University of Reading

Compacted soil adaptability of Brassica napus driven by root mechanical traits

Article

Accepted Version

Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Duan, X., Jin, K., Mao, Z., Liu, L., He, Y., Xia, S., Hammond, J. P. ORCID: https://orcid.org/0000-0002-6241-3551, White, P. J., Xu, F. and Shi, L. (2023) Compacted soil adaptability of Brassica napus driven by root mechanical traits. Soil and Tillage Research, 233. 105785. ISSN 1879-3444 doi: 10.1016/j.still.2023.105785 Available at https://centaur.reading.ac.uk/114439/

It is advisable to refer to the publisher's version if you intend to cite from the work. See Guidance on citing.

To link to this article DOI: http://dx.doi.org/10.1016/j.still.2023.105785

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the End User Agreement.

www.reading.ac.uk/centaur

University of Reading

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

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

Xianjie Duan [a, b], Kemo Jin [c, *], Zhun Mao [d], Ling Liu [a, b], Yangbo He[b], Shangwen Xia [e], John P. Hammond [f], Philip J. White [a, g], Fangsen Xu [a, b], Lei Shi [a, b, *]

[a] National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China

[b] Key Laboratory of Arable Land Conservation (Middle and Lower Reaches of Yangtze River), Ministry of Agriculture and Rural Affairs, Huazhong Agricultural University, Wuhan 430070, China

[c] College of Resources and Environmental Sciences, National Academy of Agriculture Green Development, Key Laboratory of Plant-Soil Interactions, Ministry of Education, China Agricultural University, Beijing 100193, China

[d] Univ Montpellier, AMAP, INRAE, CIRAD, CNRS, IRD, 34000 Montpellier, France

[e] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, China

[f] School of Agriculture, Policy and Development, University of Reading, Reading, United Kingdom

[g] The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK

[*]Correspondence: Lei Shi (leish@mail.hzau.edu.cn); Kemo Jin (kemo.jin@cau.edu.cn)

Address: National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China

Tel: 0086-27-87286871

Fax: 0086-27-87280016

E-mail address for other authors:

Xianjie Duan: xianjieduan23@126.com

Zhun Mao: maozhun04@126.com

29 Ling Liu: hzaulingliu@webmail.hzau.edu.cn

30 Yangbo He: kathy@mail.hzau.edu.cn

31 Shangwen Xia: xsw@xtbg.org.cn

32 John P. Hammond: j.p.hammond@reading.ac.uk

33 Philip J. white: Philip.White@hutton.ac.uk

34 Fangsen Xu: fangsenxu@mail.hzau.edu.cn

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.

Keywords: *Brassica napus*; Soil compaction; Root mechanical traits; Fine roots; Root exudates

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). 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.

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 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

206 The first-order lateral roots of more than 10 cm length of the plant were sampled to
207 test root mechanical properties. Root samples were firstly preserved in an alcohol
208 solution contained 15 % ethanol and then kept in a refrigerator at 4 °C (Bischetti et al.,
209 2003). Thirty to forty-five undamaged roots were used to test the root mechanical
210 properties with a universal testing machine (model5967, Instron® Corporation) that
211 was fitted with a 50-N load cell with an accuracy of 2 mN. Root segments were
212 manually clamped with two grips and further fixed with strips of sandpaper and 502
213 Super Waterglue to increase friction. Force of loaded was recorded during tensile
214 testing with extension at the constant rate of 5 mm min^{-1} (Giadrossich et al., 2017).
215 The diameters of root segment were gauged by vernier caliper with 0.02 mm accuracy.
216 Each root segment was measured three times, in the center of the root segment, to
217 the left and right of the center adhering to both grips, respectively. The average root
218 diameter was used to calculate the root cross-sectional area (Mao et al., 2018). The
219 root tensile force (F, N) and extension (ΔL, mm) were recorded until the root segment
220 was broken. The root tensile strength (T_r, MPa) was calculated as maximum force at
221 failure divided by root cross-sectional area. The root tensile strain (ε_r, %) was
222 calculated by dividing root extension by unstrained root length. The elasticity of
223 modulus (E_r, MPa) corresponds to the slope of the curve of stress-strain within the
224 quasi-liner elastic stage of a root in tension. The calculation method of elasticity of
225 modulus was referenced from the method by Mao et al. (2018). The crude cell wall of
226 roots was extracted by 95% ethanol and ethanol-hexane (1:2) separately and then
227 dried at 55 °C in oven. And the cellulose content was measured by the phenol–sulfuric
228 acid method based on the Masuko et al. (2005) and Nielsen (2010). Total lignin
229 content was measured by the acetyl bromide method in *Brassica napus* roots based
230 on the Iiyama and Wallis (1990).

