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The effects of soil compaction on wheat seedling root growth are specific to soil texture and soil moisture status

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ABSTRACT

Soil structure is a crucial soil physical property that determines a soil's ability to support the growth and development of plants. Soil compaction modifies soil structure by reducing pore space between soil particles thereby leading to a denser soil fabric. This often limits root growth by increasing soil strength and penetration resistance requiring roots to increase the energy needed to elongate and explore deeper soil. Apart from soil compaction, soil moisture also plays an important role in determining how resistant soil is to root penetration. An understanding of how the synergy of both compaction and moisture content affect root growth is essential to improving plant productivity. We used wheat (*Triticum aestivum*) seedlings to investigate the differences in root architectural properties using X-ray Computed Tomography imaging under three different compaction levels (1.3, 1.5 and 1.7 Mg m^{-3}) maintained at two different water contents (100% and 70% of field capacity). This was performed on soils of two different textures, a sandy loam and a sandy clay loam. Soil compaction to 1.7 g cm^{-3} significantly reduced root length, volume and surface area compared to lower compaction levels. Increased soil compaction also resulted in increased root growth angle in the sandy clay loam. Compaction reduced gas diffusivity in both soils (as determined by modelling). Soil moisture on the other hand had a significant impact on average root diameter; plants grown at 100% of field capacity had a higher average root diameter than those at 70% field capacity. Compaction up to 1.7 Mg m^{-3} adversely effected wheat root growth in both soil textures regardless of moisture content.

1. Introduction

Soil structure, the spatial arrangement of soil particles and aggregates, is a key determinant in the growth and development of plants (Bronick and Lal, 2005). The maintenance of an optimal soil structure is key as it determines crop yield via the mediation of root access to soil resources (Rabot et al., 2018). Soil compaction is a major form of soil structural degradation that is often brought about by actions that force soil components together at the expense of air, such as the frequent use of heavy machinery, excessive tillage and animal trampling (Augustin et al., 2020; Auler et al., 2016; Pillai and McGarry, 1999). A degree of soil compaction in itself is often useful to ensure good root-soil contact, especially during seedbed preparation, however, excessive soil compaction is detrimental to root growth and development which directly affects nutrient uptake and consequently plant yields (Kuht and Reintam, 2004; Lipiec and Stepniewski, 1995; Liu et al., 2021; Tracy et al., 2012a,b).

The impact of soil compaction on root growth mainly emanates from increased mechanical impedance that arises from the reduction of pore space in a compacted soil which restricts root elongation (Czarnes et al., 1999; Dexter and Hewitt, 1978; Whiteley et al., 1982). This increases soil strength and makes it more difficult for roots to penetrate and access soil resources in deeper soil layers. Recently, Pandey et al. (2021) demonstrated root growth retardation in compacted soils is linked to elevated ethylene concentrations in the soil pores around the root, as ethylene movement is restricted by lack of diffusion away from the root

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through the soil rather than as a direct response to mechanical stress imposed by the soil. Furthermore, the impact of compaction varies within and between species due to differences in root penetration capacity (Burr-Hersey et al., 2017; Colombi and Walter, 2017; Helliwell et al., 2019; Orzech et al., 2021). Generally, compaction leads to reduced root growth which subsequently limits the ability of roots to acquire essential nutrients. The morphology of plant roots is also altered as a response to increased soil strength (Tracy et al., 2012a,b). Axial roots become thicker as they attempt to force themselves through harder soil layers whilst lateral roots are severely reduced (Atwell 1990; Bengough et al., 2006). Root growth rates are also severely reduced by soil strength with a gradual decrease in root growth from 1 MPa to an almost complete elimination of root growth occurring at soil strengths higher than 5 MPa (Passioura, 2002).

The impact of soil compaction on root growth is also dependent on other soil physical properties such as soil moisture and texture (Gilker et al., 2002; Liu et al., 2021). The bulk density at which root activity is affected varies between different soil textures, mainly due to differences in pore size. For example bulk density in clay soils are often much lower than they are for sandy soils (Brady and Weil, 2017). Recently Mondal and Chakraborty (2023) showed that while compaction could reduce wheat root length and volume by up to 50% this effect was significantly reduced in a clay soil over a sandy soil, especially when water was limited. Similarly, as increased soil moisture reduces soil strength, soils at contrasting bulk densities may support root growth in different ways (Bengough et al., 2011). It is thus necessary to study soil compaction at specific soil moisture conditions.

Previous experiments have studied the effects of soil bulk density or soil water status on plant growth and yield (e.g. Houlbrooke et al., 2010; Shaxson and Barber, 2003; Stirzaker et al., 1996), but few have combined them together, especially to study early root growth. We aimed to examine the combined impact of compaction and soil moisture on root growth in wheat seedlings. We used three different levels of soil compaction combined with two different soil moisture regimes across two different soil textures. We obtained root growth metrics from X-ray Computed Tomography (CT) scanning. We hypothesised soil compaction would be a major limiting factor to root growth with soil moisture moderating its impact.

2. Materials and methods

2.1. Soils properties and preparation

Soils from two different textures, a sandy loam soil and a sandy clay loam soil were sampled from two field sites experimental farm at Bunny, University of Nottingham, (Nottinghamshire, UK, 52.52°N, 1.07°W). The soils were air-dried and passed through a 2 mm sieve to remove clods and large aggregates. Each soil was uniformly packed into polyvinyl chloride (PVC) columns (100 mm height × 51 mm diameter, with a nylon mesh base of ca. 40 μm) to three bulk densities namely of 1.3 (uncompacted treatment), 1.5 (moderate compaction) and (high compaction) 1.7 Mg m^{-3}. Each column was compacted c. 20 mm at a time to a depth of 80 mm in 4 layers of soil. After each compaction layer, the surface was lightly scarified to ensure homogeneous packing and hydraulic continuity within the column. The columns were then saturated from the base for 2 days and then allowed to freely drain for another 2 days, gravitationally. The notional field capacity water content of each soil core was then calculated.

2.2. Seedling growth experiment

Bread wheat (*Triticum aestivum* L.) seeds, variety EDSAR, were germinated in a dark chamber for 48 h. Uniform wheat seedlings were selected (determined by radical length) and planted in the centre of each soil column with one seed planted per pot. The plants were then grown for 7 days in a controlled environment chamber (Conviron A1000, Canada) set to a temperature of 18 °C (day)/12 °C (night) with supplemental lighting on a 12hr/12hr day/night cycle. The soil water content was maintained by weighing and watering using a pipette every day to ensure it remained close to 70% (≈13% (w/w) for sandy loam soil and 17% for the sandy clay loam soil) and 100% (≈18% (w/w) for sandy loam soil and 24% (w/w) for the sandy clay loam soil) of previously determined notional field capacity throughout the experiment. Three replicates for each treatment combination (soil texture x bulk density x soil moisture) were prepared resulting in a total of 36 soil columns.

