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Compacted soil adaptability of *Brassica napus* driven by root mechanical traits

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ABSTRACT

Soil compaction due to mechanized farming operations is a recurrent issue affecting crop growth and yield. Yet, how soil compaction affects plant functions and ecological strategies is poorly known. With *Brassica napus*, i.e. a widespread crop species as study object, we aim to understand (i) how soil compaction impacts root and shoot traits related to the plant's well-being, nutrient acquisition of *Brassica napus* with different mechanical robustness, as well as their trade-offs, and (ii) how such impacts vary among different cultivars. To do this, we cultivated six cultivars of *Brassica napus* in non-compacted (control) and compacted (treatment) soils, respectively, in a sand culture system. After harvesting, a series of mechanical, morphological and chemical traits of roots and/or shoots were measured. Results showed that soil compaction significantly limited root penetration depth and root system establishment in morphological traits, leading further to significant reduction in nutrients acquisition and plant biomass accumulation. However, soil compaction significantly increases the average root diameter and root/shoot ratio, and facilitate more root exudates secretion (e.g. organic acids and polysaccharides) of *Brassica napus* cultivars. The *Brassica napus* cultivars with large root mechanical traits (e.g. root tensile force, root tensile strength and modulus of elasticity) had higher root cellulose and lignin concentrations and showed a stronger response in maximum root depth and specific root length compared with *Brassica napus* cultivars with small root mechanical traits in compacted treatment, which resulted in the greater fine root length and more root exudates secretion at root-soil interface. Furthermore, deep rooting enhanced nutrients acquisition and further biomass accumulation in compacted soil. Totally, the *Brassica napus* cultivars with large root mechanical traits with more fine roots and root exudates were critical for *Brassica napus* root penetration into a deep soil layer in compacted soil.

1. Introduction

In modern agricultural system, soil compaction is mainly sourced from the improper agricultural management, such as the use of heavy machinery, soil drying, long-term no-tillage and intensive agricultural production (Shah et al., 2017; Keller et al., 2019; Mirzavand and Moradi-Talebbeigi, 2021; Ferreira et al., 2021) and is a recurrent problem worldwide. Approximately 68 million hectares of the world's land is degraded due to compaction (Flowers and Lal, 1998; Hamza and Anderson, 2005). The yield loss due to soil compaction has been estimated up to 20% (Barken et al., 1981) or even up to 50–75% (Flowers and Lal, 1998; Hoque and Kobata, 2000; Wolkowski and Lowery, 2008).

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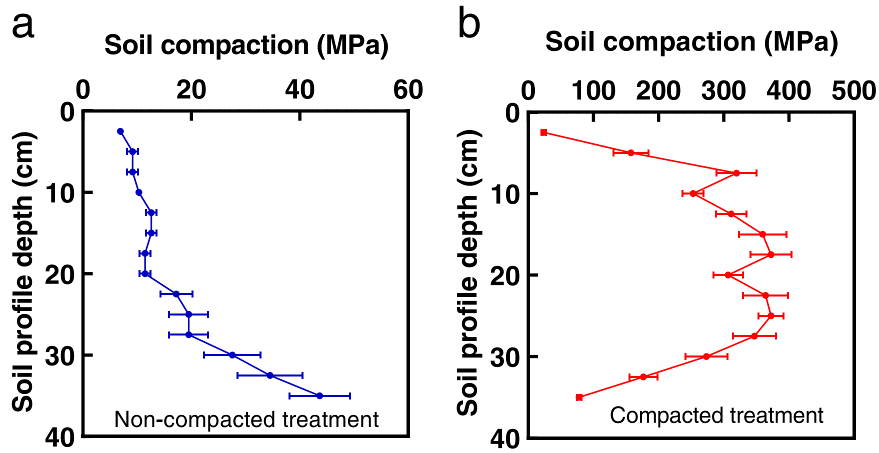

Fig. 1. Penetration resistance at different soil profile depth in non-compacted (a) and compacted (b) treatment, respectively.

Soil compaction causes a degraded soil structure, which could decrease soil void space available for displacement of soil particles, increase penetrating cost for plant roots (Hamza and Anderson, 2005; Batey, 2009) and lead to low connectivity and continuity of the pore space to reduce water and air transport capability of soil (Kuncoro et al., 2014; Keller et al., 2017).

Roots are the first and most direct plant organ subjected to soil compaction and their multifunctionality, such as water and nutrient uptake and scavenging, and resistance to uprooting, can be potentially affected in cultivated lands. Soil compaction can modify root morphological traits through limiting maximum rooting depth and decreasing the size of root system, reducing root elongation rate, increasing radial growth and changing the amount of root branching (Tracy et al., 2012; Correa et al., 2019). Besides limited root growth, soil compaction significantly affects the shoot performance by nutrients deficiency (Lipiec and Stępniewski, 1995; Colombi and Keller, 2019). Improving the adaptation ability of roots to soil compaction in deep soil layer will provide benefit for the plant establishment in shoot and root by enhancing the water and nutrients acquisition (Jin et al., 2015; Wang et al., 2019). Yet, the impact of soil compaction on roots' functions and their adaptive strategies still remains poorly understood.

Plasticity of roots to compacted soil has been studied previously mainly associated to morphological, biochemical and mechanical traits (Jin et al., 2017; Correa et al., 2019; Vanhees et al., 2020; Bello-Bello et al., 2022), which included (1) a plant with thicker roots tends to enhance its axial force and radial expansion in penetrating through the compacted soil (Chen and Weil, 2010; Colombi et al., 2017). Meanwhile, fine roots with small diameter relative to the small pores distribution in compacted soil could promote roots to penetrate and elongate in the textural pores spaces where there were sufficient small pores in compacted soil (Fukao and Bailey-Serres, 2004; Bodner et al., 2014). (2) The induction of organic and inorganic compounds in the root-soil interface by soil compaction could serve as the lubricant to decrease the resistance source from the friction between root surface and soil particles (Bengough and McKenzie, 1997; Groleau-Renaud et al., 1998; Iijima et al., 2004; More et al., 2020), mainly through improving the soil compression characteristics to ease penetration and enhance the recovery of root induced soil compaction (Oleghe et al., 2107); (3) plants with stronger (i.e., greater root tensile force and strength) and stiffer roots (i.e. greater modulus of elasticity) have an enhanced penetration ability against the strongly-compacted soil layers (Clark et al., 2008; Chimungu et al., 2015; Lee et al., 2020). Root thickening at the root tips can interpret the root penetration outcomes by increasing the root axial force in increased soil strength (Whiteley et al., 1982; Clark et al., 2002; Hanbury and Atwell, 2005; Jin et al., 2013).

Root mechanical traits are key metrics in studying the plant anchorage and root penetration into soil (Chimungu et al., 2015). Root functions in compressive, buckling, twisting and/or bending behaviour are important in response to soil compaction and root setting (Bourrier et al., 2013; Mao et al., 2014; Schwarz et al., 2015; Johnson et al., 2016). The root mechanical traits mostly related to the tensile force, tensile strength, modulus of elasticity and tensile strain. Wide variations in root mechanical traits among species mainly depends on root size (Gray and Barker, 2004; Ghestem et al., 2014; Mao et al., 2018; Xu et al., 2021), root moisture contents (Yang et al., 2016; Zhang et al., 2019; Ekeoma et al., 2021), root types (Loades et al., 2015; Mao et al., 2023), root structure (Genet et al., 2005; Zhang et al., 2014; Zhu et al., 2020) and root anatomy (Chimungu et al., 2015; Schneider et al., 2021). For example, the roots with multiseriate cortical sclerenchyma have greater root lignin concentration and root bending strength, and greater root penetration depth in compacted soils (Schneider et al., 2021). The impact of the root mechanical traits on the root penetration ability needs to be explored, which will be helpful for revealing the potential adaptative mechanism of roots' function traits driven by root mechanical traits in reaction to compacted soil (Stokes et al., 2009).