231 **2.4 Measurements of root morphological and biochemical traits**

232 The collection method of root exudates was modified from Boeuf-Tremblay et al.
233 (1995) and Pearse et al. (2006, 2007). At harvest time, the plant was lifted carefully
234 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 5810R centrifuge (Eppendorf, Hamburg, Germany) at 3000 g for 15 minutes 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 ^{o}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 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 not 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 to 0.001 (Table 2). The genotypic differences among six *Brassica napus* cultivars were also observed at P < 0.05 to 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 concentration (OAC) of root exudates at P <0.05 to 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 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 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 to 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 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 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;

437 Read and Gregory, 1997). We found that root exudates polysaccharides and organic
438 acids had significant correlations with maximum root depth in compacted treatment
439 (Fig. 7). The increase of root exudates with more sugars and organic acids can
440 decrease the penetration resistance and increase compression index of soils, and
441 facilitate the roots to grow deeper in compacted soil (Ahmed et al., 2014). In addition,
442 organic acids of exudates can disperse soil structure and decrease soil hardness
443 (Naveed et al., 2017, 2018), and thus enhancing the roots to penetrate into the soil
444 layer (Jin et al., 2013). Although sugars secretion in the soil could offset this effect to
445 stabilize soil structure (Oades, 1984), the most important function of root exudates
446 with sugars-rich mucilage formed a soil sheath to envelope the roots, and relieve the
447 friction at root-soil interface and penetrate roots deep (Bengough and McKenzie, 1997;
448 Carter et al., 2019; Liu et al., 2019). Thus, we suggest that greater root exudates
449 stimulated by mechanical impedance could facilitate roots to penetrate and elongate
450 into the deep soil layer for LRM than SRM, which was achieved by lubricating the
451 passage of biopores in the process of roots elongation (Fig. 11, Hinsinger et al., 2009;
452 Oleghe et al., 2017), and the coordination of more fine roots with more root exudates
453 in rhizosphere for LRM cultivars had the positive function in root penetration and
454 elongation in compacted soil.

455 A significant higher N, P and K contents in root and shoot, and biomass in LRM
456 cultivars than SRM cultivars were observed in compacted soil (Fig. 9, Fig. 10 and Fig.
457 11). Deeper roots and greater root proliferation in compacted soil provide benefit for
458 roots resistance to resources stress distributed in the deep soil layer, such as N and
459 water uptake (Yu et al., 2015; Battisti and Sentelhas, 2017; Xie et al., 2021; Wu et al.,
460 2022). In this study, compared with SRM cultivars, LRM cultivars had a deeper root
461 growth and greater specific root lengths, which facilitates the roots to absorbe more N,
462 P and K in compacted soil (Fig. 10), and which might be achieved by (1) greater total
463 root length and root surface area of roots dealing with the soil compaction stress
464 driven by larger root biochemical properties parameters (De Baets et al., 2008;
465 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.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant Nos. 31972498 and 31601815). P.J.W. was funded by the Scottish Government Strategic Research Programme (2022-2027).

References

Ahmed, M.A., Kroener, E., Holz, M., Zarebanadkouki, M., Carminati, A., 2014. Mucilage exudation facilitates root water uptake in dry soils. Funct. Plant Biol. 41, 1129-1137.

Alakukku, L., Elonen, P., 1995. Long-term effects of a single compaction by heavy field traffic on yield and nitrogen uptake of annual crops. Soil Till. Res. 36, 141-152.

Alameda, D., Villar, R., 2012. Linking root traits to plant physiology and growth in Fraxinus angustifolia Vahl. seedlings under soil compaction conditions. Environ. Exp. Bot. 79, 49-57.

