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Root growth and physiological responses in wheat to topsoil and subsoil compaction with or without artificial vertical macropores

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ABSTRACT

The process of soil compaction can cause various stresses on roots, ultimately limiting their growth and development within the soil. Understanding this phenomenon in real-world conditions can be challenging since the growth of roots is influenced by the soil environment. To investigate this issue, four experiments were conducted to examine the impact of topsoil (two in pots: with clay loam and sandy loam soils under two soil water regimes) and subsoil (in rhizobox: one with clay loam soil and the other with sandy loam soil, containing artificial vertical macropores) compaction on the relationship between edaphic factors and the physiological response of wheat roots. The topsoil compaction reduced root length, volume, and weight by 30–50% and the root diameter by ~15% compared to the non-compact soil. The effect was reduced in the soil with higher clay content (clay loam), especially under the limited soil water condition. Plant physiological responses were adversely affected by compaction with a reduction in plant height. The transpiration rate was highly impacted (21–47% reduction) with the build-up of intercellular CO_2 content in leaves (13–31%), especially with limited water applications. Root growth was severely restricted (>60%) in the compact subsoil layer, although the surface area and volume of roots increased in the overlying non-compact layer. Naturally occurring or artificial vertical macropores acted as escape channels, facilitating the roots to pass through the compact subsoil and grow abundantly in the loose soil below. However, plants in field conditions encounter a mix of loose and compact soil zones. By studying how roots respond to this soil heterogeneity, we can develop strategies to reduce the negative effects of soil compaction.

1. Introduction

Soil compaction, one of the major abiotic stresses to growing crops, is recognized as one of the key threats to the development of a sustainable production system in the 21st century [1,2]. It is a hidden problem occurring on or below the soil surface and mostly remains undetected. Strong soil compaction occurs when heavy machinery (e.g., combine harvester, transport vehicles, etc.) is used at high soil moisture content. It is estimated that about 68 million ha (Mha) of the global land [3] and 45% of the agricultural land [2] are affected by soil compaction. Over the years, heavy machinery has amplified soils' vulnerability to compaction [1].

The soil physical indicators mostly used for detecting soil compaction are penetration resistance, bulk density, total porosity, and

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macroporosity [4]. Root growth and proliferation are severely limited in compacted soil layers [5–7] due to higher penetration resistance [8] which limits water and nutrient uptake [9,10]. The penetration resistance is strongly related to the bulk density (positive correlation) [11] and moisture content (negative correlation) [5,12] of soil; the dependency could be more on soil water content [13]. Depending on the degree of compaction and soil texture, compaction can severely impair root growth when the soil water potential becomes less [14]. Even a compact layer may behave like a noncompact layer at high soil moisture content, allowing unhindered root growth.

Subsoil compaction and subsequent yield reduction under puddled conditions have been reported extensively [15,16]. The absence of soil inversion in no-tillage has been reported to compact the topsoil layer [17]. Growth and yield reductions due to soil compaction have been widely reported across the world [12,18–21].

A complete understanding of soil compaction is needed to meet future challenges for achieving global food security [22]. Mechanical impedance in the soil is a function of soil compaction, water content, and the relative proportion of sand-silt-clay contents. These lead to multiple stresses in the soil. Root response is an integration of soil edaphic environment. Root-to-shoot communication (root-derived long-distance mobile signal) is critical for the shoot's ability to respond to the underground conditions. Numerous studies have addressed high soil strength on root and shoot response with other associated abiotic stress parameters [9,23,24]. However, soils have always been a mixture of compact and non-compacted regions/layers due to the use of heavy machinery during tillage and land management practices, or as a natural result of soil pedological processes. This soil heterogeneity, although extremely difficult to capture, can aid in management decisions to minimize the impact of soil compaction [22]. We hypothesized that soil water potential might be managed to mitigate the adverse effects of topsoil or subsoil compaction on wheat roots in varying soil textural conditions. By monitoring edaphic factors, can we gain a deeper understanding of the connection between different edaphic factors and soil compaction? Additionally, we investigated how the existence of artificial vertical macropores impacted root growth patterns. To accomplish this, we conducted pot and rhizobox experiments in controlled and ambient environments, studying root growth and plant physiological parameters under different soil compaction, water management, and soil textures.

2. Materials and methods

2.1. Experimental design, treatments, climatic and edaphic conditions

Four independent experiments with test crop wheat (*Triticum aestivum* L.) were conducted at the Indian Agricultural Research Institute, New Delhi, India (28.639 °N, 77.161 °S) between the period 2016–2018:

Exp 1. Pot experiment with compacted topsoil in a growth chamber with two soil textures (clay loam and sandy loam) and two water regimes (adequate and limited; details follow). This experiment aimed to examine how soil compaction, water application, and soil texture impact root growth.

Exp 2. Pot experiment with compacted topsoil under ambient conditions with a sandy loam soil and water regime as in Exp. 1. This was to observe the root growth and physiological responses of plants in compact soil. Our goal was to determine whether growth parameters could be used to identify soil compaction.

Exp 3. Rhizobox experiment in a growth chamber with clay loam soil and compacted at the subsurface under an adequate water regime was carried out to visualize and document root behaviour in the presence of a subsurface compact soil layer.

Exp 4. Same as Exp 3, but with sandy loam soil under ambient conditions and artificial vertical macropores extended through the compacted sublayer. We came up with the idea of studying the impact of vertical macropores on root growth while conducting our first experiment. After seeing the results, we wanted to investigate further. Unfortunately, we could not fully execute our plan due to limited funds. We could only conduct the second year of the experiment with a few treatments, without artificial vertical macropores for two soil textures.

Topsoil and subsoil compaction indicate compaction in 0–15 and 15–30 cm soil depths, respectively.

The clay loam and sandy loam (Typic Haplustept) soils have sand, silt, and clay contents of 25.9, 39.6, 34.5, 74.7, 10.7, and 14.6%, respectively. Both soils have similar pH (7.7–7.8), but the Walkley-Black oxidizable C is 5.2 g kg^{-1} in clay loam soil compared to 1.6 g kg^{-1} in sandy loam soil. The field capacity water (θ_{FC}) contents of clay loam and sandy loam soils were 18.0 and 15.7% (w/w), respectively. Similarly, the water content at the wilting point (θ_{WP}) was 8.2 and 7.1% (w/w) for clay loam and sandy loam soils, respectively. Each pot was weighed separately on every alternate day, and water was applied at 30% depletion (adequate) and 60% depletion (limited) of θ_{FC}. When soil water remained within the available water range, between θ_{FC} and θ_{WP}, it was considered "adequate". However, when the soil dried beyond θ_{WP}, it was considered "limited" water conditions, which could cause water stress for plants. If water content was depleted by 30% θ_{FC}, the soil moisture content still remained within the available water range, but depletion of 60% resulted in water content below θ_{WP}. Water treatments were imposed after the crown root initiation stage (~21 days after sowing).

The average day and nighttime temperatures in the growth chamber were 25 and 18 °C, respectively. A day length of 12 h, and relative humidity (RH) of 55–65% (during daytime) and 75–90% (during nighttime) were maintained during the experimental period. About 900 μE m^{-2} s^{-1} of light intensity was maintained during the daytime. The ambient condition was characterized by 15.4–30.0 °C maximum and 1.1–16.0 °C minimum temperatures, and 6 mm rainfall during the experimental period (November 2017–January 2018).

2.2. *Pot experimentation (Exp 1&2)*

In Exp. 1, ~15 cm sized pots (vol. 905 cm^3) were filled up with clay loam and sandy loam soils independently at two compaction levels: a) no compaction (BD_1: bulk density, BD~1.4 Mg m^{-3}), and b) high compaction (BD_3: BD~1.8 Mg m^{-3}). The amount of soil to achieve the desired compaction or bulk density was calculated based on the pot volume and compacted incrementally (1–2 cm layer) with a broad-base hammer, and a sprinkling of water to achieve the desired compaction. The upper 3 cm soil was kept loose for proper germination of seeds. After filling, all pots were saturated by capillary wetting and equilibrated at room temperature for 24 h. Each treatment was replicated four times.

Four wheat seeds were sown in each pot, and only two seedlings (Z1.2) were retained after germination. All pots were dismantled after the ear emergence (64 days after sowing, DAS; Z5.5–5.7) for root study. In Exp. 2, pots (~20 cm diameter; 1565 cm^3 volume) were filled with sandy loam soil and with three compaction levels i.e., BD_1, BD_2 (BD~1.6 Mg m^{-3}) and BD_3. Pots were dismantled after ear emergence (Z5.7–5.9) for root study on 77 DAS. Each treatment was replicated nine times.