Oilseed rape (*Brassica napus* L.) is the most important edible oil crops and has abundant germplasm resources in China as well as in the world (Hu et al., 2017; Friedt et al., 2018; Li et al., 2020). Most of the cultivated soil in the main planting area of *Brassica napus* in Yangtze River basin of central China are poorly drained clay soils, and have poor soil pore system (Xi, 1998; Wang et al., 2021). In addition, the frequency of mechanized harvesting of *Brassica napus* has aggravated the soil compaction recently (Zhang et al., 2006; Wang et al., 2015; Correa et al., 2019). For example, the average soil bulk density at topsoil (5–10 cm) is about 1.38 g/cm^3, while the soil bulk density up to 1.52 g/cm^3 at plow pan (Ji et al., 2013), which are much higher than the ideal soil bulk density of 1.2–1.3 g/cm^3 (Li and Zhou, 1994). Oilseed rape is sensitive to soil compaction (Blake et al., 2006) and the seed yield significantly decreased under high soil compaction stress (Alakukku and Elonen, 1995; Arvidsson and Håkansson, 2014; Bogunovic et al., 2018; Orzech et al., 2021). And the adaptability of different oilseed rape species to compacted soil depends on root characteristics, such as root morphology (Wang et al., 2021), root penetration depth (Peltonen-Sainio et al., 2011), root size (Chen and Weil, 2010; Zhang et al., 2022) and root type (Chen and Weil, 2010).

In this study, we firstly determined the variation in root mechanical traits and its effect on root depth of six *Brassica napus*, and further investigated the root morphological and biochemical traits plasticity and their effects on nutrients acquisition and plant biomass accumulation of the *Brassica napus* cultivars grown in compacted soil. Thus, the objective of the study is 1) to clarify the responses of the six *Brassica napus* cultivars to soil compaction and 2) the root plasticity to soil compaction for different *Brassica napus* cultivars.

Table 1
Soil bulk density and total porosity of soil in non-compacted and compacted treatments.

Treatment	Soil bulk density (g cm^{-3})	Total porosity of soil (%)[1]
Non-compacted treatment	1.30	51.33
Compacted treatment	1.60	40.10

Note: [1] The total porosity of soil (%) was calculated with the formula by Hao et al. (2008).

2. Materials and methods

2.1. Plant materials and growth conditions

In this study, six *Brassica napus* cultivars were selected from an association panel collected from major breeding centers across China (Liu et al., 2016), and among them, *Brassica napus* cultivars of MJDT, A148 and R2 have large root mechanical traits (F, T_r and E_r) and cultivars of NY7, 11-Y7–117 and 1368 have small root mechanical traits (Table S1). A sand-culture system was used to investigate the response of *Brassica napus* to soil compaction in this study, which allows mechanical impedance to be varied independent of aeration and water status of the growing medium (Coelho Filho et al., 2013; Jin et al., 2015). Rigid plastic tubes with 45 cm in length and 15 cm in diameter were placed in tanks with nutrient solution on a base. Each tank contains six tubes, and each tube contains one *Brassica napus* seedling (Fig. S1A). The tubes were filled with mixed quartz sand (88.89% fine sand with 0.23 mm particle size on average, and 11.11% coarse sand with 0.69 mm particle size on average) and adequate nutrient solution. Compaction is directly proportional to soil bulk density (Popova et al., 2016). Low (1.30 g/cm^3) and high (1.60 g/cm^3) bulk density were quantified by adding different masses of sand soil to the tubes with the same volume, which represented non-compacted and compacted treatments, respectively. The changes of penetration resistance along soil profile depth in non-compacted and compacted treatments were shown in Fig. 1, respectively. The penetration resistance was measured by a soil compaction meter (Field Scout SC900 soil compaction meter, Spectrum Technologies, Inc., IL, USA) in 2.5 cm increments from soil surface to 30 cm depth with four repetitions. The total porosity and particle density of sand were calculated at non-compacted and compacted treatments (Table 1 and Table S2). The soil water potential is basically similar between two bulk density treatments in the well-watered sands. Each treatment for each cultivar has four replications in this study.

Seeds were sterilized using 70% (v/v) ethanol and NaOCl (2.5% active chlorine), and then placed on gauze with pure water containing 0.5 μM $CaCl_2$ for germination. The germinated seeds with about 1.0 cm length primary root were transplanted and grown in the center of sand core. *Brassica napus* seedlings were grown in an illuminated growth chamber under 16-h-light/8-h-dark photoperiod (with a photo flux density of 300–320 μmol m^{-2} s^{-1} at plant height) and 60% relative humidity. The modified Hoagland nutrient solution contains 5.0 mM $Ca(NO_3)_2{\cdot}4H_2O$, 5.0 mM KNO_3, 2.0 mM $MgSO_4{\cdot}7H_2O$, 1.0 mM KH_2PO_4, 50 μM Fe-EDTA, 50 μM H_3BO_3, 9.5 μM $MnCl_2{\cdot}4H_2O$, 0.8 μM $ZnSO_4{\cdot}7H_2O$, 0.3 μM $CuSO_4{\cdot}5H_2O$ and 0.4 μM $Na_2MoO_4{\cdot}2H_2O$. A total of 60 L nutrient solution was supplied in each tank.

Brassica napus plants were harvested at 35 d after transplanting when the difference in the growth phenotypes were observed between plants grown in non-compacted and compacted treatments. Firstly, we tested the variations of root mechanical traits and maximum root depth of the six *Brassica napus* cultivars. Secondly, the root morphological traits (total root length, coarse root length, fine root length, root surface area, average root diameter and specific root length), root biochemical traits (organic acid concentration, xylose concentration, glucose concentration and uronic acid concentration), plant biomass parameters (root and shoot dry weight, root/shoot ratio), and nitrogen (N), phosphorus (P) and potassium (K) concentrations and contents in shoot and root of plants were determined.

2.2. Measurement of maximum root depth

At harvest time, the tube grown plants were pulled out carefully from the top of the sand column, and then the sand was carefully removed

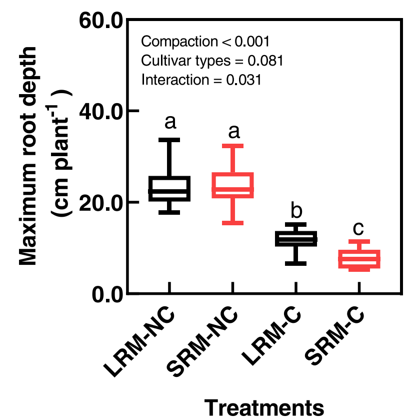

Fig. 3. Maximum root depth of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant difference among four treatments at $P < 0.05$.