493 Alves, B.J.R., Zotarelli, L., Resende, A.S., Polidoro, J.C., Urquiaga, S., Boddey, R.M.,
494 2000. Rapid and sensitive determination of nitrate in plant tissue using flow
495 injection analysis. Commun. Soil Sci. Plant Anal. 31, 2739-2750.
496 Arvidsson, J., Håkansson, I., 2014. Response of different crops to soil
497 compaction—Short-term effects in Swedish field experiments. Soil Till. Res. 138,
498 56-63.
499 Bacic, A., Moody, S.F., Clarke, A.E., 1986. Structural analysis of secreted root slime
500 from maize (*Zea mays* L.). Plant Physiol. 80, 771-777.
501 Barken, L.R., Bosrresen, T., Njoss, A., 1981. Effect of soil compaction by tractor traffic
502 on soil structure, denitrification, and yield of wheat (*Triticum aestivum* L.). J. Soil
503 Sci. 38, 541– 552.
504 Batey, T., 2009. Soil compaction and soil management–a review. Soil Use Manage.
505 25, 335-345.
506 Battisti, R., Sentelhas, P.C., 2017. Improvement of soybean resilience to drought
507 through deep root system in Brazil. Agron. J. 109, 1612-1622.
508 Bello-Bello, E., López-Arredondo, D., Rico-Chambrón, T. Y., Herrera-Estrella, L., 2022.
509 Conquering compacted soils: uncovering the molecular components of root soil
510 penetration. Trends Plant Sci. 2022, S1360138522001054.
511 Bengough, A.G., McKenzie, B.M., 1997. Sloughing of root cap cells decreases the
512 frictional resistance to maize (*Zea mays* L.) root growth. J Exp. Bot. 48, 885-893.
513 Bischetti, G.B., Bonfanti, F., Greppi, M., 2003. Root tensile strength measurement:
514 testing device and protocol. Quaderni di Idronomia Montana 21, 349-360.
515 Blake, J., Spink, J., Bingham, I., 2006. Management of oilseed rape to balance root
516 and canopy growth. HGCA Rep. 402, 22.
517 Bloom, A.J., Meyerhoff, P.A., Taylor, A.R., Rost, T.L., 2002. Root development and
518 absorption of ammonium and nitrate from the rhizosphere. J. Plant Growth Regul.
519 21, 416-431.
520 Bodner, G., Leitner, D., Kaul, H.P., 2014. Coarse and fine root plants affect pore size
521 distributions differently. Plant Soil 380, 133-151.
522 Boeuf-Tremblay, V., Plantureux, S., Guckert, A., 1995. Influence of mechanical

impedance on root exudation of maize seedlings at two development stages. Plant Soil 172, 79-287.

Bogunovic, I., Pereira, P., Kisic, I., Sajko, K., Sraka, M., 2018. Tillage management impacts on soil compaction, erosion and crop yield in Stagnosols (Croatia). Catena 160, 376-384.

Bourrier, F., Kneib, F., Chareyre, B., Fourcaud, T., 2013. Discrete modeling of granular soils reinforcement by plant roots. Ecol. Eng. 61, 646-657.

Cairns, J.E., Impa, S.M., O'Toole, J.C., Jagadish, S.V.K., Price, A.H., 2011. Influence of the soil physical environment on rice (*Oryza sativa* L.) response to drought stress and its implications for drought research. Field Crops Res. 121, 303-310.

Carter, A.Y., Hawes, M.C., Ottman, M.J., 2019. Drought-tolerant barley: I. Field observations of growth and development. Agronomy 9, 221.

Carvalhais, L.C., Dennis, P.G., Fedoseyenko, D., Hajirezaei, M.R., Borriss, R., von Wirén, N., 2011. Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. J. Plant Nutr. Soil Sci. 174, 3-11.

Chapman, N., Miller, A.J., Lindsey, K., Whalley, W.R., 2012. Roots, water, and nutrient acquisition: let's get physical. Trends Plant Sci. 17, 701-710.

Chen, G., Weil, R.R., 2010. Penetration of cover crop roots through compacted soils. Plant Soil 331, 31-43.

Chen, G.H., Weil, R.R., 2010. Penetration of cover crop roots through compacted soils. Plant Soil 331, 31-43.