2.3. CT scanning, image analysis and data collection

The columns were scanned on the eighth day after transplanting using an X-ray μCT scanner (v|tome|x M 240 kV, Waygate Technologies, Wunstorf, Germany), using an X-ray tube electron acceleration energy of 140 kV and current of 185 μA. Scans were performed in 'Fast mode' where single radiograph images are collected as the sample rotates continuously through 360°. Each scan acquired 1660 projection images, with an exposure timing of 333 ms per image. Scan time for the entire column was around 12 min. A spatial resolution of 32 μm was used in all scans and image reconstruction was performed using Datos|REC software (Waygate Technologies, Wunsdorf, Germany). Wheat seed germination, planting, culturing and X-ray μCT scanning were staggered using a randomised block design for 6 days to ensure the plants were at the same growth stage when scanning was performed. After scanning, the roots were washed from the soil and analysed using WinRHIZO® 2005c scanning equipment and software following the method of Tracy et al., (2011). The images obtained were compared with the output from the X-ray μCT scanning.

Image visualisation and root segmentation were conducted using VG StudioMAX® Version 2.2 (Volume Graphics GmbH, Heidelberg, Germany). The "Region Growing" tool in VG StudioMAX® was used to interactively extract roots from the slices as has been described in Helliwell et al. (2019). The total root volume and closed surface area were obtained from VG Studio MAX®. Total root length, root diameter and root angle were obtained using RooTH software tool as described in Mairhofer et al. (2017). Pore thresholding was carried out in AVIZO® 9.0.1 software using the auto-threshold algorithm with the isodata critereon selected. After thresholding, the pore spaces were then identified in the separate objects module using Chamfer (conservative) method and a marker extent of 2 for delineation. The pore size distribution and pore connectivity was then computed using the Label analysis module using a 3D interpolation (Houston et al., 2017).

2.4. Penetrometer resistance

Penetrometer resistance measurements were carried out using an Instron 5944 load frame fitted with a 100 N load cell, 15 cm diameter lower support anvil and 3 jaw chuck running Instron Bluehill Universal v4.03 software. The soil resistance was measured by forcing a needle with a tip diameter of 2 mm and a 60° angle at a steady state through the soil whilst measuring the force required to penetrate through a depth of 70 mm. The maximum penetrometer resistance measurable using this equipment was 31.83 MPa which was lower than that required to penetrate sandy clay loam soil at the highest compaction level (1.7 Mg m^{-3}).

2.5. Gas diffusivity

Gas diffusivity was calculated through pore-scale simulation of gas flow through the pore space revealed in the 3D X-ray CT images. Gas flow is diffusive and its movement in pore space was simulated using a lattice Boltzmann model previously developed in Li et al. (2017). The diffusivitiy of each soil sample was calculated based on the simulated gas concentration and diffusive flux in each voxel (Zhang et al., 2016).

2.6. Statistical analysis

The statistical analyses for these experiments were performed using GraphPad Prism 8.0.1. The effects of the level of compaction, soil texture and water regime had on wheat root growth parameters were evaluated using a multi-factor analysis of variance. Tukey's post hoc tests were used to evaluate for significant differences between treatments ($P < 0.05$).

3. Results

3.1. Root length

Soil compaction at 1.7 Mg m^{-3} resulted in a significant ($P = 0.0001$) reduction in wheat seedling root length (average 138 mm per plant) for both soil textures and moisture regimes as compared to compaction at 1.3 and 1.5 Mg m^{-3} as shown in Fig. 1A. Plant root lengths were reduced on average by 60% and 54% as compared to 1.3 and 1.5 Mg m^{-3} treatments, respectively. There was r no significant difference between the 1.3 and 1.5 Mg m^{-3} compaction levels with average root lengths of 328 and 301 mm per plant, respectively. There was also a significant difference ($P = 0.0063$) in root length between the different soil moisture contents with plants grown at 70% of field capacity having a root length that was on average between 14% higher than those grown in soil at 100% of field capacity (hereafter referred to as 70%FC and 100%FC respectively). There was no statistically significant interactions for root length measurements.

3.2. Root volume and surface area

Root volume and surface area exhibited a trend similar to that observed with root length with roots growing in soils at a bulk density of 1.7 Mg m^{-3} having significantly reduced root volume and surface area as compared to plants grown at 1.3 and 1.5 Mg m^{-3} as shown in Fig. 1B and E. Root volume of plants grown at 1.7 Mg m^{-3} were on average 10.55 mm^3, which was 43% lower than that of plants grown in soil at 1.3 and 1.5 Mg m^{-3}, which had an average volume of 18.62 and 18.39 mm^3 respectively. The average root surface area of plants grown at 1.7 Mg m^{-3} was 380 mm^2 which was 52 and 45% lower than that of plants grown at 1.3 and 1.5 Mg m^{-3} respectively. Unlike root length, however, root volume and root surface area were similar at both moisture levels ($P = 0.649$). Root volume and surface area were not significantly affected by soil texture ($P = 0.889$). There was also no interaction between the different factors for both measures.

3.3. Average root angle

Root angle was shallower in plants grown at 1.7 Mg m^{-3} (on average 67°) as compared to those grown at 1.3 and 1.5 Mg m^{-3} (on average 45.3 and 45.1° respectively) however, these were only statistically in the sandy clay loam soil (Figs. 1D and 2). There was a significant interaction between root angle and soil texture with the finer textured soil exhibiting shallower root angles with increased compaction. Soil moisture regime had no significant impact on root angle and there were no significant interactions for all three factors for root angle.

3.4. Average root diameter

The average root diameter was mainly affected by the soil moisture regime with a significant ($P = 0.001$) increase in root diameter at 100% FC as compared to soils maintained at 70%FC (Fig. 1E). Plants growing at 100%FC had an average diameter of 552 µm as compared to 433 µm in those grown at 70%FC. This represented a 22% increase in root diameter when plants were grown at higher soil moisture. Surprisingly, bulk density and texture did not play a significant role in determining the average root diameter. There was also no interaction between the different factors for average root diameter.