2.3. *Rhizobox experimentation (Exp 3&4)*

Custom-made transparent boxes of 15 cm × 5 cm × 75 cm (L × W × H) dimensions were used. One side of the rhizobox could be opened to facilitate the washing of roots at the end of the experiment. About 70 cm of the rhizobox was filled with <2 mm soil (clay loam) layer-wise, and the upper 5 cm was left to facilitate water application. The soil was compacted (BD_1, BD_2, and BD_3) only in the subsurface layer (15–30 cm). Water was applied every 2–3 days intervals to avoid stress. Four seeds were sown in each rhizobox, and two plants were retained after germination (Z1.2). After ear emergence (69 DAS; Z5.7–5.9), rhizobox were dismantled, and roots were washed for further observations.

The rhizobox experiment was repeated with sandy loam soil (Exp 4). About eight artificial vertical macropores were created in BD_2 and BD_3 treatments by inserting a stainless-steel wire of 1.25 mm diameter [24]. A perforated wooden block of ~7.5 cm thickness was used to keep the pores vertical, and the wire was inserted through that block up to a soil depth of 30 cm. No artificial macropores were created in BD_1, and it was used as the control. Each treatment was replicated thrice in both Exp 3 and 4.

2.4. *Root growth parameters*

The entire soil in a pot was emptied onto a 1 mm sieve and gently washed with water to remove the soil with minimum disturbance to the roots (Suppl. Fig. 1). After the washing, diluted sodium hexametaphosphate solution (~1%) was used for removing root-adhered soil particles. Washed and cleaned roots were stored in butter-paper bags at 4 °C until scanning. Roots were scanned on a root-scanner (LA-1600) to record the morphological parameters of length, surface area, volume, and diameter using the Win-RHIZO programme (Reagent Instruments Inc., Canada). Dry root mass was recorded after oven-drying at 60 °C for 48 h. In the case of rhizobox, one side was opened, the entire profile was washed slowly to get complete root architecture and then the roots were cut depth-wise for scanning. All root parameters were expressed per unit of soil volume.

2.5. *Plant growth parameters*

Plant height (Exp. 2) was measured thrice (on 46, 57, and 77 DAS) with a ruler. Photosynthesis rate, stomatal conductance, intercellular CO_2 concentration, and transpiration of the fully expanded uppermost leaf of the wheat plant were measured using a portable InfraRed Gas Analyzer (IRGA; Model LI6400XT, Li-COR Ltd.) between 10:30 and 13:30 h on 66 DAS. Relative leaf water content (RLWC) was determined by the method given by Weatherley [25] on 68 DAS while the carbohydrate concentration (CC, %) of flag leaf was measured on 67 DAS by following Dubois [26]. The uppermost leaf was collected, and fresh weight (FW) was noted. The leaf was then soaked in distilled water for 4 h to record its turgid weight (TW). The leaf was oven-dried at 60 °C till constant weight, and the weight (DW) was recorded. The RLWC was measured in triplicate for each treatment and calculated by the following formula:

$$\mathrm{RLWC}\ (\%) = \frac{\mathrm{FW} - \mathrm{DW}}{\mathrm{TW} - \mathrm{DW}} \times 100$$

For the CC in leaves, ~500 mg of leaf sample was taken and hydrolyzed with 5 ml of 2.5 N HCl followed by neutralization with sodium carbonate. The entire content was centrifuged, and 1 ml aliquot was taken for colour development. One ml of 5% phenol and 5 ml of 96% H_2SO_4 were added to the aliquot and the concentration was determined at 490 nm using a spectrophotometer (Shimadzu, UV–Visible Spectrophotometer, Model 1900). The CC was read from a standard curve prepared with glucose and calculated by the following formula:

$$\text{Carbohydrate concentration } (\%) = \frac{\text{Sugar concentration} \times \text{Volume of extract}}{\text{Aliquot of sample} \times \text{Weight of leaf sample} \times 1000}$$

2.6. *Statistical analysis*

All data were analyzed using the Statistical Analysis System available at the Indian NARS Statistical Computing Portal (Indian NARS Statistical Computing Portal (http://stat.iasri.res.in/sscnarsportal) and Minitab. For all root and plant growth parameters, a

Table 1

Significance of factors and their interactions on root growth parameters in wheat (Exp. 1 & 2). '*', '**', and 'ns' indicate statistically significant at $p < 0.05$ and $p < 0.01$, and non-significant, respectively, by Tukey's Honestly significant difference (HSD) test.

Factors	Length density	Surface area density	Volume density	Average diameter	Weight density
Exp. 1					
Compaction (C)	**	**	**	*	**
Soil texture (S)	**	**	ns	ns	**
Water application (W)	**	**	ns	ns	**
C × S	*	**	ns	ns	ns
S × W	*	ns	ns	ns	ns
C × W	*	ns	ns	ns	ns
C × S × W	*	ns	ns	ns	ns
Exp. 2					
Compaction (C)	**	**	**	**	**
Water application (W)	**	ns	ns	**	ns
C × W	*	**	**	*	**

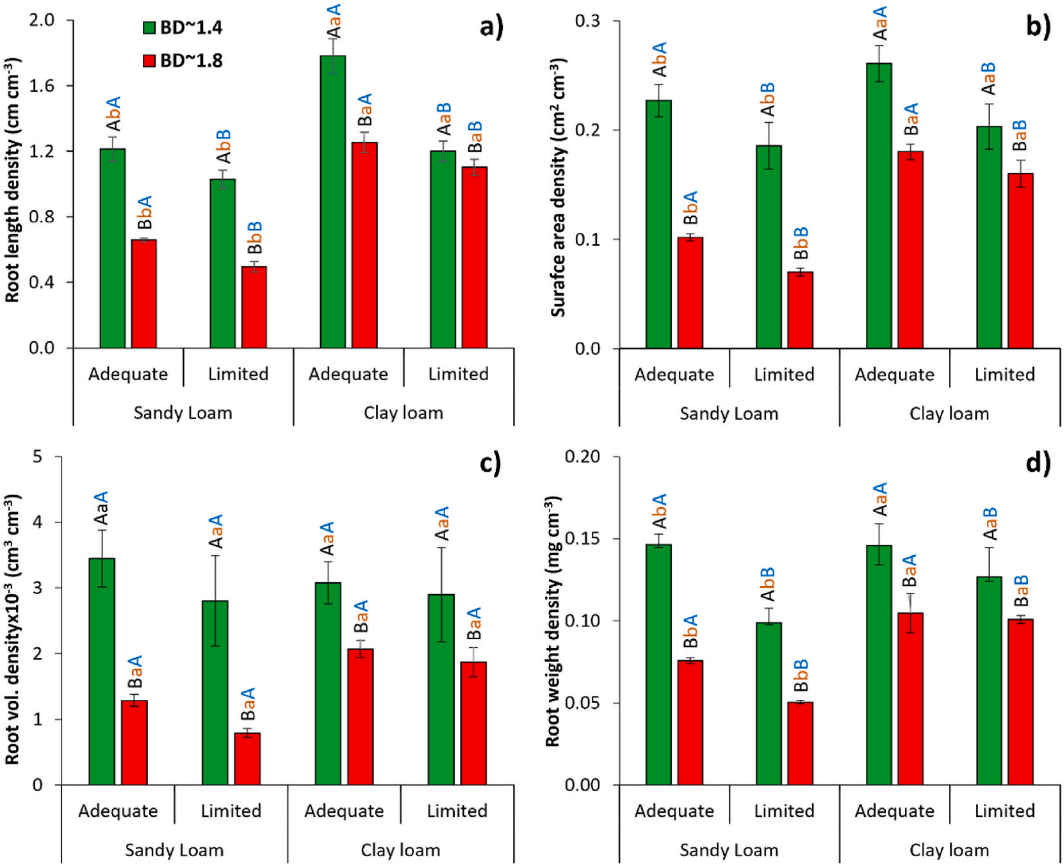

Fig. 1. Impact of soil compaction (BD∼1.8 Mg m^{-3}) on root growth parameters in wheat in sandy loam and clay loam soils under adequate and limited water supply (Exp. 1). Vertical bars indicate ± standard errors of means. Bars followed by different uppercase (first, black), lowercase (brown) and uppercase (second, blue) letters are significantly different at $p < 0.05$ for compaction (within same water application and soil texture), soil texture (within same compaction and water application) and water application (within same compaction and soil texture), respectively by Tukey's HSD test.