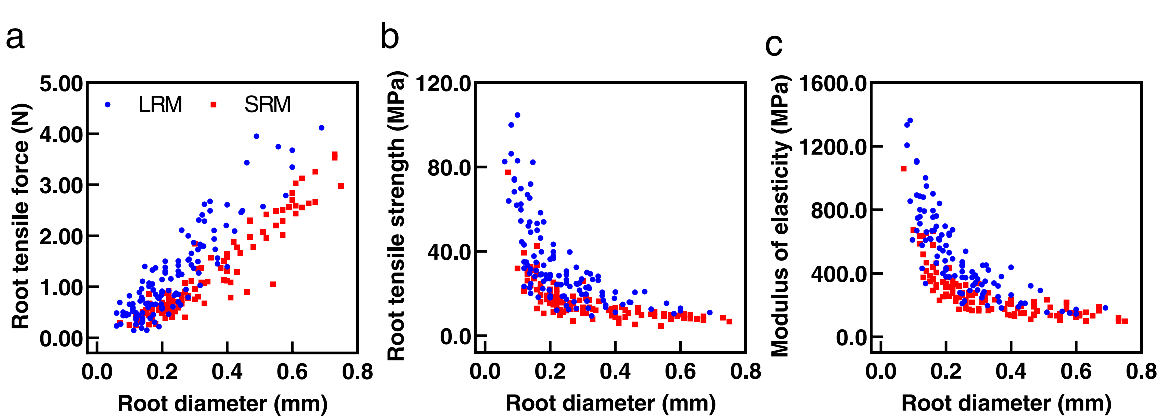

Fig. 2. Correlations between root tensile force (a), root tensile strength (b), modulus of elasticity (c) and root diameter of LRM or SRM cultivars in compacted treatment. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits.

Table 2
The effects of soil compaction on the root morphological and biochemical traits of six *Brassica napus* cultivars.

	Root morphological traits							Root biochemical traits			
Effect	TRL (cm plant^{-1})	RSA (cm^2 plant^{-1})	ARD (mm plant^{-1})	SRL (m root length g^{-1} RDW)	CRL (cm plant^{-1})	FRL (cm plant^{-1})	MRD (cm plant^{-1})	GC (mg g^{-1} RDW)	XC (mg g^{-1} RDW)	UAC (mg g^{-1} RDW)	OAC (mmol g^{-1} RDW)
Compaction	38.13 * **	40.56 * **	16.67 * **	7.79 * **	5.90 *	41.95 * **	167.02 * **	10.57 * *	10.72 * **	25.93 * **	10.37 * *
Cultivars	7.96 * *	9.34 * *	1.32 ns	7.07 *	1.01 ns	3.63 *	1.52 ns	48.07 * **	75.73 * **	3.43 *	7.35 * *
Compaction × Cultivars	0.93 ns	4.21 *	4.43 *	0.04 ns	1.47 ns	0.07 ns	2.71 ns	0.71 ns	0.05 ns	1.11 ns	0.16 ns

Note: TRL, total root length; RSA, root surface area; ARD, average root diameter; SRL, specific root length; CRL, coarse root length; FRL, fine root length; MRD, maximum root depth; GC, glucose concentration; XC, xylose concentration; UAC, uronic acid concentration; OAC, organic acid concentration and RDW, root dry weight. A two-way ANOVA was conducted to test the significance of genotypes, treatments and their interaction on the investigated traits. ns, no significant differences, * : $P < 0.05$, * *: $P < 0.01$, * ** : $P < 0.001$.

from the tube bottom till the root tips appeared (Fig. S1B). The maximum root depth was determined by the vertical distance measured from the primary root base to the root tips by ruler with the accuracy of 0.1 cm.

2.3. Measurements of root mechanical traits and root cellulose and lignin content

The first-order lateral roots of more than 10 cm length of the plant were sampled to test root mechanical properties. Root samples were firstly preserved in an alcohol solution contained 15% ethanol and then kept in a refrigerator at 4 °C (Bischetti et al., 2003). Thirty to forty-five undamaged roots were used to test the root mechanical properties with a universal testing machine (model5967, Instron® Corporation) that was fitted with a 50-N load cell with an accuracy of 2 mN. Root segments were manually clamped with two grips and further fixed with strips of sandpaper and 502 Super Waterglue to increase friction. Force of loaded was recorded during tensile testing with extension at the constant rate of 5 mm min^{-1} (Giadrossich et al., 2017). The diameters of root segment were gauged by vernier caliper with 0.02 mm accuracy. Each root segment was measured three times, in the center of the root segment, to the left and right of the center adhering to both grips, respectively. The average root diameter was used to calculate the root cross-sectional area (Mao et al., 2018). The root tensile force (F, N) and extension (ΔL, mm) were recorded until the root segment was broken. The root tensile strength (T_r, MPa) was calculated as maximum force at failure divided by root cross-sectional area. The root tensile strain (ε_r, %) was calculated by dividing root extension by unstrained root length. The elasticity of modulus (E_r, MPa) corresponds to the slope of the curve of stress-strain within the quasi-liner elastic stage of a root in tension. The calculation method of elasticity of modulus was referenced from the method by Mao et al. (2018). The crude cell wall of roots was extracted by 95% ethanol and ethanol-hexane (1:2) separately and then dried at 55 °C in oven. And the cellulose content was measured by the phenol–sulfuric acid method based on the Masuko et al. (2005) and Nielsen (2010). Total lignin content was measured by the acetyl bromide method in *Brassica napus* roots based on the Iiyama and Wallis (1990).

2.4. Measurements of root morphological and biochemical traits

The collection method of root exudates was modified from Boeuf--Tremblay et al. (1995) and Pearse et al., (2006, 2007). At harvest time, the plant was lifted carefully from the plastic tube and bulk soil (sand) was shaken off from the root system immediately, and the sand adhering to the roots was defined as rhizosphere soil. Roots were then immersed into a 200 mL container with 40 mL 0.2 mM $CaCl_2$ solution for 1–2 min to remove mostly rhizosphere soil. All extracts were poured into a 50 mL centrifuge tube and then centrifugated using an Eppendrof 5810 R centrifuge (Eppendorf, Hamburg, Germany) at 3000 g for 15 min to discard root debris and sloughed cells. The supernatant was freeze-dried and redissolved in 8 mL of distilled water.

The extracts of separate 2 mL were used to quantify the glucose and xylose concentrations by anthrone-sulfuric acid assay, respectively (Leyva et al., 2008). A hydroxybiphenyl method was used to test the uronic acid concentration with 2 mL suspension (Filisetti-Cozzi and Carpita, 1991). The rest of the 2 mL extract was used to analyze carboxylates by a reversed phase high-performance liquid chromatography (HPLC) system on an Agilent column (Agilent 1200, equipped with a C18 250 ×4.6 mm ion-exclusion column, Alltima, America) (Wang et al., 2007; Li et al., 2016).

After collection of root exudates, the roots were cleaned by flow water and then scanned with a modified flatbed scanner (Epson V700, Nagano-ken, Japan). The total root length, fine root length, coarse root length, root surface area and average root diameter were analyzed by WinRHIZO software (Regent Instruments Inc., Quebec, Canada).

2.5. Plant biomass and nutrients analyses

Shoots and roots were dried at 80 °C for 3 days to test the root and shoot dry weight. Then, the dried samples were ground to powder and digested with sulfuric acid and hydrogen peroxide in a microwave oven. The N and P concentrations were determined using a fully automated flow-injection system and colorimetry (Sullivan and Havlin, 1991; Alves et al., 2000). The K concentration was determined by a flame photometry (Gao et al., 2005).

2.6. Statistical analyses

The statistical analysis of the data was conducted by SPSS software (SPSS 19.0; IBM Corporation, Armonk, NY, USA). Analysis of Variance (ANOVA) was used to compare the effects of soil compaction on root morphological traits, root biochemical traits, plant biomass and nutrients concentrations and contents in root and shoot among six *Brassica napus* cultivars. Pearson's correlation analysis was used to test the linear correlations among root morphological and root biochemical traits. Principal component analysis (PCA) was used to evaluate the relationships among eleven root traits (including root morphological traits and root biochemical traits) in non-compacted and compacted treatments, respectively. The first three principal components were used to describe the relationships among eleven root traits.