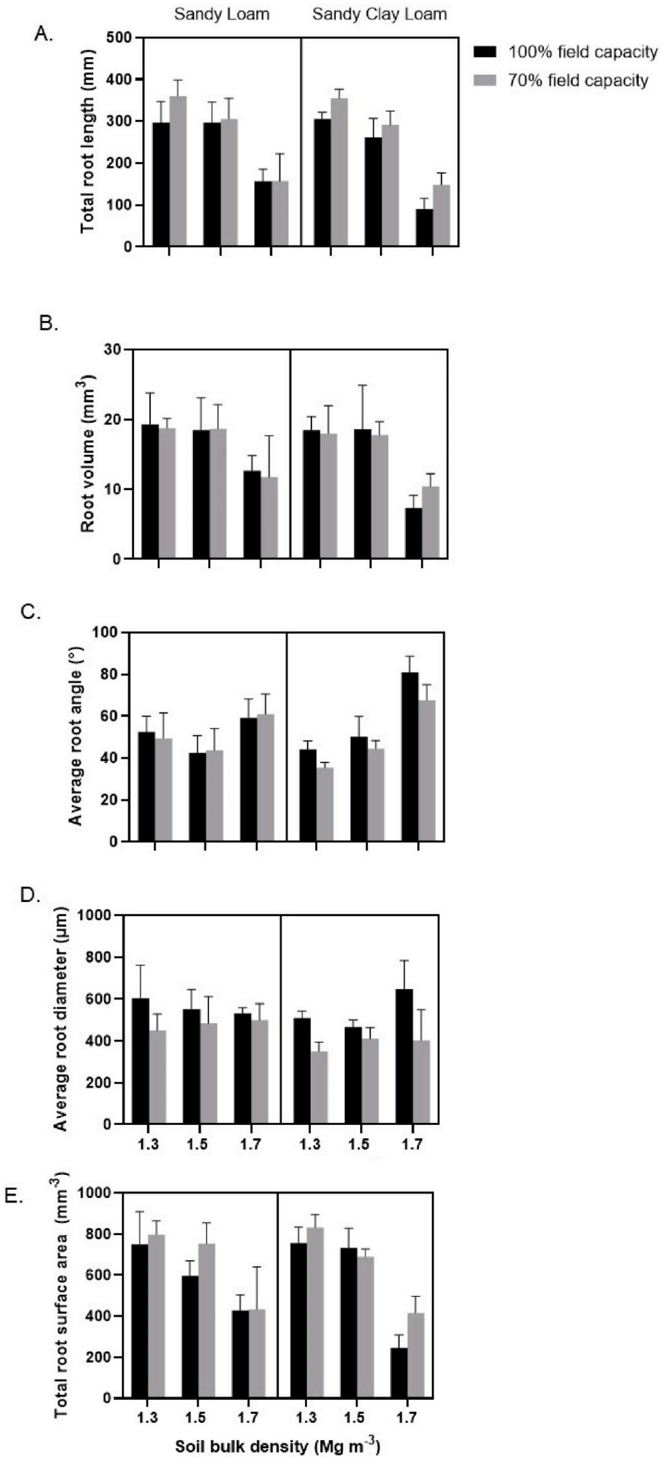

Fig. 1. The effects of soil bulk density and soil moisture regime on A. root length, B. root volume, C. average root angle, D. average root diameter and E. total surface area of 8-day wheat grown in either Sandy Loam or Sandy Clay Loam soil.

3.5. Pore size distribution

The pore size distribution of the soils varied significantly with bulk density (Fig. 3) as soils at the lowest compaction level (1.3 Mg m^{-3}) had a greater proportion of larger pores (>3 mm) as compared to soil at higher bulk densities. These pores contributed to more than 50% of the