Chimungu, J.G., Loades, K.W., Lynch, J.P., 2015. Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea mays*). J. Exp. Bot. 66, 3151-3162.

Clark, L.J., Cope, R.E., Whalley, W.R., Barraclough, P.B., Wade, L.J., 2002. Root penetration of strong soil in rainfed lowland rice: comparison of laboratory screens with field performance. Field Crops Res. 76, 189-198.

Clark, L.J., Price, A.H., Steele, K.A., Whalley, W.R., 2008. Evidence from near-isogenic lines that root penetration increases with root diameter and

553 bending stiffness in rice. Funct. Plant Biol. 35, 1163-1171.
554 Coelho Filho, M.A., Colebrook, E.H., Lloyd, D., Webster, C.P., Mooney, S.J., Phillips,
555 A.L., Hedden, P., Whalley, W.R., 2013. The involvement of gibberellin signalling
556 in the effect of soil resistance to root penetration on leaf elongation and tiller
557 number in wheat. Plant Soil 371, 81-94.
558 Colombi, T., Keller, T., 2019. Developing strategies to recover crop productivity after
559 soil compaction—A plant eco-physiological perspective. Soil Till. Res. 191,
560 156-161.
561 Colombi, T., Kirchgessner, N., Walter, A., Keller, T., 2017. Root tip shape governs root
562 elongation rate under increased soil strength. Plant Physiol. 174, 2289-2301.
563 Comas, L.H., Becker, S.R., Cruz, V.M.V., Byrne, P.F., Dierig, D.A., 2013. Root traits
564 contributing to plant productivity under drought. Front. Plant Sci. 4, 442.
565 Correa, J., Postma, J.A., Watt, M., Wojciechowski, T., 2019. Soil compaction and the
566 architectural plasticity of root systems. J. Exp. Bot. 70, 6019-6034.
567 De Baets, S., Poesen, J., Reubens, B., Wemans, K., De Baerdemaeker, J., Muys, B.,
568 2008. Root tensile strength and root distribution of typical Mediterranean plant
569 species and their contribution to soil shear strength. Plant Soil 305, 207-226.
570 Degenhardt, B., Gimmler, H. 2000. Cell wall adaptations to multiple environmental
571 stresses in maize roots. J. Exp. Bot. 51, 595-603.
572 Ekeoma, E.C., Boldrin, D., Loades, K.W., Bengough, A.G., 2021. Drying of fibrous
573 roots strengthens the negative power relation between biomechanical properties
574 and diameter. Plant Soil 469, 321-334.
575 Ferreira, C J.B., Tormena, C.A., Severiano, E.D.C., Zotarelli, L., Betioli Júnior, E.,
576 2021. Soil compaction influences soil physical quality and soybean yield under
577 long-term no-tillage. Arch. Agron. Soil Sci. 67, 383-396.
578 Filisetti-Cozzi, T.M., Carpita, N.C., 1991. Measurement of uronic acids without
579 interference from neutral sugars. Anal. Biochem. 197, 157-162.
580 Flowers, M.D., Lal, R., 1998. Axle load and tillage effects on soil physical properties
581 and soybean grain yield on a mollic ochraqualf in northwest Ohio. Soil Till. Res.
582 48, 21-35.