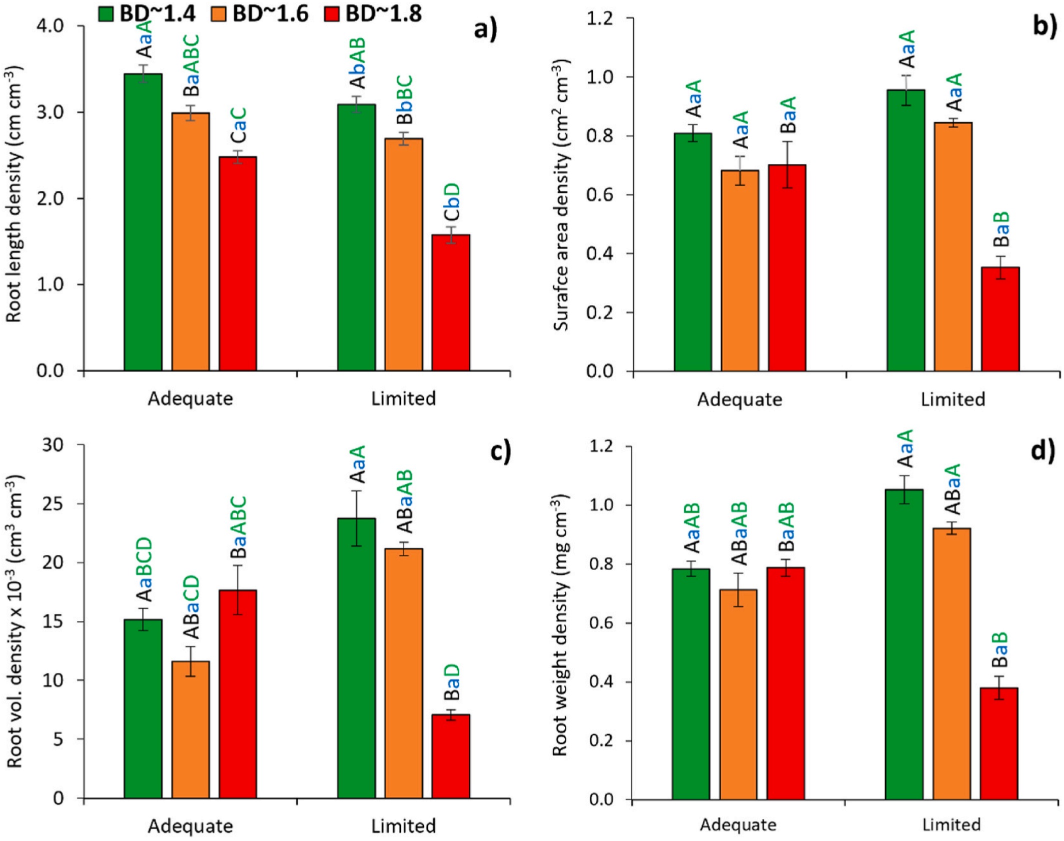

Fig. 2. Root growth parameters of wheat in noncompact (Bulk density, BD∼1.4 Mg m^{-3}), and compact (BD∼1.6 and ∼1.8 Mg m^{-3}) sandy loam soils under adequate and limited water supply (Exp. 2). Bars followed by different uppercase (first, black), lowercase (blue) and uppercase (second, green) letters are significantly different ($p < 0.05$) for compaction (C, within same water application), water application (W, within same compaction) and C × W interaction, respectively by Tukey's HSD test. Vertical bars indicate ± standard errors of means.

Table 2

Significance of factors and their interactions on plant growth parameters in wheat (Exp. 2). '*', '**', and 'ns' indicate statistically significant at $p < 0.05$ and $p < 0.01$, and non-significant, respectively, by Tukey's HSD test. DAS: Days after sowing; RLWC: Relative leaf water content.

Factors	Photosynthetic rate	Stomatal Conductance	Transpiration rate	Intercellular CO_2	Plant height			Carbohydrates in leaves	RLWC
					46 DAS	57 DAS	77 DAS		
Compaction (C)	**	*	**	**	**	**	**	**	**
Water application (W)	**	ns	**	ns	ns	**	ns	**	**
C × W	ns	ns	**	**	ns	ns	ns	ns	ns

general linear model was fitted for analysis of variance (ANOVA) taking compaction, water management, and soil texture as factors. Pairwise means were compared at $p < 0.05$ or $p < 0.01$ level by Tukey's Honest Significant Test (HSD).

3. Results

3.1. Root growth parameters as affected by water applications, soil textures, and topsoil compactions

Results demonstrated the potential impacts of soil compaction, texture, and water application on root growth in wheat (Table 1). Significant interactions of soil compaction, soil texture, and water application were found for root length density (RLD) ($p < 0.05$) and compaction and texture for surface area density (SAD) ($p < 0.01$) in Exp. 1, and significant interaction between compaction and water for all the root parameters in Exp 2.

There were 30 and 8% reductions in RLD by compaction in the clay loam soil compared to 46 and 52% reductions in sandy loam soil

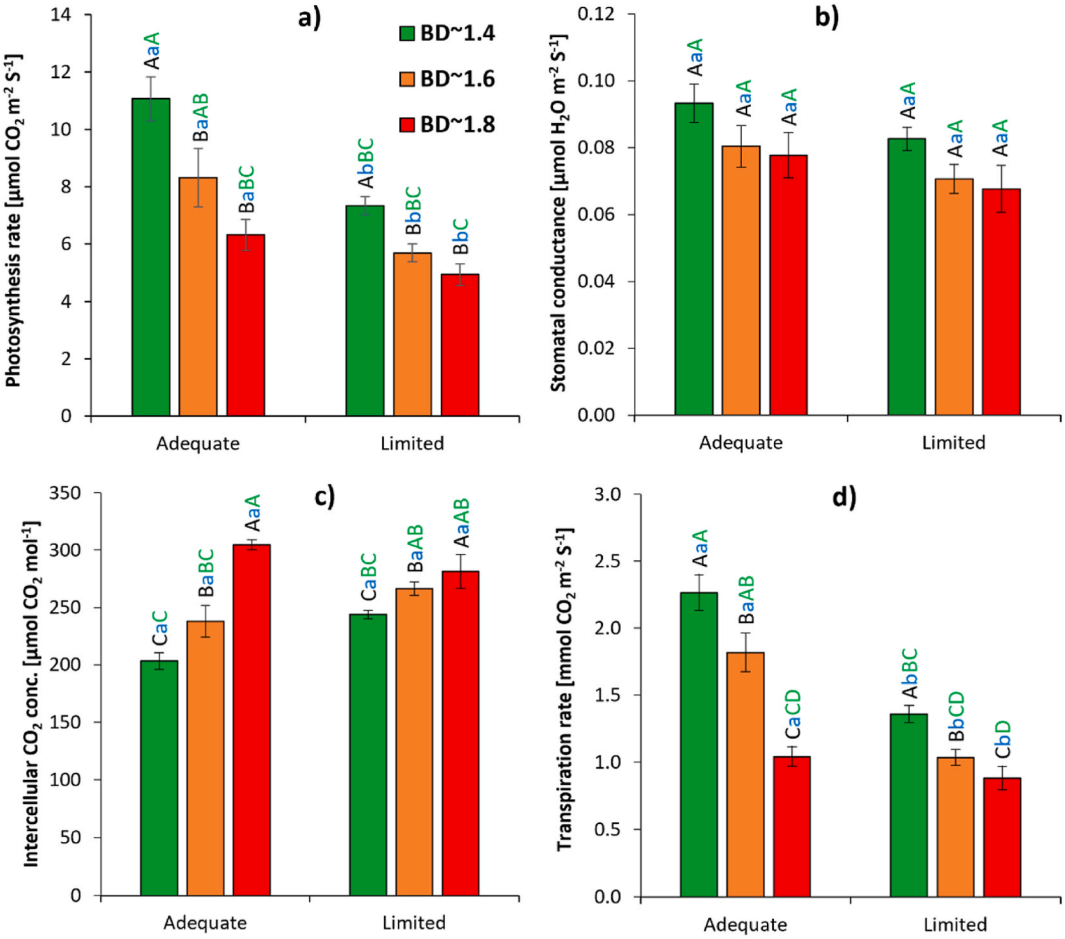

Fig. 3. Plant growth parameters of wheat at 66 days after sowing in noncompact (Bulk density, BD~1.4 Mg m^{-3}) and compact (BD~1.6 and ~1.8 Mg m^{-3}) sandy loam soils with adequate and limited water applications (Exp. 2). Bars followed by different uppercase (first, black), lowercase (blue), and uppercase (second, green) letters are significantly different ($p < 0.05$) for compaction (C, within same water application), water application (W, within same compaction), and C × W interaction, respectively by Tukey's HSD test. Vertical bars indicate ± standard errors of means.

under adequate and limited water application, respectively (Exp. 1; Fig. 1). With an adequate water supply, the non-compact clay loam soil recorded 47% higher RLD than the sandy loam soil (Fig. 1a). It was 90% higher in the compact clay loam soil compared to the sandy loam soil under similar conditions. The clay loam soil also supported higher root growth under compaction even with a limited water supply (RLD = 1.10 cm cm^{-3}) compared to 0.50 cm cm^{-3} in sandy loam soil or sustained similar root growth to the non-compact sandy loam soil with adequate soil water. The clay loam soil recorded higher SAD in noncompact (0.23 cm^2 cm^{-3}) and compact (0.17 cm^2 cm^{-3}) conditions compared to the sandy loam soil (0.21 and 0.09 cm^2 cm^{-3}, respectively) (Fig. 1b). Soil compaction significantly reduced root volume density (RVD, 51%) (Fig. 1c), average root diameter (RAD, 15%) (data not presented), and root weight density (RWD, 36%) (Fig. 1d).