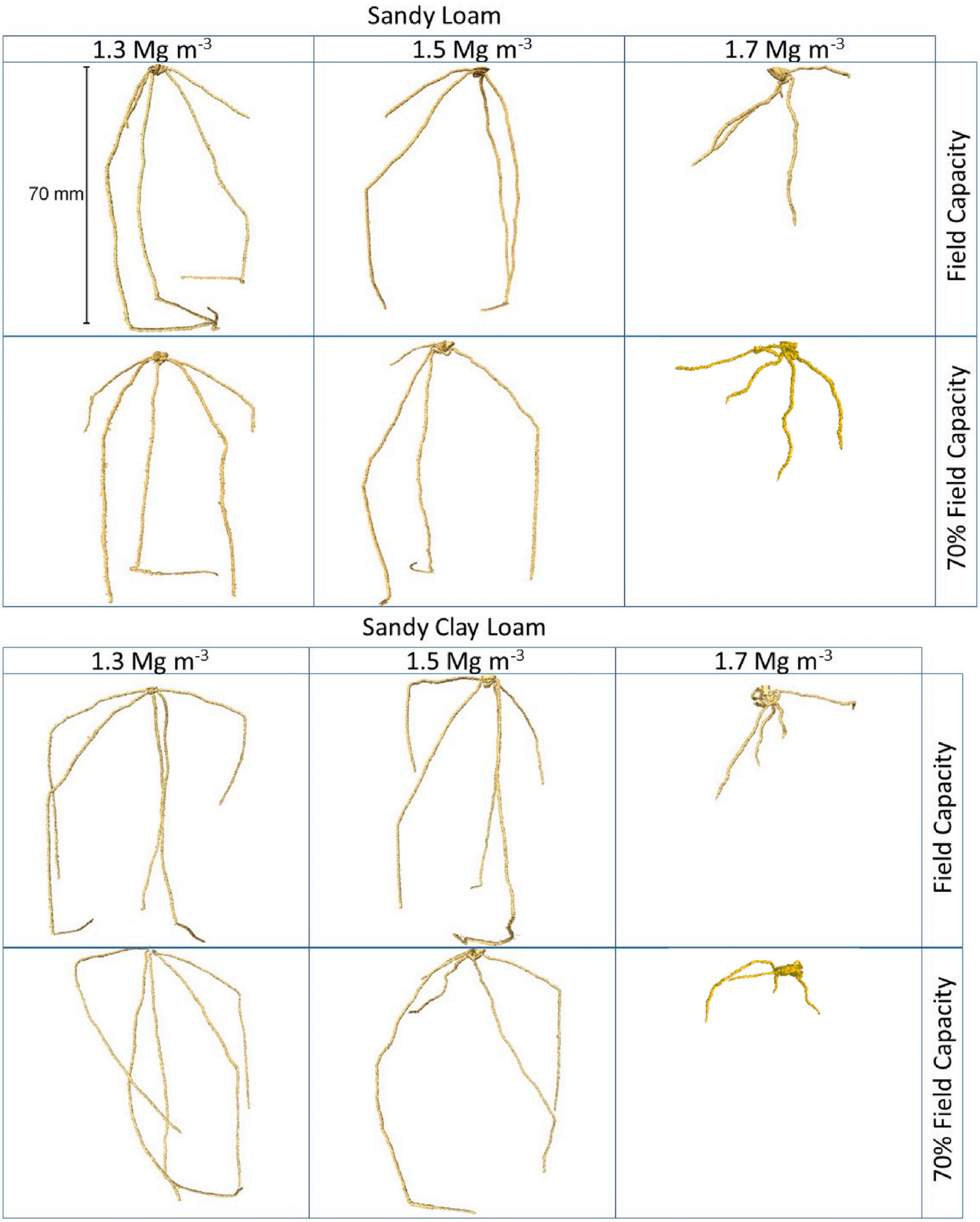

Fig. 2. Images of the root system architecture of wheat seedlings grown in Sandy Loam and Sandy Clay Loam soils at different bulk densities and moisture regimes.

total pore volume in soils at this compaction level in both soil textures. At the 1.5 Mg m^{-3} and 1.7 Mg m^{-3}, pores were more evenly distributed with the contribution of smaller pores to total pore volume being increasingly more dominant as the compaction level increases. Sandy loam soil had a higher proportion of larger pores at all the compaction levels.

3.6. *Penetrometer resistance*

Penetrometer resistance ranged from 1.3 MPa to 29 MPa and was dependent on bulk density, texture and soil moisture content (Fig. 4). The sandy clay loam soil had significantly higher ($P = 0.027$) penetrometer resistance as compared to the sandy loam at similar bulk densities in soils at 70%FC, whilst there were no significant differences at 100%FC. The penetrometer resistance in the sandy clay loam at the bulk density of 1.7 Mg m^{-3} exceeded the maximum limit of the penetrometer. The soils at 100%FC had significantly ($P < 0.001$) lower penetrometer resistance as compared to those at 70%FC with a difference of at least 50% between the different moisture contents in both textures.

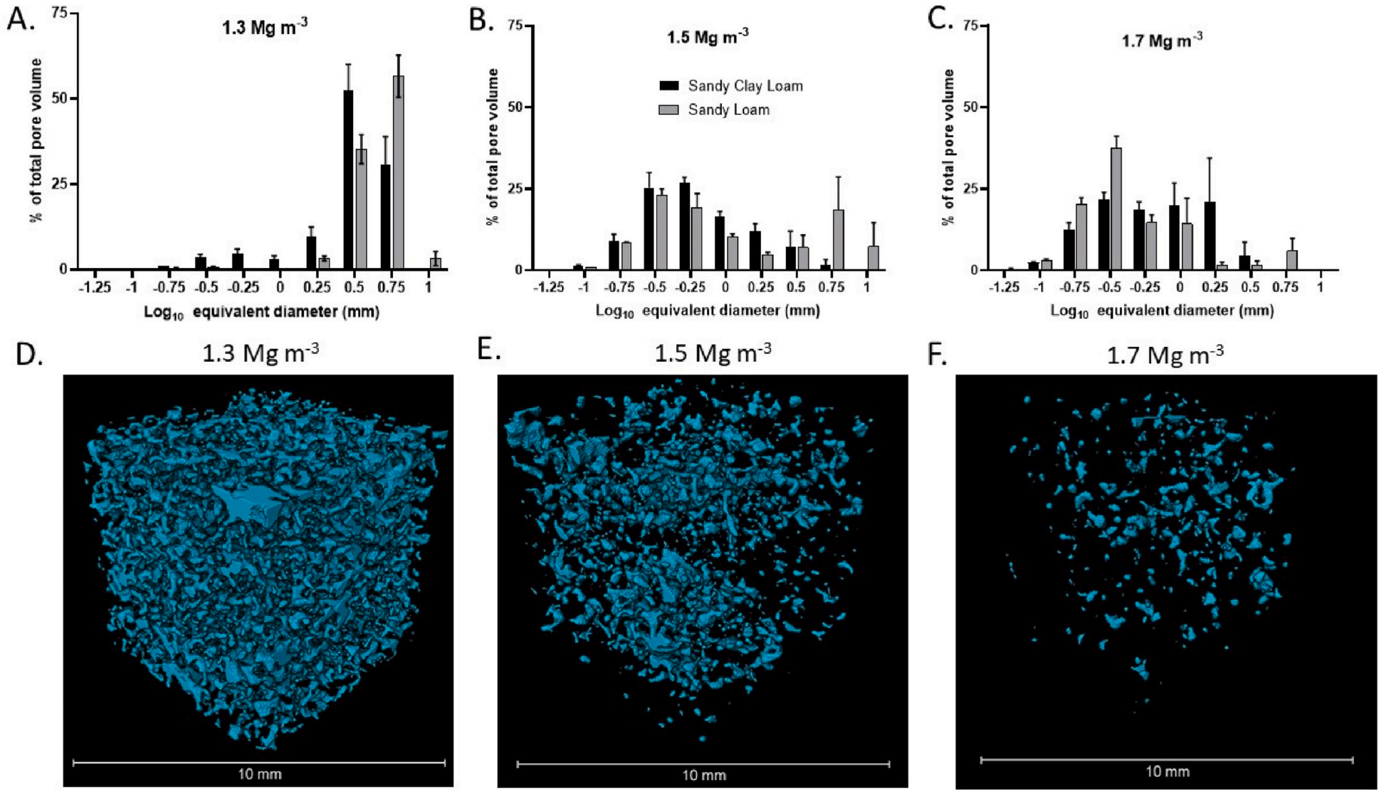

Fig. 3. Average pore size distribution of cores at A) 1.3 Mg m^{-3}, B) 1.5 Mg m^{-3}, and C) 1.7 Mg m^{-3} in Sandy Clay Loam and Sandy Loam soil. D, E, F shows example three-dimensional visualisations of the pores at different compaction levels in the Sandy Loam soil.

