. The conductance of the leaves to water vapour was sharply reduced by high soil strength.

What are possible explanations for these effects on the early behaviour of the shoot? We have alluded to several in the Introduction, namely:

1. The root system is so restricted by the strength of the soil that it is unable to supply enough water or nutrients to the shoot. This is an unlikely explanation. Differences in the seedlings' behaviour occurred very early, at a time when the plants were still relying almost exclusively on their seed for nutrients. The phosphorus content of the soil had no effect on these differences for several days after they had become visible, and neither did the addition of other macro- and micronutrients (tested in a preliminary experiment). At the high phosphorus level, the concentrations of phosphorus and nitrogen in the shoot tissue remained similar regardless of soil strength, even though the growth rate was reduced by up to 60%; and they were higher than the critical concentrations measured in wheat or similar grasses (Masle-Meynard 1981; Smith et al. 1985; Meynard 1985).

Although nutrient deficiency was an unlikely cause of the onset of the effects of soil strength on growth, it is possible that nutrient deficiency may develop later as a consequence of the restriction of root growth caused by soil strength, and thus may limit shoot growth in the long term. This is a likely explanation for the increased severity and earliness of the phosphorus deficiency at low phosphorus level when soil strength was high (Fig. 3).

The supply of water to the leaves seemed adequate, for the leaf water potentials measured throughout the experiment (−0.65 to −0.5 MPa) were much higher than any
values that we are aware of for wheat leaves whose growth has been reduced by water deficiency. Also leaf water potential was generally uniform across treatments or even higher at high soil strength (final harvest), even when the plants were growing more slowly than at low soil strength. We cannot completely exclude the possibility that a larger overall hydraulic resistance in plants growing in tough soil might have induced stomatal closure, thus maintaining $\Psi$ approximately constant. However, that such an effect could result in $\Psi$ actually increasing, as in the final harvest, seems very unlikely. We therefore conclude that the lower leaf conductance in the plants growing in tough soil was not induced by changes in the water status of the leaves. It is nevertheless possible that growth may have been limited by insufficient turgor if, say, the osmotic pressure of the growing cells happened to be lower at high soil strength, but we have no information on the turgor of these cells.

(2) The growth of the shoot is limited by an insufficient supply of carbohydrates, because a higher proportion of carbohydrate is directed to the roots, or because the photosynthetic rate is small due to a small stomatal conductance. Both possibilities are unlikely explanations for the early onset of the effects of soil strength on shoot growth. These effects occur when the seed is still the main source of carbon for growth, and starch and the enzymes necessary for its breakdown are presumably present in large amounts. Removing a large part of this starch (experiment 2) did not produce any additional reduction of growth in leaf area or dry weight.

However, it is possible that carbohydrate may limit shoot growth at a later stage: although the net assimilation rate apparently increased at high soil strength, the carbon supply to the shoot may nevertheless have been limiting, because a higher proportion of the carbohydrate available to the whole plant is required for the growth of the roots (because of the higher root/shoot ratio). Conclusive evidence on this possibility would require measurements of shoot and root growth at various soil strengths combined with various rates of carbon supply to the plant.

(3) The shoot growth is controlled by hormones produced in the roots. This is the only conclusion left if the onset of the slower growth cannot be explained by a reduced supply of water or nutrients, or by an excessive demand for carbohydrates by the roots, or by the roots being anaerobic. There is increasing evidence that hormones control the response of root elongation to mechanical resistance. Hormones involved might include auxins and ethylene (Kays et al. 1974; Lachno et al. 1982). Cytokinins and gibberellins also may play a role, as suggested by Richards and Rowe (1977) and Carmi and Heuer (1981), respectively, for plants grown on restricting volumes of soil, which in several respects behave similarly to plants grown at high soil strength.

The response of shoot growth to soil strength described here corresponds to that obtained with soil compaction in the field, in its earliness and also in its nature (see for example, Chevalier and Cih 1986) or Brereton et al. (1986) on barley; Whiteley and Dexter (1982) on wheat; Tardieu (1987) on maize. Despite large effects on early growth, it does not necessarily follow that high soil strength results in lower final yield. Indeed, from the reduction of leaf area and the fall in stomatal conductance, one can expect that crops grown on soils of high strength will use a reduced amount of water; such behaviour has been reported in several field studies (e.g. Brereton et al. 1986; Chevalier and Cih 1986; Tardieu 1987). It is also possible that, in dry environments, the growth rate may be improved in later stages, because of more water remaining available in the root zone. The interactions among tillage treatment, seasonal rainfall, and yield, observed by Mason and Fischer (1986), namely that direct-drilled crops yield more than conventionally cultivated ones in dry years, but less in wet years, is consistent with this idea, for the direct-drilled crops experience a much higher soil strength during establishment.

The growth response obtained in our study is more severe than that observed in most field experiments on compaction. One reason for this severity may be that in our con-
ditions the roots experienced high soil strength as soon as they began to elongate. Furthermore, soil strength in a given pot was similar for all roots, and was maintained constant through time, whereas in the field it is not. This is another complication, because there is circumstantial evidence that the conditions experienced by only part of the root system may influence the behaviour of the shoot (see Crossett et al. 1975 and Whiteley and Dexter 1982 for soil strength; Blackman and Davies 1985 for water stress). But the way the plant integrates variable conditions around its roots is at present unknown.

To identify the hormones that might be involved in regulating shoot growth by roots when soil strength varies, and to demonstrate how they work in a complex metabolic network, is very difficult (Trewavas 1986), but is fundamentally important to our understanding of how the plant adapts to its environment. The responses to high strength observed in our experiment — reduced growth, mainly of the shoot, stomatal closure, higher net assimilation rate — suggest that the plant might have evolved an early warning system which results in conservative behaviour where continued poor root growth could lead to a shortage of water in the shoot.

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References

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