Water supply had no impact on root growth in noncompact sandy loam soil or when it was compacted at BD_2 (Exp. 2; Fig. 2). When the soil was compacted at BD_3, limited water supplies reduced RLD and SAD by 37% and 50%, respectively compared to an adequate supply of water (Fig. 2a & b). At this compaction level, limited water supplies reduced RVD, RWD, and SAD by one-third of their values in non-compact soil, while RLD and RAD reduced by half and by a quarter compared to these in non-compact soil (Fig. 2c & d).

3.2. *Plant growth parameters as affected by topsoil compaction*

The effect of compaction was apparent in all plant growth parameters of wheat in Exp. 2 (Table 2). Water application impacted photosynthesis, transpiration rates, and relative water content in leaves (RLWC). The interaction between compaction and water was significant only for the transpiration rate and intercellular CO_2 concentration. Soil compaction at BD_2 and BD_3 reduced the photosynthesis rate by 24 and 39% ($p < 0.01$) and stomatal conductance by 14 and 17% ($p < 0.05$), respectively compared to non-compact soil (Fig. 3a & b). Limited water supply reduced the photosynthetic rate by 30% compared to the adequate water supply. Reduction in

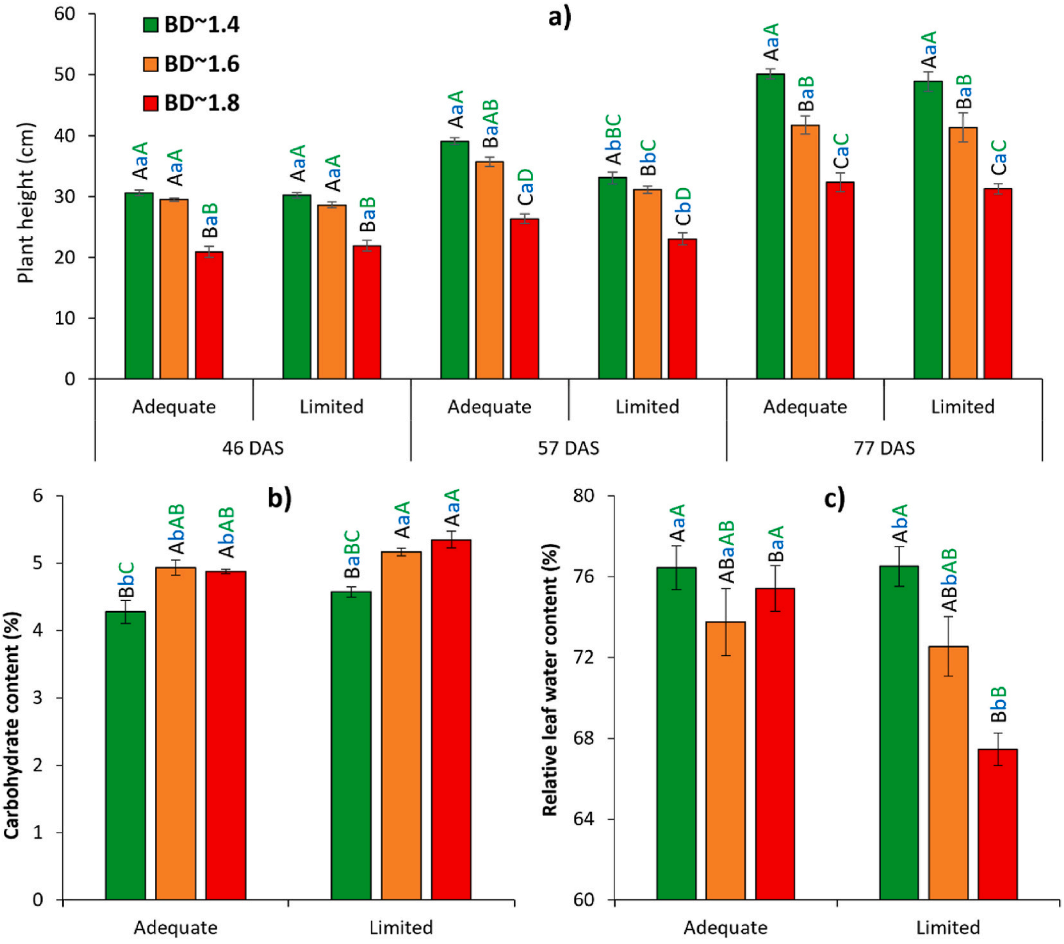

Fig. 4. Plant height, carbohydrates, and relative leaf water content under noncompact (Bulk density BD~1.4 Mg m^{-3}) and two levels of soil compaction (BD~1.6 and ~1.8 Mg m^{-3}), and differential water applications (Exp. 2). Bars followed by different uppercase (first, black), lowercase (blue), and uppercase (second, green) letters are significantly different ($p < 0.05$) for compaction (C, within same water application), water application (W, within same compaction), and C × W interaction, respectively by Tukey's HSD test. Vertical bars indicate ± standard error of mean.

transpiration rate was only significant at BD_3 under both the water levels compared to noncompact soil (Fig. 3d). However, limited water supply reduced ($p < 0.01$) transpiration rate in non-compact and compact soils (BD_2) by 40 and 43%, respectively compared to adequate water but was similar at the BD_3 level. Intercellular CO_2 increased by 50% ($p < 0.01$) with compaction at BD_3 compared to the non-compact soil but was unaffected by compaction at BD_2 (Fig. 3c). The water supply did not make a difference at each level of BD. The effect of soil compaction on plant height increased with the progress in crop growth and recorded 27–32, 30–33, and 35–36% reductions at 46, 57, and 77 DAS in BD_3, respectively, compared to BD_1 (Fig. 4a). The soil compaction increased the carbohydrate concentration by 14–15 and 13–17% under adequate and limited water supply, respectively (Fig. 4b). Compaction at BD_3 resulted in a 7% decrease in RLWC (Fig. 4c). Limited water supply reduced RWC by 4% ($p < 0.01$).

3.3. Root growth under the subsoil compaction

Subsoil compaction at 15–30 cm significantly reduced RLD (~63%), SAD (62–66%), and RVD (71–72%) in this layer (Fig. 5a, b & 5c). This was associated with increases in SAD and RVD in the surface 0–15 cm soil, although RLD remained unaffected. In this layer, SAD increased by 20 and 45%, and RVD by 64 and 113% in BD_2 and BD_3, respectively, compared to BD_1. The average diameter of roots increased by 41–51% at 0–15 cm layer following the subsoil compaction (Fig. 5d). Marginal differences were recorded at 30–45 cm layer, while traces of roots were found in deeper soil, and no analyses could be performed.

3.4. Root growth in the presence of artificial macropores extending through the compact subsoil

Artificial macropores significantly altered the root growth below the compact subsoil (Fig. 6). Although compaction reduced RLD by 20–26% in the 15–30 cm layer, it increased by 62–66% and 48–58% in the 30–45 and 45–60 cm layers, respectively (Fig. 6a).