3.7. Gas diffusivity

Gas diffusion was derived from soil pore network data obtained by X-ray CT imaging. At 32 μm resolution most pores in the images for soils at 70%FC are likely to air-filled, while for soils at 100%FC some pores might be filled by water. As it is not readily possible to distinguish between water and air filled pores at this resolution, we calculated the gas diffusivity assuming all pores were air-filled (Fig. 5A). We then plotted the change in diffusivity with porosity to elucidate how the diffusivity would vary according to a change in soil water content (Fig. 5B). As we observed no significant difference in the diffusion coefficient between the 70% and 100%FC we pooled the results for the two water treatments in Fig. 5. Diffusive flux in the pore space depends on molecular diffusion which varies between gases. As ethylene is a crucial gas affecting root growth and penetration, in the pore-scale simulation we used the molecular diffusion coefficient of ethylene at 25 °C and one atmospheric pressure to simulate gas diffusion and calculate gas diffusivity. Gas diffusivity deceased exponentially as porosity decreased (i.e. as bulk density increased), thus the impact of bulk density on diffusivity of ethylene is more profound than on soil porosity. Significant differences in diffusivity of ethylene between the soil types were observed at the lowest bulk density only (Fig. 5).

4. Discussion

A high level of compaction had a negative effect on early wheat root growth which was observed as a reduction of root length, volume and surface area at the highest compaction level (1.7 Mg m^{-3}). This was consistent for both soil moisture regimes and textures implying that at this compaction level, plant roots struggle to penetrate the soil regardless of other soil conditions pertinent to root growth similar to Bengough et al. (2006) and Bingham and Bengough (2003). Surprisingly, soil bulk densities at 1.5 Mg m^{-3} and 1.3 Mg m^{-3} did affect root diameter in the different soils, suggesting these lie within the optimal range for root growth for wheat, or at least one in which wheat plants can readily adapt to (noting that only one variety was examined here). Interestingly, Tracy et al. (2012a,b) found the highest root growth at a bulk density of 1.5 g cm^{-3} as compared to soil at 1.1 g cm^{-3} in wheat seedlings suggesting low bulk densities are not favourable. In our experiments, however, wheat root growth in soil with a bulk density of 1.3 Mg m^{-3} was only marginally higher than root grown at 1.5 Mg m^{-3} which suggested that within our optimal range, lower bulk densities were preferable. Atwell (1990) found that wheat roots growing at a bulk density of 1.6 Mg m^{-3} in the field were generally shorter, thicker and more contorted than those growing under less compacted conditions, We found a consistent increase in penetrometer resistance as bulk density increased in both soils explained by the decrease in pores size with the reduction of larger pores resulting in an increased force required for penetrometer penetration (Bengough and Mullins, 1991; Menon et al., 2015). There was also a consistent reduction in penetrometer resistance as moisture content increased, explained by decreased friction between soil particles and the penetrometer probe thus reducing the soil's resistance to penetration. Soils with increased moisture content are also more prone to aggregate deformity which can increase their penetrability (Ball et al., 2005; Clark and Barraclough, 1999). Our penetrometer resistance values were significantly higher than those reported to limit cereal root growth (about 1.3 MPa), however, it is known that penetrometer resistance is often several magnitudes greater than those imposed by growing roots (Bengough and Mullins, 1990, 1991; Whiteley et al., 1981). Our results were in line with those reported in young wheat seedlings by Masle and Farquhar (1988) (range between 1.5 and 5.5 MPa) albeit in a silty loam soil. In our experiment, the penetrometer resistance was highly dependent on soil texture with roots growing at higher resistance levels in sandy clay loam soil as compared to the sandy loam soil. This is most likely due to the increased clay content in the former which can be displaced more readily than coarser material (Bodner et al., 2014).

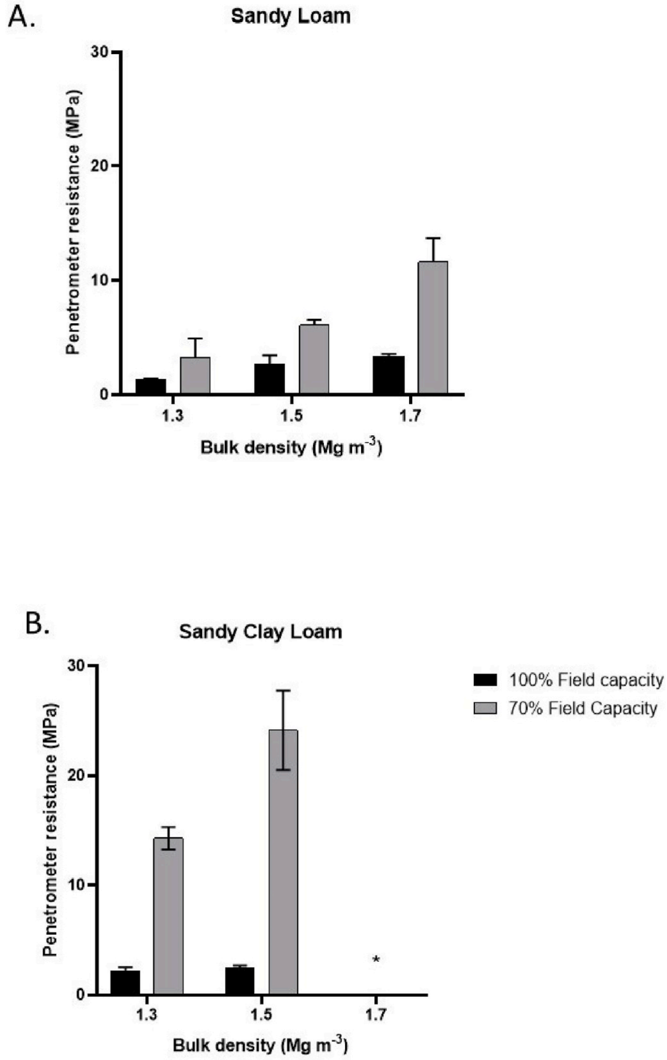

Fig. 4. Penetrometer resistance of cores at different moisture contents in A) Sandy Loam and B) Sandy Clay Loam soil. * Indicates values that could not be measured as they exceeded the maximum penetrometer resistance of the equipment used.