583 Friedt, W., Tu, J., Fu, T., 2018. Academic and economic importance of *Brassica napus*
584 rapeseed. In The *Brassica napus* genome. Springer, 1-20, Cham, Germany.
585 Fukao, T., Bailey-Serres, J., 2004. Plant responses to hypoxia–is survival a balancing
586 act?. Trends Plant Sci. 9, 449-456.
587 Gao, W., Watts, C.W., Ren, T., Whalley, W.R., 2012. The effects of compaction and
588 soil drying on penetrometer resistance. Soil Till. Res. 125, 14-22.
589 Gao, X., C. Ma, S. Du., 2005. Techniques on formula fertilization by soil testing.
590 Chinese Agriculture Press, 94-96, Beijing, China.
591 Genet, M., Stokes, A., Salin, F., Mickovski, S.B., Fourcaud, T., Dumail, J.F., Van Beek,
592 R., 2005. Plant Soil 278, 1-9.
593 Gharu, A., Tarafdar, J.C., 2004. Influence of organic acids on mobilization of inorganic
594 and organic phosphorus in soil. J. Indian Soc. Soil Sci. 52, 248-253.
595 Ghestem, M., Cao, K.F., Ma, W.Z., Rowe, N., Leclerc, R., Gadenne, C., Stokes, A.,
596 2014. A framework for identifying plant species to be used as 'ecological
597 engineers' for fixing soil on unstable slopes. Plos One 9. e95876.
598 Giadrossich, F., Schwarz, M., Cohen, D., Cislaghi, A., Vergani, C., Hubble, T., Phillips,
599 C., Stokes, A., 2017. Methods to measure the mechanical behaviour of tree roots:
600 a review. Ecol. Eng. 109, 256-271.
601 Gray, D.H., Barker, D., 2004. Root-soil mechanics and interactions. In: Bennett JJ,
602 Simon A (eds) Riparian vegetation and fluvial geomorphology. Water Science and
603 Application 8. American Geophyisical Union, New York, pp 113–123.
604 Groleau-Renaud, V., Plantureux, S., Guckert, A., 1998. Influence of plant morphology
605 on root exudation of maize subjected to mechanical impedance in hydroponic
606 conditions. Plant Soil 201, 231-239.
607 Grzesiak, S., Grzesiak, M. T., Hura, T., Marcińska, I., Rzepka, A., 2013. Changes in
608 root system structure, leaf water potential and gas exchange of maize and
609 triticale seedlings affected by soil compaction. Environ. Exp. Bot. 88, 2-10.
610 Hamza, M.A., Anderson, W.K., 2005. Soil compaction in cropping systems: A review
611 of the nature, causes and possible solutions. Soil Till. Res. 82, 121-145.
612 Hanbury, C.D., Atwell, B.J., 2005. Growth dynamics of mechanically impeded lupin

613 roots: does altered morphology induce hypoxia?. Ann. Bot. 96, 913-924.
614 Hinsinger, P., Bengough, A.G., Vetterlein, D., Young, I.M., 2009. Rhizosphere:
615 biophysics, biogeochemistry and ecological relevance. Plant Soil 321, 117-152.
616 Ho, M.D., Rosas, J.C., Brown, K.M., Lynch, J.P., 2005. Root architectural tradeoffs for
617 water and phosphorus acquisition. Funct. Plant Biol. 32, 737-748.
618 Hoorman, J.J., Sá, J.C.M., Reeder, R., 2011. The biology of soil compaction. Science
619 68, 49-57.
620 Hoque, M., Kobata, T., 2000. Effect of soil compaction on the grain yield of rice (*Oryza*
621 *sativa* L.) under water-deficit stress during the reproductive stage. Plant Prod. Sci.
622 3, 316–322.
623 Hu, Q., Hua, W., Yin, Y., Zhang, X.K., Liu, L.J., Shi, J.Q., Zhao, Y.G., Qin, L., Chen, C.,
624 Wang, H.Z., 2017. Rapeseed research and production in China. Crop J. 5, 127–
625 135.
626 Iijima, M., Barlow, P. W., Bengough, A.G., 2003. Root cap structure and cell
627 production rates of maize (*Zea mays*) roots in compacted sand. New Phytol. 160,
628 127-134.
629 Iijima, M., Higuchi, T., Barlow, P.W., 2004. Contribution of root cap mucilage and
630 presence of an intact root cap in maize (*Zea mays*) to the reduction of soil
631 mechanical impedance. Ann. Bot. 94, 473-477.
632 Iiyama, K., Wallis, A.F., 1990. Determination of lignin in herbaceous plants by an
633 improved acetyl bromide procedure. J. Sci. Food Agr. 51, 145-161.
634 Ji, B., Zhao, Y., Mu, X., Liu, K., Li, C., 2013. Effects of tillage on soil physical
635 properties and root growth of maize in loam and clay in central China. Plant Soil
636 Environ. 59, 295-302.
637 Jin, K., Shen, J., Ashton, R.W., Dodd, I.C., Parry, M.A., Whalley, W.R., 2013. How do
638 roots elongate in a structured soil?. J. Exp. Bot. 64, 4761-4777.
639 Jin, K., Shen, J., Ashton, R.W., White, R.P., Dodd, I.C., Phillips, A.L., Whalley, W.R.,
640 2015. The effect of impedance to root growth on plant architecture in wheat. Plant
641 Soil 392, 323-332.