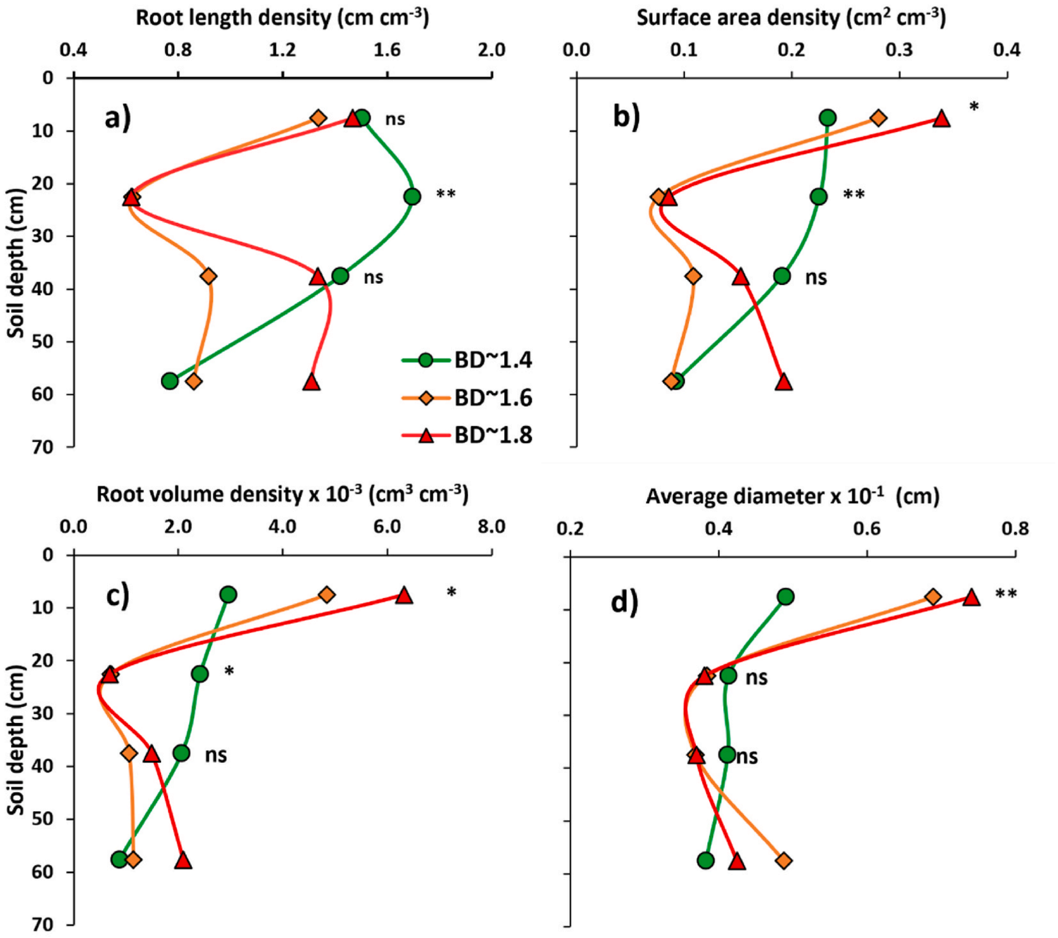

Fig. 5. Root growth in wheat as affected by subsoil (15–30 cm) compaction in rhizobox experimentation (Exp. 3). BD_1, BD_2, and BD_3 refer to bulk densities of ~1.4, ~1.6 and ~1.8 Mg m^{-3}, respectively at 15–30 cm layer; '*', '**' and 'ns' denote significant at $p < 0.05$ and < 0.01 levels, and non-significant, respectively by Tukey's HSD test.

Similarly, SAD increased by 31–41% in the 30–45 cm, but ~2 times in the 45–70 cm layer (Fig. 6b). In the case of RVD and RAD, values were similar at 30–45 cm, but RVD increased by 3–5 times in the 45–70 cm layer in the compacted subsoil treatments (Fig. 6c & d). There were, however, significant reductions in RLD (56–60%) and SAD (44–55%) at 0–15 cm compared to noncompacted subsoil treatment.

4. Discussions

Root growth parameters were modified by soil compaction for the topsoil (pot experimentation; homogeneous soil bulk density) or the subsoil (rhizobox; layer heterogeneity of bulk density). An increase in bulk density increased the soil mechanical impedance, resulting in detrimental effects on root length, surface area, volume, and mass within a given soil volume. This restricted the assemblage of roots, resulting in poor growth and uneven distribution [5,11,12,27,28].

A substantial reduction in root length density was measured in the sandy loam soil (14.6% clay) compared to the clay loam soil (34.5% clay) with a limited water supply when both soils were compacted. It could be attributed to a greater water content in clay loam soil (at any given soil water potential) owing to its higher clay content, which reduced the impact of compacted soil on roots. A 20% higher clay content (clay loam) could support a comparable root length density in compact soil even with limited soil water to that in non-compact soil with adequate water supply. However, the consequence of soil water in relieving the compaction force in the soil with a low clay content (sandy loam) was also evident. The soil-wetness dependency of the impact of compaction on plant roots has been aptly demonstrated [5,12,29]. The average diameter of roots was either similar or larger in compact soil, indicating radial expansion of the root – a morphological modification of its trait [30]. The contrasting response of roots to variations in bulk density of different soil textures was documented [31]. The soil texture effect was evident in root weight, and not in its volume, indicating a possible change in root air space volume in diverse soil types.

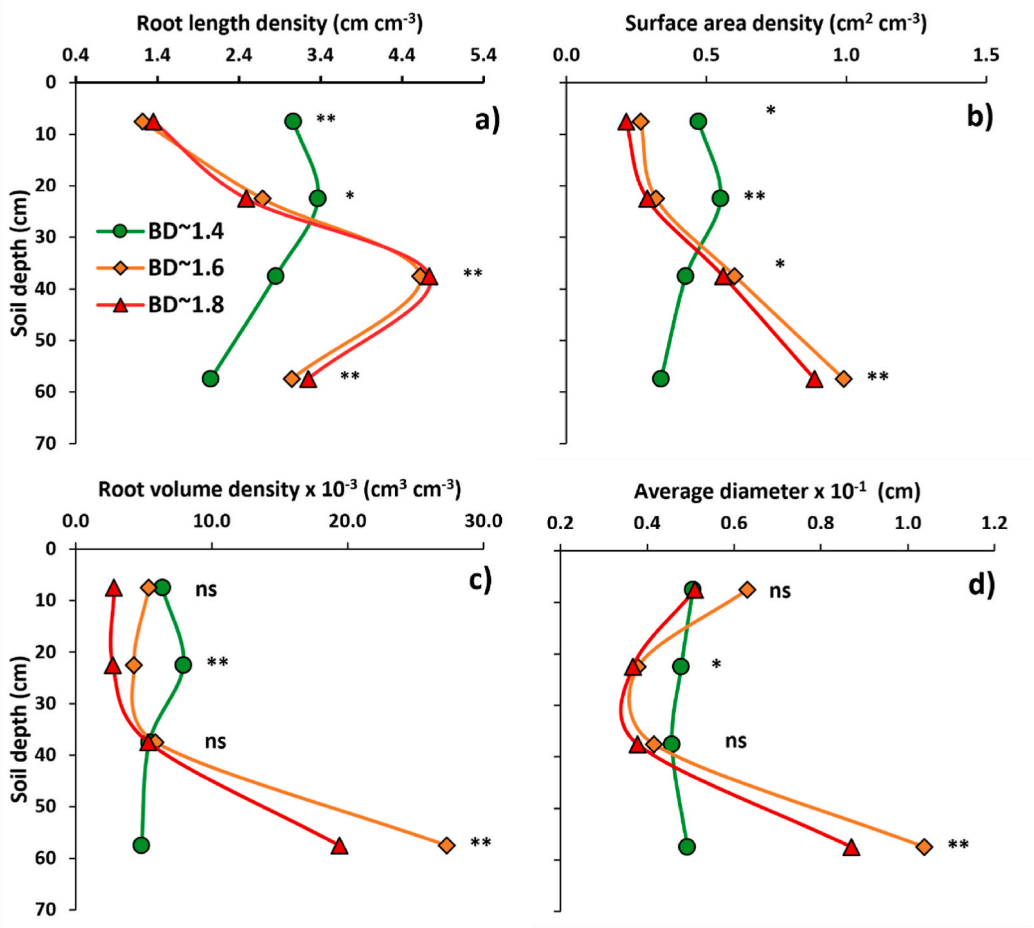

Fig. 6. Root growth in wheat across the soil profile in rhizobox in presence of vertical artificial macropores extending through the subsurface (15–30 cm) layer (Exp. 4). BD_1, BD_2, and BD_3 refer to bulk densities of ~1.4, ~1.6 and ~1.8 Mg m^{-3} at 15–30 cm layer, respectively; '*', '**' and 'ns' denote significant at $p < 0.05$ and < 0.01 levels, and non-significant, respectively by Tukey's HSD test.

The adverse effects of soil compaction were evident in the plant growth parameters. The transpiration rate appeared to be the most sensitive, affected by soil compaction, water application, and their interactions. Lower rates of photosynthesis and transpiration, higher intercellular CO_2 concentration, and lower relative leaf water content proved the adverse soil edaphic environment [32]. Mechanical constraints intensified under limited soil water conditions [5,12]. Soil compaction reduces the proportion of larger pores and consequently lowers the total pore volume which has detrimental effects on water movement, solute transport, soil aeration and root growth [33,34]. A compacted soil restricts root elongation even though water may be available. Plants require considerable effort or metabolic costs to uptake the water [24,35]. A stunted root system makes the uptake even more difficult [9,27,28]. A lower transpiration rate and lower relative water content in leaves corroborated this. A decline in turgor pressure due to water stress in soils accompanied by a drop in root local water potential produces root-derived hydraulic signals to regulate stomatal closure [36]. A lower transpiration rate under compacted soil indicates partial closure of stomata [9,37] and therefore, the exchange of gases and water vapour with the atmosphere was impaired [38]. This adversely affected the rate of photosynthesis and allowed a build-up of CO_2 in the plants. A lower relative leaf water content adversely impacted carbohydrate translocation within the plant system. Higher carbohydrate concentration in leaves substantiates poor translocation under soil compaction than in noncompacted conditions [39]. This might influence the sugar budget in plants and sucrose allocation towards roots [40]. Irrespective of growth stages, soil compaction reduced the plant height significantly [41]. Many researchers have observed reduced plant vigour in compact soil [11,12,42,43]. However, the root-shoot communication through mobile signals in response to abiotic stress has been poorly understood [44,45].