Soil moisture regime played an important role in determining root growth as it interacted with bulk density and hence pore size distribution to affect total root length. The lower soil moisture regime (70%FC) resulted in consistently higher total root length across all soil types and bulk densities. This is an interesting result as field capacity is often considered an idealised soil water status for plant growth in terms of both water and air availability, although field capacity in a soil column is likely to be greater than in the field due to constrained drainage (Khalil et al., 2020). This suggests the wheat seedlings preferred the increased aeration in these soils at 70%FC which may also improve the diffusion of ethylene gas that has been shown to accumulate in roots grown in compact or waterlogged soils (Ali and Kim, 2018; Pandey et al., 2021). Soil moisture regime was also a factor in determining average root diameter, surprisingly more so than bulk density which has been shown to be important by Tracy et el. (2012) with higher soil moisture content increasing wheat seedling root diameter. As was postulated by Khalil et al. (2020) in a study also using wheat, maintaining soil moisture at 100%FC may reduce root growth without affecting photosynthetic processes albeit in a pot study.

Average root diameter was consistently higher in soils maintained at field capacity. This result was surprising as we hypothesised root diameter would be lower under higher moisture contents as increased soil moisture reduces soil strength thus minimising root radial expansion (Logsdon, 2013; Logsdon et al., 1987). Although it is possible that this was influenced by ethylene, which is produced more under wetter conditions and may have retarded growth (Lang et al., 2023). Growing under reduced moisture conditions can negatively impact on root growth, particularly in terms of lateral root growth. Similarly, we also expected the root diameter to have been thicker in the more compact soils with higher soil strength (Bengough et al., 2011). However, surprisingly soil bulk density did not seem to have an impact on root thickness suggesting moisture content and aeration status played a more important role in determining root thickness.

Root angle is an important root system architectural property that determines the direction of root elongation into the soil with a steeper root angle often resulting in deeper growing roots (Richard et al., 2015; Uga et al., 2013). Bulk density significantly affected root angle as soils with higher bulk densities produced steeper root angles. This translated into roots growing more laterally in response to soil hardness. This may have been due to the inability of root tips to grow vertically as the strength of the soil below was more resistant to root penetration. Our results are consistent with Tracy et al. (2012a,b) who also reported higher root angles in response to increased soil strength. This may lead to poor water and nutrient uptake as roots do not explore the entire depth of the soil preferentially exploring shallow depths of soil.

By pore network modelling we showed an important, significant

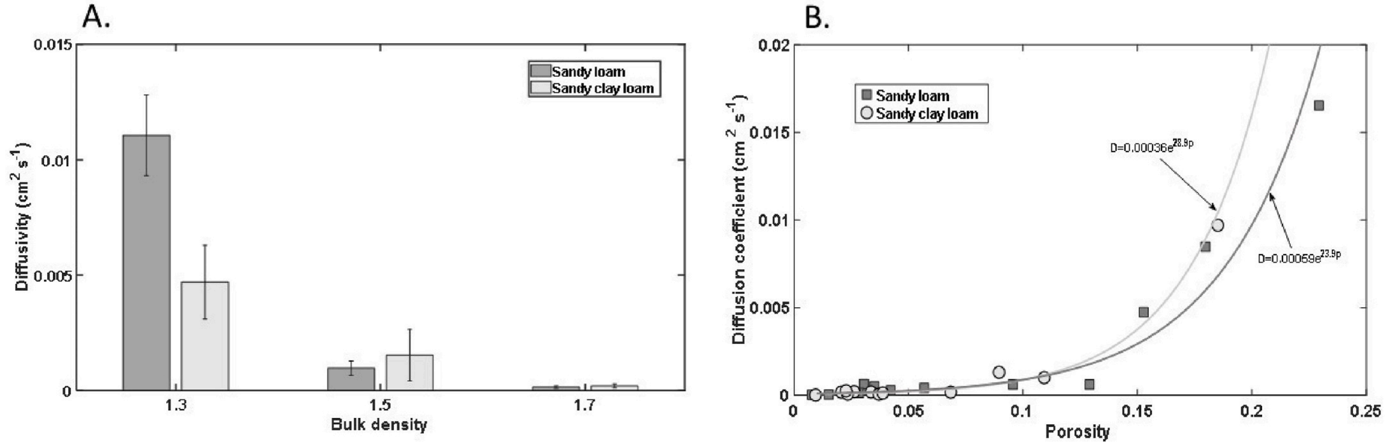

Fig. 5. (A) Variation in diffusivity of ethylene between different soil types and bulk densities (Mg m^{-3}) as derived from lattice-Boltzmann modelling. (B) The diffusivity of ethylene increases with porosity but differently between the two soil types.

increase in diffusivity of ethylene as bulk density decreases for both soils because the gas diffusion coefficient increases with air-filled porosity approximately exponentially (Fig. 5B). The observation that diffusion is reduced with increased bulk density is consistent with the previous finding that roots penetrate deep in soil with high diffusivity for ethylene (Pandey et al., 2021), though reduced penetration resistance also plays an important role. There appears to be a critical value for ethylene diffusivity below which the ethylene starts to inhibit root growth penetration. In this experiment, this critical diffusivity is approximately 0.002 cm^2 s^{-1}. The impact of compaction was more noticeable in the sandier soil due to the larger pores in the lower bulk density treatments which are lost following moderate and major compaction. As diffusivity increases with the proportion of air-filled pores exponentially for both soil types (Fig. 5B), a small decrease in air-filled porosity due to an increase in soil water content or soil compaction could substantially reduce the diffusivity of ethylene and root growth as a result.

5. Conclusions

The interactions between soil type, bulk density and soil water content are complex and not always as hypothesised. Higher soil compaction generally reduced root growth under both soil moisture conditions. However, the wheat plants we examined performed similarly at both low and moderate bulk densities, each of which could be considered compact if under field conditions. This is important as reducing tillage is gaining popularity as part of the regenerative agriculture movement and the harder soils that emerge under these conditions have been considered potentially problematic for germination and establishment. We identified roots grown under drier conditions can grow deeper into the soil due to their steeper root angle. Under a changing climate where soil moisture is likely to be limiting and irrigation available at a significant cost this could be important, especially when calculating the soil moisture budget. We also observed that the diffusion of ethylene is reduced with increased bulk density which was more noticeable in sandy soils due to a higher proportion of large pores.