3. Results

3.1. Root mechanical traits and maximum root depth of Brassica napus in response to compacted soil

The root tensile force (F) increased significantly with increasing diameter of six *Brassica napus* cultivars regardless of the compaction treatment (non-compacted versus compacted) (Fig. 2a, Fig. S2a and Table S3). The root tensile strength (T_r) and elasticity of modulus (E_r) of *Brassica napus* cultivars decreased with increasing diameter following a non-linear relationship (Fig. 2b, c, Fig. S2b, c and Table S3). There was

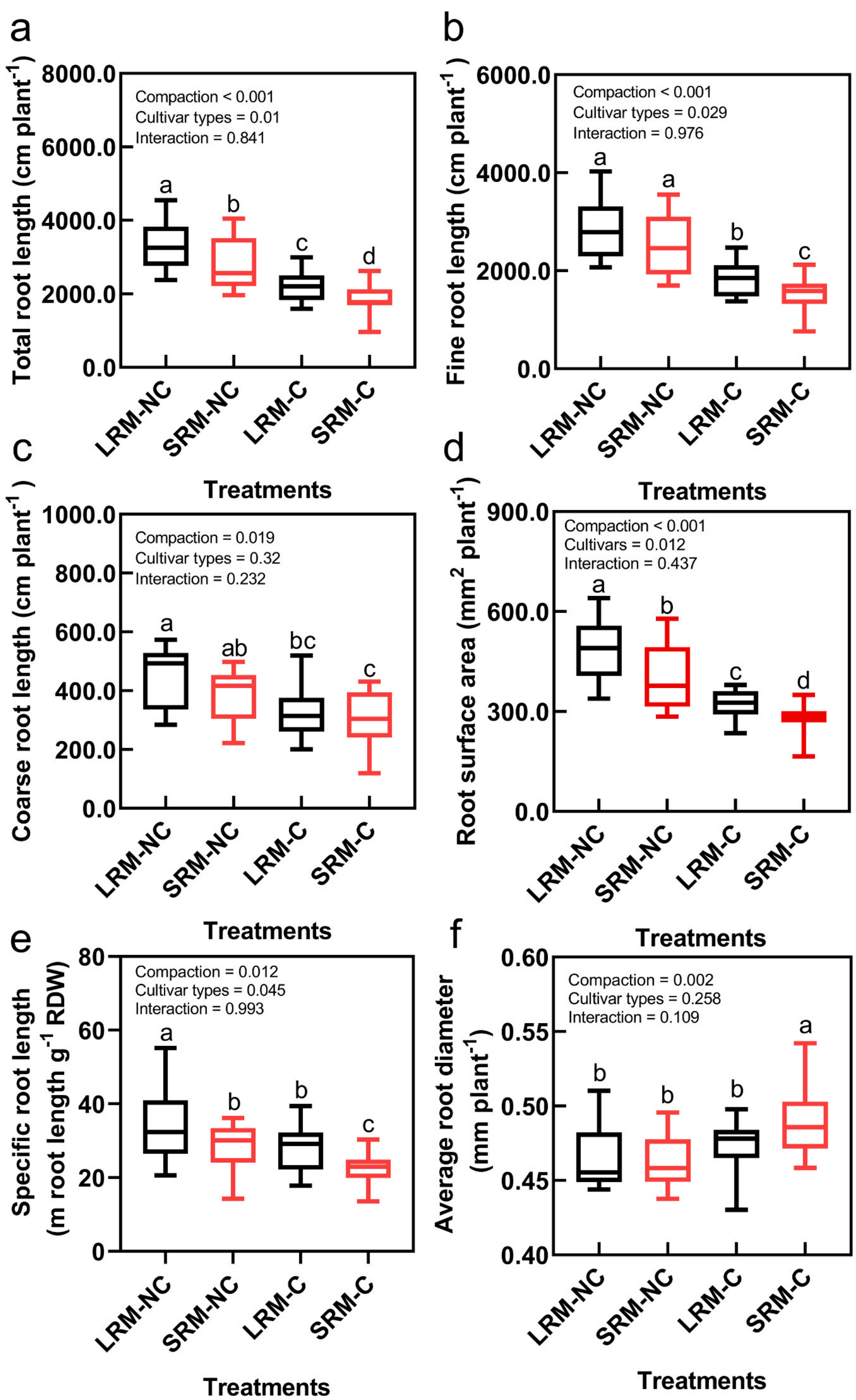

Fig. 4. Root morphological traits of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. Total root length (a), fine root length (b), coarse root length (c), root surface area (d), specific root length (e) and average root diameter (f). LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant difference among four treatments at $P < 0.05$.

no significant difference in root mechanical traits (F, T_r and E_r) among six *Brassica napus* cultivars in non-compacted treatment (Fig. S2). However, in the compacted treatment, the three LRM cultivars (MJDT, A148 and R2) had significantly larger root mechanical traits (F, T_r and E_r) than SRM cultivars (NY7, 11-Y7–117 and 1368) (Fig. 2). There was no significant difference among six *Brassica napus* cultivars for root tensile strain (ε_r) whether in non-compacted or compacted treatments (Fig. S3). And we also found higher cellulose and lignin concentration in roots of LRM cultivars compared with SRM cultivars, especially in compacted treatment (Fig. S4). The maximum root depth (MRD) of all the six cultivars of the compacted treatment was 59.4% smaller than that of the non-compacted treatment (Fig. 3). In compacted treatment, LRM cultivars had a significantly larger maximum root depth compared with SRM cultivars (Fig. 3), while no significant difference between LRM and SRM cultivars was found in non-compacted treatment (Fig. 3).

3.2. Root morphological and biochemical traits of Brassica napus in response to compacted soil

The effects of soil compaction on root morphological and biochemical traits of *Brassica napus* were significant at $P < 0.05$–0.001 (Table 2). The genotypic differences among six *Brassica napus* cultivars were also observed at $P < 0.05$–0.01 in total root length (TRL), root surface area (RSA), specific root length (SRL) and fine root length (FRL). Significant differences were also observed in glucose concentration (GC), xylose concentration (XC), uronic acid concentration (UAC) and organic acid