The subsoil (15–30 cm) compaction in the rhizobox restricted root growth in the compact layer progressively from a bulk density of 1.6 to 1.8 Mg m^{-3} (Fig. 7–c). However, the impact was not necessarily limited to the compacted layer (15–30 cm), but was registered in the entire profile (0–70 cm). Significant reductions (>60%) in root length, surface area, and volume in the compacted layer were associated with increases in surface area and root volume in the 0–15 cm layer, with marginal changes in root length. This implied radial expansion of roots (bulky roots) in the non-compact layer just above the compact layer with a higher mechanical impedance [5, 9,20,23,30,46]. Radial expansion of the root with fewer appearances has been documented as an acclimatization strategy to overcome

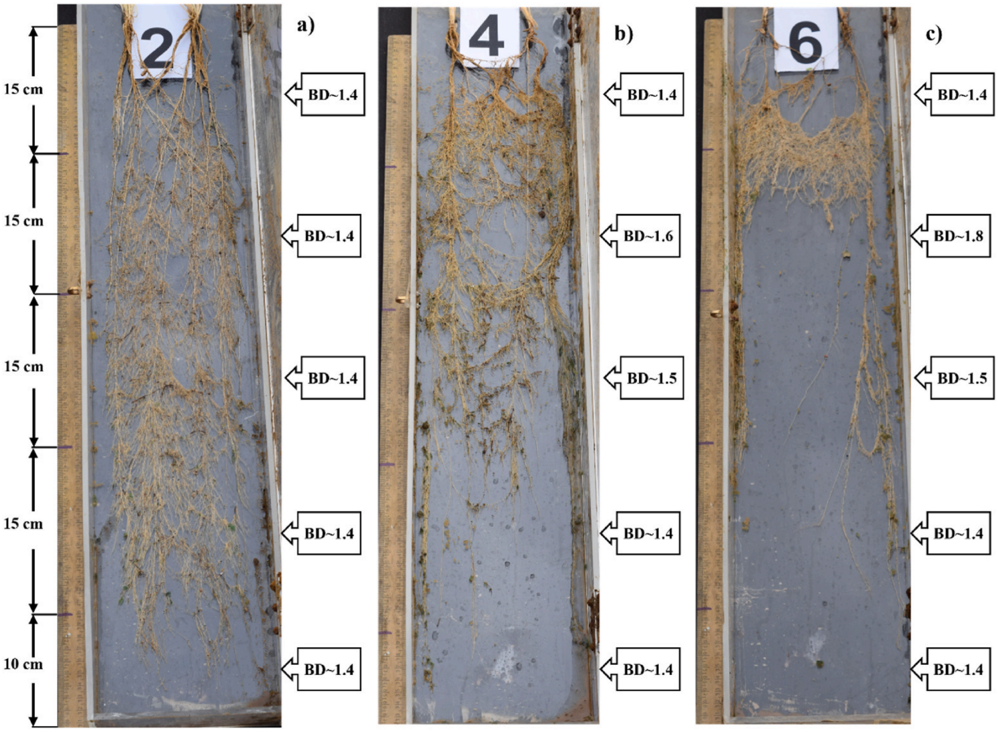

Fig. 7. Visual pattern of root distribution in the rhizobox (a–c) under subsoil (15–30 cm) compaction (Exp. 3). BD refers to soil bulk density (Mg m^{-3}).

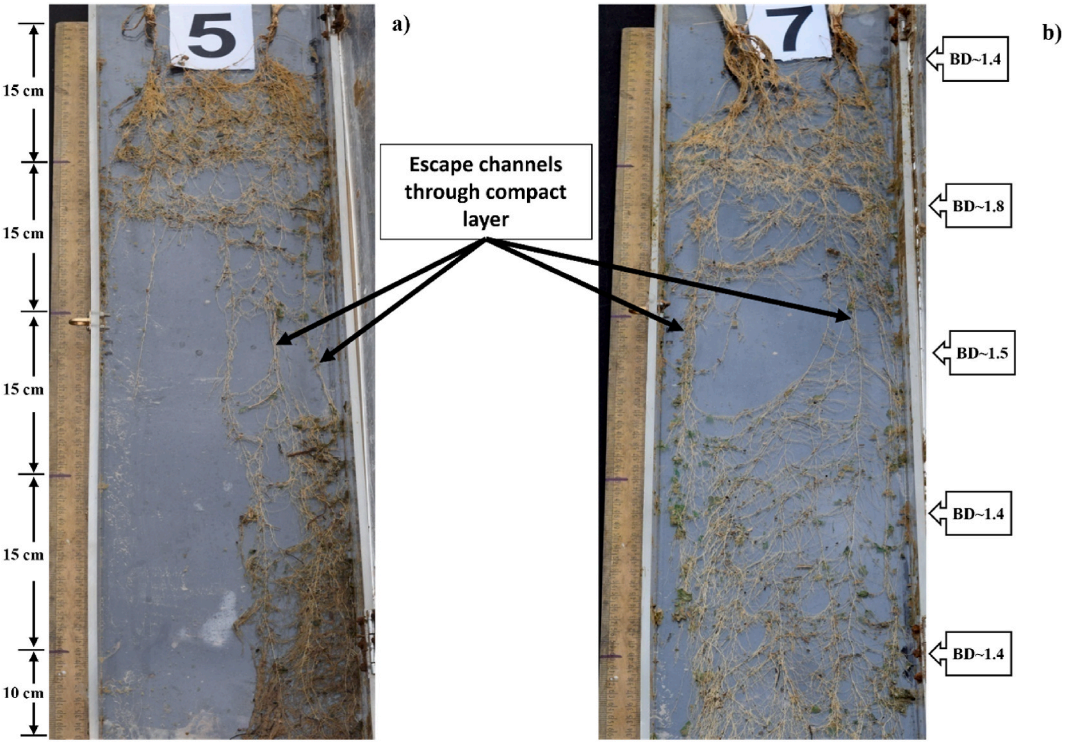

Fig. 8. Escape channels through compact 15–30 cm layer favouring root growth in the rhizobox (Exp. 3) (a–b). BD refers to soil bulk density (Mg m^{-3}).

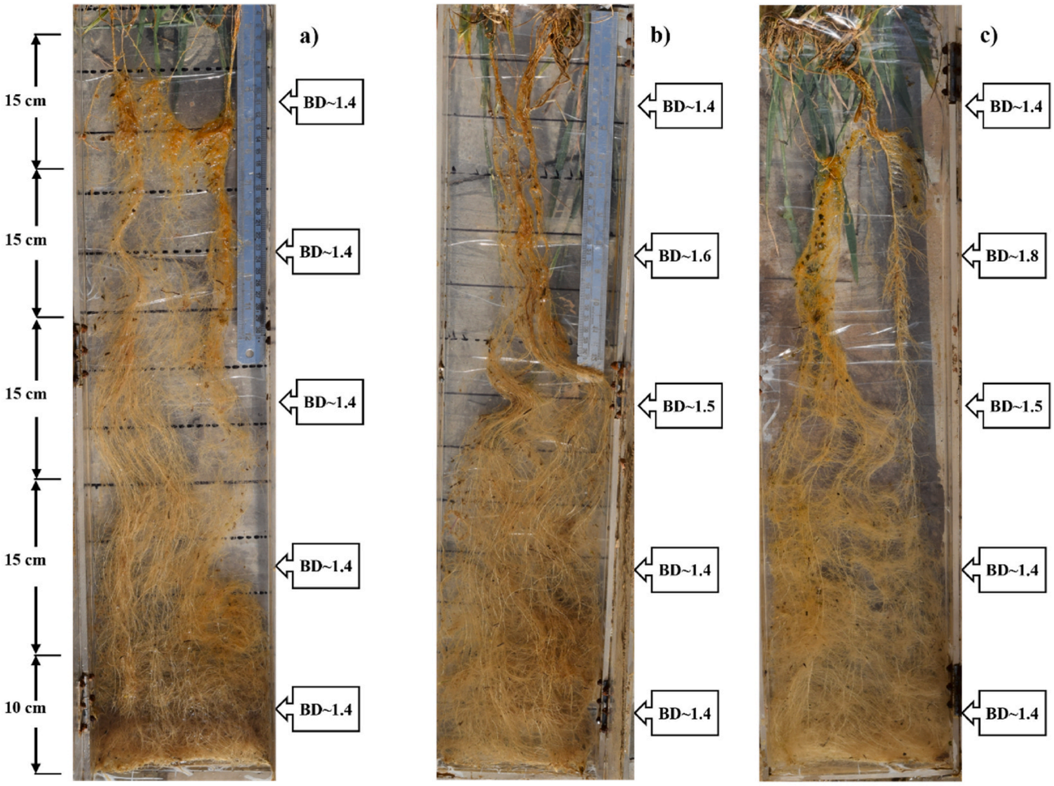

Fig. 9. Image of the root growth pattern in soil profile in presence of artificial vertical macropores extending through the compact subsoil (15–30 cm) (a–c). BD refers to soil bulk density (Mg m^{-3}).