CRediT authorship contribution statement

Cailian Yu: Data curation, Formal analysis, Methodology, Writing - original draft. **Tinashe Mawodza:** Visualization, Writing - original draft, Writing - review & editing. **Brian S. Atkinson:** Methodology, Writing - review & editing. **Jonathan A. Atkinson:** Conceptualization, Formal analysis, Writing - original draft. **Craig J. Sturrock:** Funding acquisition, Investigation, Methodology, Validation, Writing - original draft. **Richard Whalley:** Conceptualization, Funding acquisition, Writing - original draft. **Malcolm J. Hawkesford:** Conceptualization, Funding acquisition, Writing - original draft. **Hannah Cooper:** Visualization, Writing - original draft, Writing - review & editing. **Xiaoxian Zhang:** Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Hu Zhou:** Data curation, Formal analysis, Investigation, Validation, Visualization, Writing - original draft. **Sacha J. Mooney:** Conceptualization, Methodology, Project administration, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Ali, S., Kim, W.C., 2018. Plant growth promotion under water: decrease of waterlogging-induced ACC and ethylene levels by ACC deaminase-producing bacteria. Front. Microbiol. 9, 1096. https://doi.org/10.3389/FMICB.2018.01096.

Atwell, B.J., 1990. The effect of soil compaction on wheat during early tillering. New Phytol. 115, 29–35. https://doi.org/10.1111/j.1469-8137.1990.tb00918.x.

Augustin, K., Kuhwald, M., Brunotte, J., Duttmann, R., 2020. Wheel load and wheel pass frequency as indicators for soil compaction risk: a four-year analysis of traffic intensity at field scale, 2020 Geosci. 10. https://doi.org/10.3390/GEOSCIENCES10080292. Page 292 10, 292.

Auler, A.C., Galetto, S.L., Hennipman, F.S., Guntzel, E.D., 2016. Soil Structural Quality Degradation by the Increase in Grazing Intensity in Integrated Crop-Livestock System 1–7.

Ball, B.C., Bingham, I., Rees, R.M., Watson, C.A., Litterick, A., 2005. The role of crop rotations in determining soil structure and crop growth conditions. Can. J. Soil Sci. 85, 557–577. https://doi.org/10.4141/S04-078.

Bengough, A.G., Bransby, M.F., Hans, J., McKenna, S.J., Roberts, T.J., Valentine, T.A., 2006. Root responses to soil physical conditions; growth dynamics from field to cell. J. Exp. Bot. 57, 437–447. https://doi.org/10.1093/JXB/ERJ003.

Bengough, A.G., McKenzie, B.M., Hallett, P.D., Valentine, T.A., 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. J. Exp. Bot. 62, 59–68. https://doi.org/10.1093/JXB/ERQ350.

Bengough, A.G., Mullins, C.E., 1991. Penetrometer resistance, root penetration resistance and root elongation rate in two sandy loam soils. Plant Soil 131, 59–66. https://doi.org/10.1007/BF00010420.

Bengough, A.G., Mullins, C.E., 1990. Mechanical impedance to root growth: a review of experimental techniques and root growth responses. J. Soil Sci. 41, 341–358. https://doi.org/10.1111/j.1365-2389.1990.tb00070.x.

Bingham, I.J., Bengough, A.G., 2003. Morphological plasticity of wheat and barley roots in response to spatial variation in soil strength. Plant Soil 250, 273–282. https://doi.org/10.1023/A:1022891519039.

Bodner, G., Leitner, D., Kaul, H.P., 2014. Coarse and fine root plants affect pore size distributions differently. Plant Soil 380, 133–151. https://doi.org/10.1007/s11104-014-2079-8.

Brady, N.C., Weil, R.R., 2017. The Nature and Properties of Soils, fifteenth ed. Pearson.

Bronick, C.J., Lal, R., 2005. Soil structure and management: a review. Geoderma 124, 3–22. https://doi.org/10.1016/j.geoderma.2004.03.005.

Burr-Hersey, J.E., Mooney, S.J., Bengough, A.G., Mairhofer, S., Ritz, K., 2017. Developmental morphology of cover crop species exhibit contrasting behaviour to changes in soil bulk density, revealed by X-ray computed tomography. PLoS One 12, 1–18. https://doi.org/10.1371/journal.pone.0181872.

Clark, L.J., Barraclough, P.B., 1999. Do dicotyledons generate greater maximum axial root growth pressures than monocotyledons? J. Exp. Bot. 50, 1263–1266. https://doi.org/10.1093/jxb/50.336.1263.

Colombi, T., Walter, A., 2017. Genetic diversity under soil compaction in wheat: root number as a promising trait for early plant vigor. Front. Plant Sci. 8, 1–14. https://doi.org/10.3389/fpls.2017.00420.

Czarnes, S., Hiller, S., Dexter, A.R., Hallett, P.D., Bartoli, F., 1999. Root:Soil adhesion in the maize rhizosphere: the rheological approach. Plant Soil 211, 69–86. https://doi.org/10.1023/A:1004656510344.

Dexter, A.R., Hewitt, J.S., 1978. The deflection of plant roots. J. Agric. Eng. Res. 23, 17–22. https://doi.org/10.1016/0021-8634(78)90075-6.

Gilker, R.E., Weil, R.R., Krizek, D.T., Momen, B., 2002. Eastern gamagrass root penetration in adverse subsoil conditions. Soil Sci. Soc. Am. J. 66, 931–938. https://doi.org/10.2136/SSSAJ2002.9310.

Helliwell, J.R., Sturrock, C.J., Miller, A.J., Whalley, W.R., Mooney, S.J., 2019. The role of plant species and soil condition in the structural development of the rhizosphere. Plant Cell Environ. 42, 1974–1986. https://doi.org/10.1111/PCE.13529.

Houlbrooke, D.J., Thom, E.R., Chapman, R., McLay, C.D.A., 2010. A study of the effects of soil bulk density on root and shoot growth of different ryegrass lines, pp. 429–435. https://doi.org/10.1080/00288233.1997.951326540.

Houston, A.N., Otten, W., Falconer, R., Monga, O., Baveye, P.C., Hapca, S.M., 2017. Quantification of the pore size distribution of soils: assessment of existing software using tomographic and synthetic 3D images. Geoderma 299, 73–82.

Khalil, A.M., Murchie, E.H., Mooney, S.J., 2020. Quantifying the influence of water deficit on root and shoot growth in wheat using X-ray Computed Tomography. AoB Plants 12, 1–13. https://doi.org/10.1093/aobpla/plaa036.

Kuht, J., Reintam, E., 2004. Soil compaction effect on soil physical properties and the content of nutrients in spring barley (Hordeum vulgare L.) and spring wheat (Triticum aestivum L.). Agron. Res. 2, 187–194.

Lang, V., Schneider, V., Puhlmann, H., Schengel, A., Seitz, S., Schack-Kirchner, H., Schaffer, J., Maier, M., 2023. Spotting ethylene in forest soils—what influences the occurrence of the phytohormone? Biol. Fertil. Soils. https://doi.org/10.1007/s00374-023-01763-z.