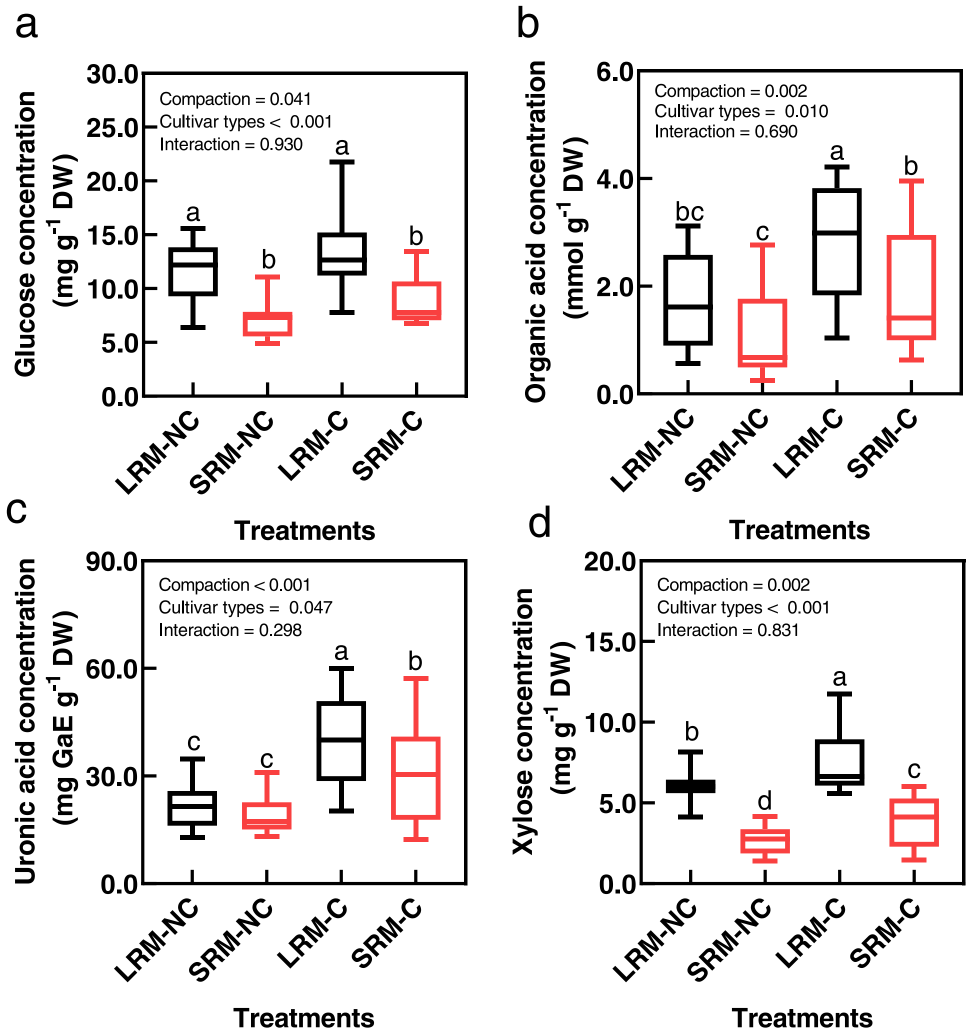

Fig. 5. The concentrations of glucose (a), organic acids (b), uronic acid (c) and xylose (d) of root exudates of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant difference among four treatments at $P < 0.05$.

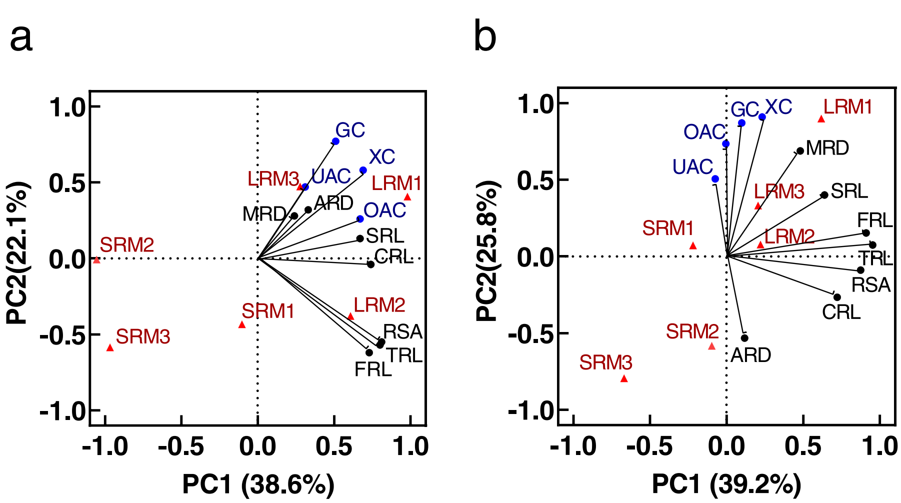

Fig. 6. Principal component analysis of root morphological traits (TRL, CRL, FRL, RSA, SRL, ARD and MRD) and root biochemical traits (UAC, GC, XC and OAC) of six *Brassica napus* cultivars (LRM1, LRM2, LRM3, SRM1, SRM2 and SRM3) in non-compacted (a) and compacted (b) treatments, respectively. TRL, total root length; CRL, coarse root length; FRL, fine root length; RSA, root surface area; SRL, specific root length; ARD, average root diameter; MRD, maximum root depth; GC, glucose concentration; XC, xylose concentration; UAC, uronic acid concentration; OAC, organic acid concentration; LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits.

concentration (OAC) of root exudates at $P < 0.05$–0.001 (Table 2). The interaction effects between compaction treatment and cultivars were observed only in RSA and average root diameter (ARD) ($P < 0.05$) (Table 2).

The mechanical impedance significantly impeded root growth and elongation in TRL, RSA, SRL, FRL and CRL, but increased ARD (Fig. 4). Compared with SRM cultivars, LRM cultivars were 23.4% greater in TRL, 17.8% greater in RSA, 22.8% greater in FRL, 6.8% greater in CRL

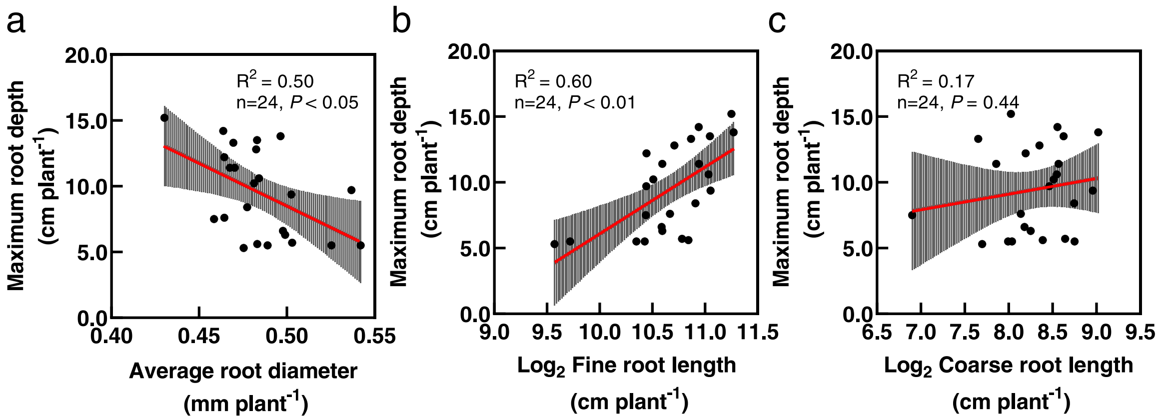

Fig. 7. Correlations between maximum root depth and average root diameter (a), fine root length (b) and coarse root length (c) of six *Brassica napus* cultivars in compacted treatment. The shaded areas indicate the 95% confidence range, derived from the models.