the growth limitations imposed by the compact layer [20,47,48]. We, however, failed to obtain a change in the non-compact layers below, or the roots needed to be more to be traced. Large continuous pores (naturally formed as the passage of drainage during the experimentation) acted as channels to facilitate the roots to escape through the compact subsoil and proliferate down (Fig. 8a & b). Decayed root channels or root biopores under the no-tillage have been reported as effective pathways to link the surface and subsurface soil through a compact layer in between without affecting the root growth [49–51].

The presence of artificial vertical macropores in the soil with a compact subsoil layer modified the root distribution across soil layers, significantly below the compacted layer. Although the presence of root was limited in the compact 15–30 cm layer, ~1.5 times increase in root length, surface area, and volumes were recorded in the below layers. It was likely that the roots extended through the artificial macropores to the zone underlying the compact layer (Fig. 9a, b & 9c). The ability of roots to sense the path of least resistance (macropores) and move to higher oxygenated zones (non-compact layers below) has been widely documented [52–55]. Root system response to heterogeneous soil conditions has significant practical implications. Dense subsoil underlying the loosened topsoil is typical of cultivated fields, where roots can proliferate to the non-compact soil layers. Several authors have reported preferential growth of roots towards either natural macropores [56–59] or artificial macropores [24,60,61]. The tendency of roots to use lower resistance paths increases following strong mechanical impedance as experienced in compacted soils [58,59].

5. Limitations

The collected field soils were repacked into pots or rhizoboxes, causing a difference in soil structural orientation compared to the natural field conditions. Root growth may have been restricted due to the small volume of the pots, leading to roots following the pot walls. Water was applied based on field capacity, but soil compaction can alter water content at this level and was not taken into account. Additionally, soil textures can affect bulk density values critical for root growth and were not addressed in this study.

6. Conclusions

Our research clearly shows that surface and subsoil compaction negatively affect plant growth, particularly root growth. Surface compaction results in shorter, smaller, and lighter roots with a reduced surface area and average diameter. Meanwhile, subsoil compaction limits root proliferation into deeper soil layers, affecting water and nutrient use efficiency. However, we found that soil with higher clay content can mitigate the harmful effects of compaction since it retains moisture and remains softer for growing roots. The negative effects of compaction are worsened under limited water conditions since drier soils offer more resistance to root growth. The presence of vertical macropores is beneficial for roots to escape compacted sublayers. In this regard, conservation tillage could help grow roots since it increases soil bulk density, creating more vertical macropores in the form of root biopores, macropores created by earthworms or other faunal activities, and cracks due to soil drying.

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Author contribution statement

Surajit Mondal: Conceived and designed the experiments; Performed the experiments, Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Debashis Chakraborty: Conceived and designed the experiments; Performed the experiments, Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Data availability

Data will be made available on request.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at 10.1016/j.heliyon.2023.e18834.

References

[1] T. Keller, M. Sandin, T. Colombi, R. Horn, D. Or, Historical increase in agricultural machinery weights enhanced soil stress levels and adversely affected soil functioning, Soil Till. Res. 194 (2019), 104293.

[2] P. Schjønning, J.J. van den Akker, T. Keller, M.H. Greve, M. Lamandé, A. Simojoki, H. Breuning-Madsen, Driver-pressure-state-impact-response (DPSIR) analysis and risk assessment for soil compaction—a European perspective, Adv. Agron. 133 (2015) 183–237.

[3] L. Montanarella, M. Badraoui, V. Chude, I.D.S.B. Costa, T. Mamo, M. Yemefack, N. McKenzie, Status of the World's Soil Resources: Main Report. Embrapa Solos-Livro Científico (ALICE), FAO, Rome, 2015.

[4] T. Keller, A.P. da Silva, C.A. Tormena, N.F.B. Giarola, K.M.V. Cavalieri, M. Stettler, J. Arvidsson, SoilFlex-LLWR: linking a soil compaction model with the least limiting water range concept, Soil Use Manag. 31 (2) (2015) 321–329.

[5] A.G. Bengough, B.M. McKenzie, P.D. Hallett, T.A. Valentine, Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits, J. Exp. Bot. 62 (1) (2011) 59–68.

[6] W.R. Whalley, P.B. Leeds-Harrison, L.J. Clark, D.J.G. Gowing, Use of effective stress to predict the penetrometer resistance of unsaturated agricultural soils, Soil Till. Res. 84 (1) (2005) 18–27.

[7] A.P. Whitmore, W.R. Whalley, Physical effects of soil drying on roots and crop growth, J. Exp. Bot. 60 (10) (2009) 2845–2857.

[8] M.T. de Moraes, H. Debiasi, R. Carlesso, J.C. Franchini, V.R. da Silva, F.B. da Luz, Soil physical quality on tillage and cropping systems after two decades in the subtropical region of Brazil, Soil Till. Res. 155 (2016) 351–362.

[9] A. Nosalewicz, J. Lipiec, The effect of compacted soil layers on vertical root distribution and water uptake by wheat, Plant Soil 375 (1) (2014) 229–240.

[10] A. Schnepf, D. Leitner, S. Klepsch, Modeling phosphorus uptake by a growing and exuding root system, Vadose Zone J. 11 (3) (2012) vzj2012-0001.

[11] T. Colombi, L.C. Torres, A. Walter, T. Keller, Feedbacks between soil penetration resistance, root architecture and water uptake limit water accessibility and crop growth–A vicious circle, Sci. Total Environ. 626 (2018) 1026–1035.

[12] S. Grzesiak, M.T. Grzesiak, T. Hura, I. Marcińska, A. Rzepka, Changes in root system structure, leaf water potential and gas exchange of maize and triticale seedlings affected by soil compaction, Environ. Exp. Bot. 88 (2013) 2–10.

[13] P. Thomas, S. Mondal, D. Roy, M. Meena, B. Aggarwal, A. Sharma, D. Chakraborty, Exploring the relationships between penetration resistance, bulk density and water content in cultivated soils, J. Agric. Phys. 20 (1) (2020) 22.

[14] T. Batey, Soil compaction and soil management–a review, Soil Use Manag. 25 (4) (2009) 335–345.

[15] S. Mondal, D. Chakraborty, T.K. Das, M. Shrivastava, A.K. Mishra, K.K. Bandyopadhyay, P. Aggarwal, S.K. Chaudhari, Conservation agriculture had a strong impact on the sub-surface soil strength and root growth in wheat after a 7-year transition period, Soil Till. Res. 195 (2019), 104385.

[16] M. Ahmad, D. Chakraborty, P. Aggarwal, R. Bhattacharyya, R. Singh, Modelling soil water dynamics and crop water use in a soybean-wheat rotation under chisel tillage in a sandy clay loam soil, Geoderma 327 (2018) 13–24.