Li, Z., Zhang, X., Liu, Y., 2017. Pore-scale simulation of gas diffusion in unsaturated soil aggregates: accuracy of the dusty-gas model and the impact of saturation. Geoderma 303, 196–203.

Lipiec, J., Stepniewski, W., 1995. Effects of soil compaction and tillage systems on uptake and losses of nutrients. Soil Tillage Res. 35, 37–52. https://doi.org/10.1016/0167-1987(95)00474-7.

Liu, H., Colombi, T., Jäck, O., Keller, T., Weih, M., 2021. Effects of soil compaction on grain yield of wheat depend on weather conditions. Sci. Total Environ. 807, 150763 https://doi.org/10.1016/j.scitotenv.2021.150763.

Logsdon, S.D., 2013. Root effects on soil properties and processes: synthesis and future. Res. Needs 4, 173–196. https://doi.org/10.2134/advagricsystmodel4.c8.

Logsdon, S.D., Parker, J.C., Reneau, R.B., 1987. Root growth as influenced by aggregate size. Plant Soil 99, 267–275. https://doi.org/10.1007/BF02370873.

Mairhofer, S., Pridmore, T., Johnson, J., Wells, D.M., Bennett, M.J., Mooney, S.J., Sturrock, C.J., 2017. X-ray computed tomography of crop plant root systems grown in soil. Curr. Protoc. Plant Biol. 2, 270–286. https://doi.org/10.1002/cppb.20049.

Masle, J., Farquhar, G.D., 1988. Effects of soil strength on the relation of water-use efficiency and growth to carbon isotope discrimination in wheat seedlings. Plant Physiol. 86, 32–38. https://doi.org/10.1104/pp.86.1.32.

Menon, M., Jia, X., Lair, G.J., Faraj, P.H., Blaud, A., 2015. Analysing the impact of compaction of soil aggregates using X-ray microtomography and water flow simulations. Soil Tillage Res. 150, 147–157. https://doi.org/10.1016/j.still.2015.02.004.

Mondal, S., Chakraborty, D., 2023. Root growth and physiological responses in wheat to topsoil and subsoil compaction with or without artificial vertical macropores. Heliyon 9 (8), e18834. https://doi.org/10.1016/j.heliyon.2023.e18834.

Orzech, K., Wanic, M., Załuski, D., 2021. The effects of soil compaction and different tillage systems on the bulk density and moisture content of soil and the yields of winter oilseed rape and cereals. Agric 11, 1–17. https://doi.org/10.3390/agriculture11070666.

Pandey, B.K., Huang, G., Bhosale, R., Hartman, S., Sturrock, C.J., Jose, L., Martin, O.C., Karady, M., Voesenek, L.A.C.J., Ljung, K., Lynch, J.P., Brown, K.M., Whalley, W.R., Mooney, S.J., Zhang, D., Bennett, M.J., 2021. Plant roots sense soil compaction through restricted ethylene diffusion. Science 371, 276–280. https://doi.org/10.1126/SCIENCE.ABF3013.

Passioura, J.B., 2002. Soil conditions and plant growth. Plant Cell Environ. 25, 311–318. https://doi.org/10.1046/j.0016-8025.2001.00802.x.

Pillai, U.P., McGarry, D., 1999. Structure repair of a compacted vertisol with wet-dry cycles and crops. Soil Sci. Soc. Am. J. 63, 201–210. https://doi.org/10.2136/sssaj1999.03615995006300010029x.

Rabot, E., Wiesmeier, M., Schlüter, S., Vogel, H.J., 2018. Soil structure as an indicator of soil functions: a review. Geoderma 314, 122–137. https://doi.org/10.1016/j.geoderma.2017.11.009.

Richard, C., Hickey, L., Fletcher, S., Chenu, K., Borrell, A., Christopher, J., 2015. High-throughput phenotyping of wheat seminal root traits in a breeding context. Procedia Environ. Sci. 29, 102–103. https://doi.org/10.1016/J.PROENV.2015.07.179.

Shaxson, T.F., Barber, R.G., 2003. Optimizing soil moisture for plant production: the significance of soil porosity. FAO Soils Bull. 107.

Stirzaker, R.J., Passioura, J.B., Wilms, Y., 1996. Soil structure and plant growth: impact of bulk density and biopores. Plant Soil 185, 151–162. https://doi.org/10.1007/BF02257571.

Tracy, Saoirse R., Black, C.R., Roberts, J.A., McNeill, A., Davidson, R., Tester, M., Samec, M., Korošak, D., Sturrock, C., Mooney, S.J., 2012a. Quantifying the effect of soil compaction on three varieties of wheat (Triticum aestivum L.) using X-ray Micro Computed Tomography (CT). Plant Soil 353, 195–208. https://doi.org/10.1007/s11104-011-1022-5.

Tracy, S.R., Black, C.R., Roberts, J.A., Mooney, S.J., 2011. Soil compaction: a review of past and present techniques for investigating effects on root growth. J. Sci. Food Agric. 91, 1528–1537. https://doi.org/10.1002/jsfa.4424.

Tracy, Saoirse R., Black, C.R., Roberts, J.A., Sturrock, C., Mairhofer, S., Craigon, J., Mooney, S.J., 2012b. Quantifying the impact of soil compaction on root system architecture in tomato (Solanum lycopersicum) by X-ray micro-computed tomography. Ann. Bot. 110, 511–519. https://doi.org/10.1093/aob/mcs031.

Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, H., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J., Matsumoto, T., Takai, T., Okuno, K., Yano, M., 2013. Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat. Genet. 45, 1097–1102. https://doi.org/10.1038/ng.2725.

Whiteley, G.M., Hewitt, J.S., Dexter, A.R., 1982. The buckling of plant roots. Physiol. Plant. 54, 333–342. https://doi.org/10.1111/j.1399-3054.1982.tb00268.x.

Whiteley, G.M., Utomo, W.H., Dexter, A.R., 1981. A comparison of penetrometer pressures and the pressures exerted by roots. Plant Soil 61, 351–364. https://doi.org/10.1007/BF02182016.

Zhang, X., Crawford, J.W., Flavel, R.J., Young, I.M., 2016. A multi-scale Lattice Boltzmann model for simulating solute transport in 3D X-ray micro-tomography images of aggregated porous materials. J. Hydrol. 541 (Part B), 1020–1029.