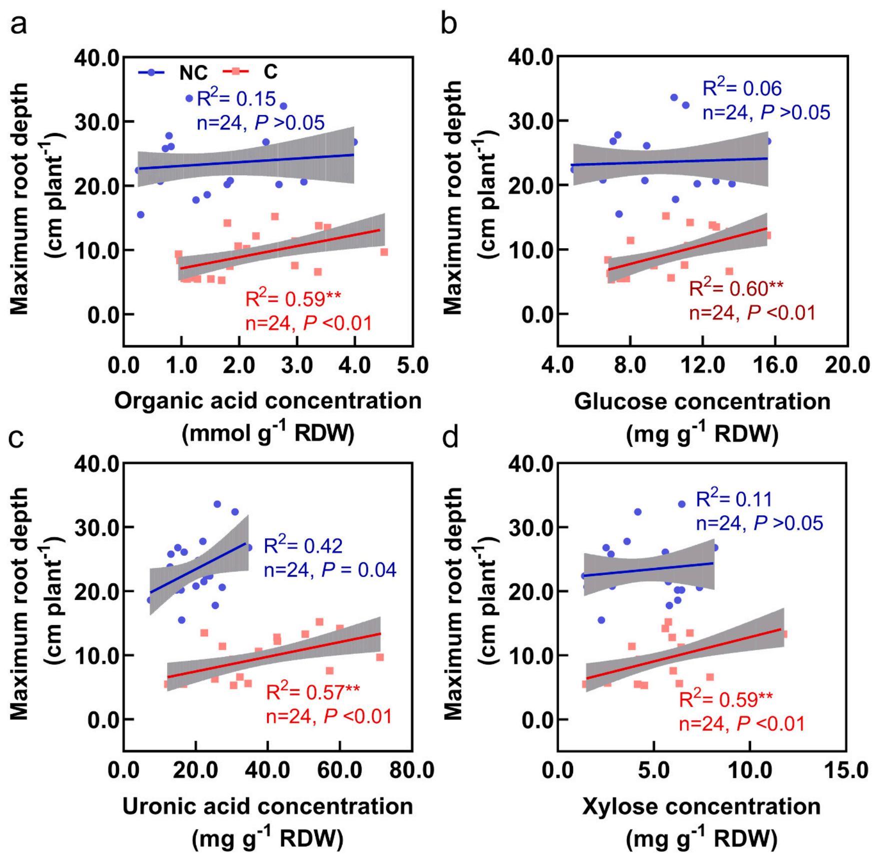

Fig. 8. Correlations between maximum root depth and organic acids (a), glucose (b), uronic acid (c) and xylose (d) concentrations of six *Brassica napus* cultivars in both non-compacted (NC) and compacted (C) treatments. The shaded areas indicate the 95% confidence range, derived from the models. * $P < 0.05$, $^{**}P < 0.01$.

and 23.9% greater in SRL, but 3.6% less in ARD in compacted treatment (Fig. 4). The mechanical impedance also stimulates *Brassica napus* roots to secrete more glucose, uronic acid, xylose and organic acid components in the rhizosphere (Fig. 5 and Table S4). Compared with SRM cultivars, LRM cultivars were 49.0% greater in glucose, 91.7% greater in xylose, 28.3% greater in uronic acid and 47.6% greater in organic acid of root exudates (Fig. 5).

3.3. Trade-offs among root-related traits in response to compacted soil

The principal component analysis of the eleven root functional traits of six *Brassica napus* cultivars in non-compacted treatment explained 77.2% of the variation in the first three principal components, and the first component (PC1) represented 38.6% of the variability and was dominated by TRL, CRL, SRL, RSA, OAC and XC; the second component (PC2) represented 22.1% of the variability and was dominated by UAC and GC; the third component (PC3) accounted for 16.4% of the variability and was dominated by ARD and MRD (Fig. 6a and Table S5). And the LRM cultivar was clustered in the direction of OAC (e.g. LRM1), the direction of GC, UAC and MRD (e.g. LRM3) and the direction of RSA and TRL (e.g. LRM2). In compacted treatment, the first three traits of the PCA accounted for 39.2%, 25.8% and 10.9% of the total variation, respectively. The root morphological traits (such as TRL, CRL, FRL, MRD, SRL, RSA) scored high in PC1, the root biochemical traits (such as

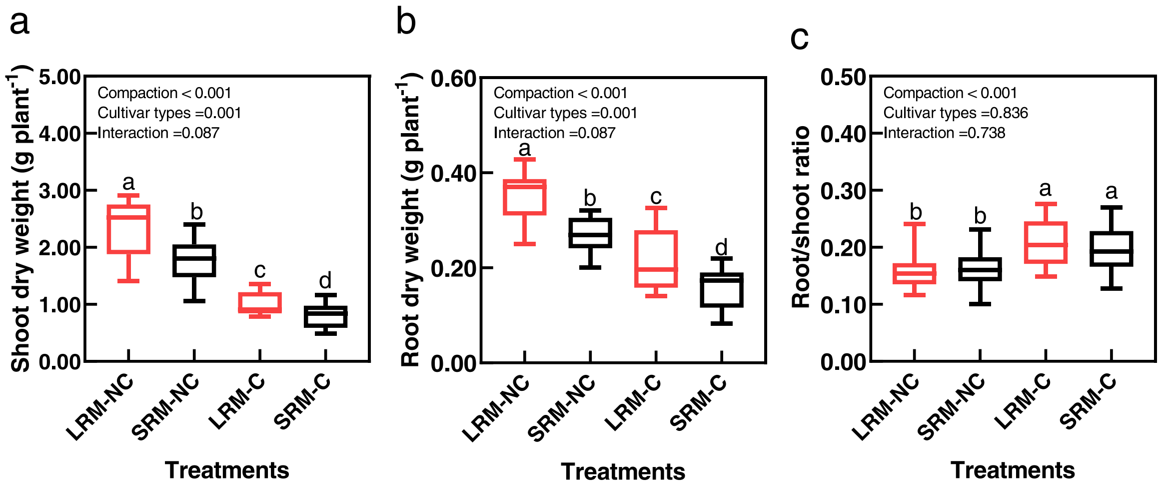

Fig. 9. Shoot dry weight (a), root dry weight (b) and root/shoot ratio (c) of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant difference among four treatments at $P < 0.05$.

UAC, OAC, GC and XC) scored high in PC2, and the ARD and MRD scored high in PC3 (Fig. 6b and Table S5). Cultivars LRM1 and LRM3 were clusters in the direction of MRD, and the cultivar LRM2 was cluster in the direction of FRL and SRL (Fig. 6b).

3.4. *Correlations between maximum root depth and root morphological, biochemical traits of Brassica napus in compacted soil*

Across six *Brassica napus* cultivars, the MRD and CRL had significant positive correlation with ARD, and the FRL and RSA both had significant positive correlations with CRL in non-compacted treatment ($P < 0.01$–0.001, Fig. S5). However, in compacted treatment, MRD had significant negative correlation with ARD ($P < 0.05$, Fig. 7a). In addition, MRD had significant positive correlation with FRL ($P < 0.05$, Fig. 7b), but had no significant correlation with CRL ($P = 0.44$) in compacted treatment (Fig. 7c). Meanwhile, SRL had significant positive correlation with glucose, xylose, uronic acid and organic acid concentrations in compacted treatment (Fig. S6). The maximum root depth also had significant correlation with organic acid, glucose, xylose and uronic acid concentrations in compacted treatment (Fig. 8).

3.5. *Plant biomass and nutrients acquisition of Brassica napus in response to soil compaction*

A significant reduction of shoot dry weight (SDW), root dry weight (RDW) and nutrients (N, P and K) concentrations and contents of *Brassica napus* were observed in compacted treatment (Fig. 9a, b, Fig. 10 and Fig. S7). However, the root/shoot ratio significantly increased in compacted treatment compared with non-compacted treatment in both LRM and SRM cultivars (Fig. 9c). The genotypic differences were observed among six *Brassica napus* cultivars both in SDW and RDW ($P = 0.001$, Fig. 9), and also in N, P and K contents of root ($P = 0.001$) and shoot ($P = 0.013$ to < 0.001) in both non-compacted and compacted treatments (Fig. 10). Soil compaction had significant effects on the nutrient concentrations of N, P and K in shoot and root ($P < 0.001$, Fig. S7). There was no significant difference in shoot N, P and K concentrations among six cultivars, however, significant differences were found in root N and K concentrations among cultivars both in non-compacted and compacted treatments (Fig. S7). Compared with SRM cultivars, LRM cultivars had significantly larger SDW and RDW, and N, P and K contents in shoot and root both in compacted and non-compacted treatments (Fig. 9 and Fig. 10); and higher N, P and K concentrations in root in compacted treatment. There was no significant difference in shoot N, P and K concentrations whether in compacted or non-compacted treatment (Fig. S7).