[17] P.L. Fernández, C.R. Alvarez, M.A. Taboada, Topsoil compaction and recovery in integrated no-tilled crop–livestock systems of Argentina, Soil Till. Res. 153 (2015) 86–94.
[18] D. Sidhu, S.W. Duiker, Soil compaction in conservation tillage: crop impacts, Agron. J. 98 (5) (2006) 1257–1264.
[19] T. Batey, D.C. McKenzie, Soil compaction: identification directly in the field, Soil Use Manag. 22 (2) (2006) 123–131.
[20] T. Colombi, A. Walter, Genetic diversity under soil compaction in wheat: root number as a promising trait for early plant vigor, Front. Plant Sci. 8 (2017) 420.
[21] T. Sonderegger, S. Pfister, Global assessment of agricultural productivity losses from soil compaction and water erosion, Environ. Sci. Technol. 55 (18) (2021) 12162–12171.
[22] M.F. Nawaz, G. Bourrie, F. Trolard, Soil compaction impact and modelling. A review, Agron. Sustain. Dev. 33 (2) (2013) 291–309.
[23] J. Pfeifer, M. Faget, A. Walter, S. Blossfeld, F. Fiorani, U. Schurr, K.A. Nagel, Spring barley shows dynamic compensatory root and shoot growth responses when exposed to localised soil compaction and fertilisation, Funct. Plant Biol. 41 (6) (2014) 581–597.
[24] T. Colombi, S. Braun, T. Keller, A. Walter, Artificial macropores attract crop roots and enhance plant productivity on compacted soils, Sci. Total Environ. 574 (2017) 1283–1293.
[25] P. Weatherley, Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves, New Phytol. 49 (1950) 81–97.
[26] M. Dubois, K.A. Gilles, J.K. Hamilton, P.A. Rebers, F.A.J.N. Smith, A colorimetric method for the determination of sugars, Nature 168 (4265) (1951) 167, 167.
[27] J. Lipiec, R. Horn, J. Pietrusiewicz, A. Siczek, Effects of soil compaction on root elongation and anatomy of different cereal plant species, Soil Till. Res. 121 (2012) 74–81.
[28] T.A. Valentine, P.D. Hallett, K. Binnie, M.W. Young, G.R. Squire, C. Hawes, A.G. Bengough, Soil strength and macropore volume limit root elongation rates in many UK agricultural soils, Ann. Bot. 110 (2) (2012) 259–270.
[29] M.A. Hamza, W.K. Anderson, Soil compaction in cropping systems: a review of the nature, causes and possible solutions, Soil Till. Res. 82 (2) (2005) 121–145.
[30] A.G. Bengough, M.F. Bransby, J. Hans, S.J. McKenna, T.J. Roberts, T.A. Valentine, Root responses to soil physical conditions; growth dynamics from field to cell, J. Exp. Bot. 57 (2) (2006) 437–447.
[31] S.R. Tracy, C.R. Black, J.A. Roberts, S.J. Mooney, Exploring the interacting effect of soil texture and bulk density on root system development in tomato (*Solanum lycopersicum* L.), Environ. Exp. Bot. 91 (2013) 38–47.
[32] D. Wang, Y. Sun, J. Zheng, N. Zhao, L. Wang, Effects of soil compaction stress on carbohydrate metabolismo of cucumber, J. Plant Nutr Fert. Sci., Pequim 19 (1) (2013) 159–175.
[33] J.M. Arocena, Cations in solution from forest soils subjected to forest floor removal and compaction treatments, For. Ecol. Manag. 133 (1–2) (2000) 71–80.
[34] G.P. Matthews, G.M. Laudone, A.S. Gregory, N.R.A. Bird, A.G. de G Matthews, W.R. Whalley, Measurement and simulation of the effect of compaction on the pore structure and saturated hydraulic conductivity of grassland and arable soil, Water Resour. Res. 46 (5) (2010).
[35] S. Ruiz, I. Straub, S.J. Schymanski, D. Or, Experimental evaluation of earthworm and plant root soil penetration–cavity expansion models using cone penetrometer analogs, Vadose Zone J. 15 (3) (2016) vzj2015.09.0126.
[36] A. Christmann, E.W. Weiler, E. Steudle, E. Grill, A hydraulic signal in root-to-shoot signalling of water shortage, Plant J. 52 (1) (2007) 167–174.
[37] J. Lipiec, V.V. Medvedev, M. Birkas, E. Dumitru, T.E. Lyndina, S. Rousseva, E. Fulajtar, Effect of soil compaction on root growth and crop yield in Central and Eastern Europe, Int. Agrophys. 17 (2) (2003) 61–69.
[38] H. Komatsu, A. Katayama, S. Hirose, A. Kume, N. Higashi, S. Ogawa, K. Otsuki, Reduction in soil water availability and tree transpiration in a forest with pedestrian trampling, Agric. For. Meteorol. 146 (1–2) (2007) 107–114.
[39] B.J. Atwell, The effect of soil compaction on wheat during early tillering: II. Concentrations of cell constituents, New Phytol. 115 (1) (1990) 37–41.
[40] M. Thalmann, D. Santelia, Starch as a determinant of plant fitness under abiotic stress, New Phytol. 214 (3) (2017) 943–951.
[41] N.H. Abu-Hamdeh, Thermal properties of soils as affected by density and water content, Biosyst. Eng. 86 (1) (2003) 97–102.
[42] C.T.S. Beckett, D. Glenn, K. Bradley, A.L. Guzzomi, D. Merritt, A.B. Fourie, Compaction conditions greatly affect growth during early plant establishment, Ecol. Eng. 106 (2017) 471–481.
[43] M. Wang, D. He, F. Shen, J. Huang, R. Zhang, W. Liu, Q. Zhou, Effects of soil compaction on plant growth, nutrient absorption, and root respiration in soybean seedlings, Environ. Sci. Pollut. Res. 26 (22) (2019) 22835–22845.
[44] H. Li, C. Testerink, Y. Zhang, How roots and shoots communicate through stressful times, Trends Plant Sci. 26 (9) (2021) 940–952.
[45] S. Mondal, S. Christopher, D. Chakraborty, P.K. Mandal, Soil compaction affects root growth and gene expression of major N-assimilating enzymes in wheat, J. Soil Sci. Plant Nutr. 22 (3) (2022) 3958–3967.
[46] G. Hernandez-Ramirez, E.J. Lawrence-Smith, S.M. Sinton, F. Tabley, A. Schwen, M.H. Beare, H.E. Brown, Root responses to alterations in macroporosity and penetrability in a silt loam soil, Soil Sci. Soc. Am. J. 78 (4) (2014) 1392–1403.
[47] Y.L. Chen, J. Palta, J. Clements, B. Buirchell, K.H. Siddique, Z. Rengel, Root architecture alteration of narrow-leafed lupin and wheat in response to soil compaction, Field Cro. Res. 165 (2014) 61–70.
[48] T. Colombi, A. Walter, Root responses of triticale and soybean to soil compaction in the field are reproducible under controlled conditions, Funct. Plant Biol. 43 (2) (2016) 114–128.
[49] J.C. Calonego, C.A. Rosolem, Soybean root growth and yield in rotation with cover crops under chiseling and no-till, Eur. J. Agron. 33 (3) (2010) 242–249.
[50] M.T. de Moraes, H. Debiasi, J.C. Franchini, A.A. Mastroberti, R. Levien, D. Leitner, A. Schnepf, Soil compaction impacts soybean root growth in an Oxisol from subtropical Brazil, Soil Till. Res. 200 (2020), 104611.
[51] K. Jin, J. Shen, R.W. Ashton, I.C. Dodd, M.A. Parry, W.R. Whalley, How do roots elongate in a structured soil? J. Exp. Bot. 64 (15) (2013) 4761–4777.
[52] A.R. Dexter, Model experiments on the behaviour of roots at the interface between a tilled seed-bed and a compacted sub-soil: III. Entry of pea and wheat roots into sub-soil cracks, Plant Soil 95 (1) (1986) 149–161.
[53] A.R. Dexter, Amelioration of soil by natural processes, Soil Till. Res. 20 (1) (1991) 87–100.
[54] D.M. Porterfield, M.E. Musgrave, The tropic response of plant roots to oxygen: oxytropism in *Pisum sativum* L, Planta 206 (1) (1998) 1–6.
[55] K.D. Montagu, J.P. Conroy, B.J. Atwell, The position of localized soil compaction determines root and subsequent shoot growth responses, J. Exp. Bot. 52 (364) (2001) 2127–2133.
[56] M. Athmann, T. Kautz, R. Pude, U. Köpke, Root growth in biopores–evaluation with in situ endoscopy, Plant Soil 371 (1) (2013) 179–190.
[57] E. Han, T. Kautz, U. Perkons, D. Uteau, S. Peth, N. Huang, U. Köpke, Root growth dynamics inside and outside of soil biopores as affected by crop sequence determined with the profile wall method, Biol. Fertil. Soils 51 (7) (2015) 847–856.
[58] T. Kautz, U. Perkons, M. Athmann, R. Pude, U. Köpke, Barley roots are not constrained to large-sized biopores in the subsoil of a deep Haplic Luvisol, Biol. Fertil. Soils 49 (7) (2013) 959–963.
[59] R.G. White, J.A. Kirkegaard, The distribution and abundance of wheat roots in a dense, structured subsoil–implications for water uptake, Plant Cell Environ. 33 (2) (2010) 133–148.
[60] T. Nakamoto, The distribution of maize roots as influenced by artificial vertical macropores, Jpn. J. Crop Sci. 66 (2) (1997) 331–332.
[61] R.J. Stirzaker, J.B. Passioura, Y. Wilms, Soil structure and plant growth: impact of bulk density and biopores, Plant Soil 185 (1) (1996) 151–162.