4. Discussion

It is an important strategy to enhance the biological potential with superior root traits to break the limitation of soil compaction stress by plants (Alameda and Villar, 2012; Grzesiak et al., 2013; Correa et al., 2019). In this study, the *Brassica napus* cultivars with large root mechanical traits (LRM) had higher root lignin and cellulose concentrations and greater rooting depth compared with *Brassica napus* cultivars with small root mechanical traits (SRM) in compacted soil (Fig. 2, Fig. 3, Fig. 11 and Fig. S4). Additionally, the former had more fine roots accompanied by more root exudates in rhizosphere than the latter in compacted treatment. These result in more nutrients uptake and higher biomass accumulation in LRM cultivars than SRM cultivars (Fig. 4, Fig. 5, Fig. 9 and Fig. 10). The penetration of roots through the compacted soil promotes plant growth while increasing soil voids due to the large taproot system of *Brassica napus* (Kautz, 2015; Semwal et al., 2020). It is beneficial for the root establishment of staple crops along the soil pores in structural soil and adherence to more water and nutrients (Gao et al., 2012; Jin et al., 2013).

Deep root development in compacted soil is associated with the root traits modification, maximum root system establishment and elongation in vertical and horizontal directions (Comas et al., 2013; Pérez-Ramos et al., 2013; Zwicke et al., 2015; Wu et al., 2022). However, the soil properties significantly affect deep root development, especially in the drought and high soil bulk density condition associated to the soil compaction (Cairns et al., 2011; Correa et al., 2019). In this study, rooting depth of *Brassica napus* in compacted treatment was 59.4% smaller than in non-compacted treatment (Fig. 3). In addition, LRM cultivars had larger root biomechanical properties parameters including tensile force, tensile strength and modulus of elasticity, and had a deeper rooting growth compared with SRM (Fig. 3). These are consistent with previous studies that stiffer roots with large tensile force, tensile strength and modulus of elasticity are associated with greater rooting depth in strong soil (Clark et al., 2008; Chimungu et al., 2015; Lee et al., 2020). Meanwhile, high cellulose or lignin concentrations in cell wall are associated with larger root tensile strength and modulus of elasticity values (Marga et al., 2003; Genet et al., 2005; Zhang et al., 2014), especially for lignin, deposited in the walls of secondarily thickened cells, making them rigid and impervious (Degenhardt and Gimmler, 2000; Zhang et al., 2011). Lee et al. (2020) has reported tree species with large root tensile strength and Young's modulus has deeper and more abundant root system. We hypothesized that large root mechanical traits

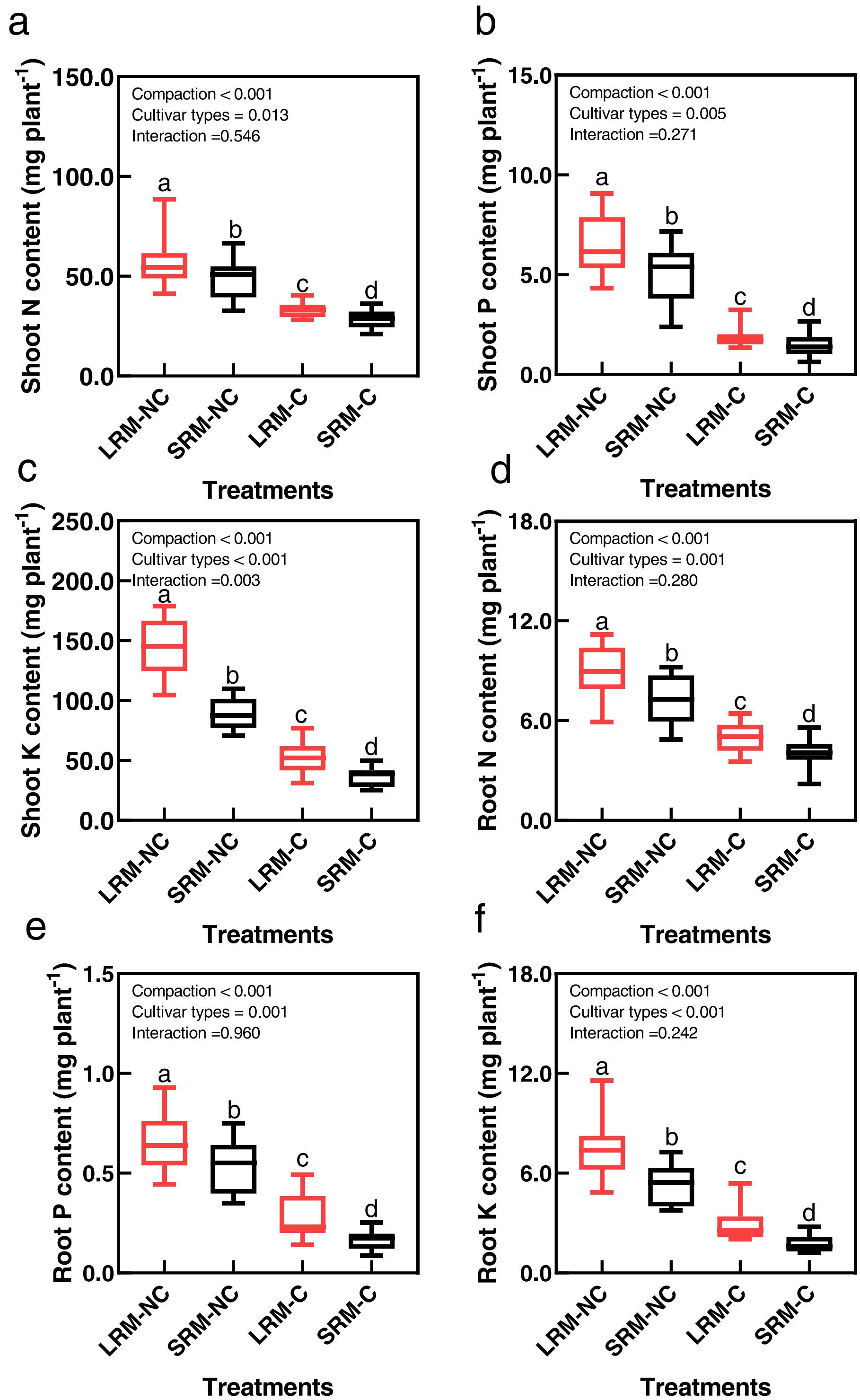

Fig. 10. The contents of nitrogen (N), phosphorus (P) and potassium (K) in shoot (a-c) and root (d-f) of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant difference among four treatments at $P < 0.05$.

might be attributed to the stiff root cell wall structure decided by the cell wall components (Fig. 3 and Fig. S5).

In this study, with the increasing root diameter, the root tensile force of *Brassica napus* grows larger in both non-compacted and compacted treatments (Fig. 2 and Fig. S3). Generally, compared with fine roots, coarse roots with a large axial force and radial expansion could increase root penetration probability when roots encounter a strong soil layer (Whiteley et al., 1982; Clark et al., 2008). However, our results showed that the trade-offs of root morphological traits with more fine roots, rather than coarse roots, had significant positive correlation with root penetration depth in compacted treatment (Fig. 7). Fine roots had an important function in resistance to compacted soil stress, which might be depended on that (1) the shorter and narrower root caps benefit to increase axial force per root cross-sectional area and facilitate penetration through the dense soil layer in mechanical impedance (Souty and Rode, 1987; Iijima et al., 2003) and that (2) the micro-pores proportion

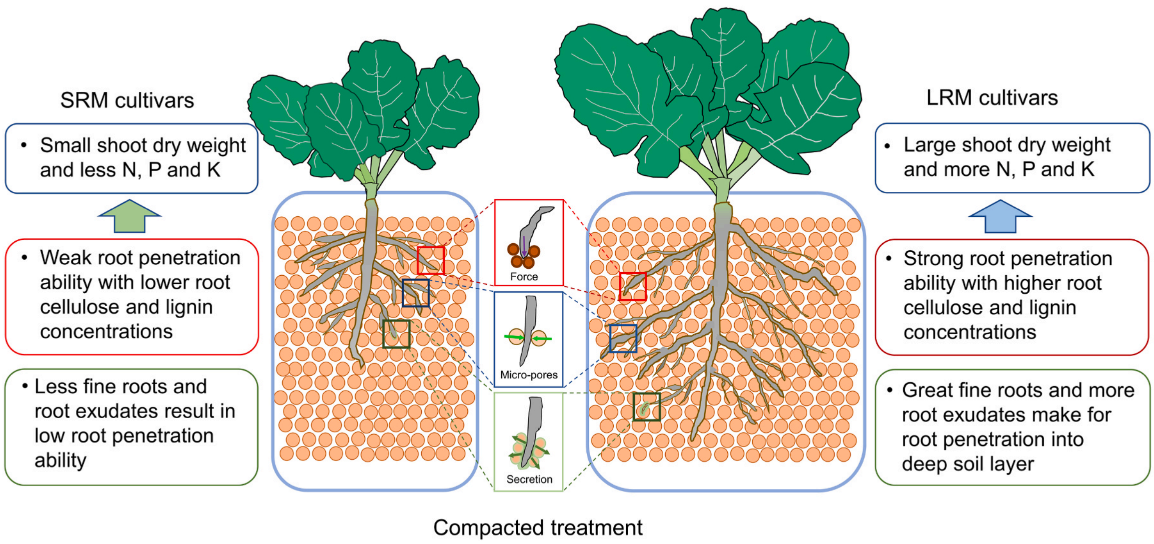

Fig. 11. A proposed diagram on how root traits (especially fine roots and root exudates) of *Brassica napus* contribute to root penetration through the compacted soil. LRM: *Brassica napus* cultivars with large root mechanical traits, SRM: *Brassica napus* cultivars with small root mechanical traits.

increased in compacted soil with the decreasing total soil priority, and the fine roots had a strongly adaptive response to the local constriction in micropores in compacted soil (Fig. 7, Fig. 11 and Table 1). Additionally, a larger fine root length was found in LRM cultivars than SRM cultivars in compacted treatment (Fig. 4b). Specially, LRM cultivars tend to have larger SRL and finer and larger MRD in compacted treatment compared with SRM cultivars (Fig. 6). Thus, we suggest that greater fine roots with large root tensile strength and modulus of elasticity facilitate roots to penetrate into the deep soil layer in compacted soil, and increase the soil volume exploring and nutrients acquisition by proliferating more roots per unit carbon investment (Fig. 3 and Fig. 4) (Ho et al., 2005; Laliberté et al., 2015).

In our study, greater specific root length and larger rooting depth were also found in LRM cultivars than SRM cultivars in compacted soil stress (Fig. 3 and Fig. 4e). In maize, roots with larger specific root length stimulated by localized fertilizer application had more fine roots proliferation, which could further facilitate the roots to grow into the small pores and elongate into the deep soil layers in compacted soil (Wu et al., 2022). In addition, under compacted soil stress, the organic acids secretion was significantly induced (Ahmed et al., 2014; Oleghe et al., 2017) and the reduction of soil pore size could limit soil solution movement and restrict proton diffusion, all leading to the rhizosphere acidified (McNear, 2013). Low rhizosphere soil pH could regulate root proliferation and cell wall mechanical properties to contribute to the root proliferation (Bloom et al., 2002). This might be supported by our results that specific root length had significant positive correlation with organic acids concentration under compacted soil stress (Fig. S6b). Greater specific root length could be associated with more organic acids secretion in the rhizosphere, and contributed to roots proliferation in compacted soil.

Previous studies reported that root secreted mucilage from root tip could lubricate roots to reduce friction as they penetrate through deeper soil layers (Bacic et al., 1986; Read and Gregory, 1997). We found that root exudates polysaccharides and organic acids had significant correlations with maximum root depth in compacted treatment (Fig. 7). The increase of root exudates with more sugars and organic acids can decrease the penetration resistance and increase compression index of soils, and facilitate the roots to grow deeper in compacted soil (Ahmed et al., 2014). In addition, organic acids of exudates can disperse soil structure and decrease soil hardness (Naveed et al., 2017, 2018), and thus enhancing the roots to penetrate into the soil layer (Jin et al., 2013). Although sugars secretion in the soil could offset this effect to stabilize soil structure (Oades, 1984), the most important function of root exudates with sugars-rich mucilage formed a soil sheath to envelope the roots, and relieve the friction at root-soil interface and penetrate roots deep (Bengough and McKenzie, 1997; Carter et al., 2019; Liu et al., 2019). Thus, we suggest that greater root exudates stimulated by mechanical impedance could facilitate roots to penetrate and elongate into the deep soil layer for LRM than SRM, which was achieved by lubricating the passage of biopores in the process of roots elongation (Fig. 11, Hinsinger et al., 2009; Oleghe et al., 2017), and the coordination of more fine roots with more root exudates in rhizosphere for LRM cultivars had the positive function in root penetration and elongation in compacted soil.

A significant higher N, P and K contents in root and shoot, and biomass in LRM cultivars than SRM cultivars were observed in compacted soil (Fig. 9, Fig. 10 and Fig. 11). Deeper roots and greater root proliferation in compacted soil provide benefit for roots resistance to resources stress distributed in the deep soil layer, such as N and water uptake (Yu et al., 2015; Battisti and Sentelhas, 2017; Xie et al., 2021; Wu et al., 2022). In this study, compared with SRM cultivars, LRM cultivars had a deeper root growth and greater specific root lengths, which facilitates the roots to absorb more N, P and K in compacted soil (Fig. 10), and which might be achieved by (1) greater total root length and root surface area of roots dealing with the soil compaction stress driven by larger root biochemical properties parameters (De Baets et al., 2008; Vergani et al., 2014); and (2) more nutrients mobilization by root secreting organic acids into the rhizosphere that increased the bioavailability of nutrients (Ström et al., 2002; Gharu and Tarafdar, 2004; Carvalhais et al., 2011; Terzano et al., 2015) and (3) a deeper root system beneficial to the nutrients absorption from the tank by shortening the distance of mass flow between roots and nutrients (Lipiec and Stępniewski, 1995; Chapman et al., 2012).

5. Conclusion

Soil compaction limited root penetration depth and root system establishment, while facilitating root exudates secretion of *Brassica napus*. LRM cultivars had higher root penetration ability, greater fine roots and more exudates, more biomass accumulation and nutrients uptake than SRM cultivars in the compacted treatments. LRM cultivars could be planted in the agricultural soils where soil compaction increases due to the intensity of agricultural activities or the pressure of heavy farm machinery.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2023.105785.

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