642 Johnson, D.M., Wortemann, R., McCulloh, K.A., Jordan-Meille, L., Ward, E., Warren,
643 J.M., Palmroth, S., Domec, J.C., 2016. A test of the hydraulic vulnerability
644 segmentation hypothesis in angiosperm and conifer tree species. Tree Physiol.
645 36, 983-993.
646 Kautz, T., 2015. Research on subsoil biopores and their functions in organically
647 managed soils: A review. Renew. Agr. Food Syst. 30, 318-327.
648 Keller, T., Colombi, T., Ruiz, S., Manalili, M. P., Rek, J., Stadelmann, V., Wunderli, H.,
649 Breitenstein, D., Reiser, R., Oberholzer, H.-R., Schymanski, S., Romero-Ruiz, A.,
650 Linde, N., Weisskopf, P., Walter, A., Or, D., 2017. Long-term soil structure
651 observatory for monitoring post-compaction evolution of soil structure. Vadose
652 Zone J. 16, 1-16.
653 Keller, T., Sandin, M., Colombi, T., Horn, R., Or, D., 2019. Historical increase in
654 agricultural machinery weights enhanced soil stress levels and adversely affected
655 soil functioning. Soil Till. Res. 194, 104293.
656 Kuncoro, P.H., Koga, K., Satta, N., Muto, Y., 2014. A study on the effect of compaction
657 on transport properties of soil gas and water I: Relative gas diffusivity, air
658 permeability, and saturated hydraulic conductivity. Soil Till. Res. 143, 172-179.
659 Laliberté, E., Lambers, H., Burgess, T.I., Wright, S.J., 2015. Phosphorus limitation,
660 soil‐borne pathogens and the coexistence of plant species in hyperdiverse
661 forests and shrublands. New Phytol. 206, 507-521.
662 Lee, J.T., Chu, M.Y., Lin, Y.S., Kung, K.N., Lin, W.C., Lee, M.J., 2020. Root traits and
663 biomechanical properties of three tropical pioneer tree species for forest
664 restoration in landslide areas. Forests 11, 179.
665 Leyva, A., Quintana, A., Sánchez, M., Rodríguez, E.N., Cremata, J., Sánchez, J.C.,
666 2008. Rapid and sensitive anthrone–sulfuric acid assay in microplate format to
667 quantify carbohydrate in biopharmaceutical products: method development and
668 validation. Biologicals 36, 134-141.
669 Li, C., Zhou, S., 1994. Effects of soil bulk density on the growth of maize seeding
670 stage. Acta Agriculturae Boreali-Sinica (In Chinese), 9, 49-54.
671 Li, H., Xia, H., Mei, Y., 2016. Modeling organic fouling of reverse osmosis membrane:

From adsorption to fouling layer formation. Desalination 386, 25-31.

Li, L.X., Chen, B.Y., Yan, G.X., Gao, G.Z., Xu, K., Xie, T., Zhang, F.G., 2020. Proposed strategies and current progress of research and utilization of oilseed rape germplasm in China. J. Plant Genet. Resour. 21, 1–19.

Lipiec, J., Stępniewski, W., 1995. Effects of soil compaction and tillage systems on uptake and losses of nutrients. Soil Till. Res. 35, 37-52.

Liu, S., Fan, C.C., Li, J.N., Cai, G.Q., Yang, Q.Y., Wu, J., Yi, X.Q., Zhang, C.Y., Zhou, Y.M., 2016. A genome-wide association study reveals novel elite allelic variations in seed oil content of *Brassica napus*. Theor. Appl. Genet. 129, 1203-1215.

Liu, T.Y., Ye, N., Song, T., Cao, Y., Gao, B., Zhang, D., Zhu, F.Y., Chen, M., Zhang, Y.J., Xu, W.F., Zhang, J., 2019. Rhizosheath formation and involvement in foxtail millet (*Setaria italica*) root growth under drought stress. J. Integr. Plant Biol. 61, 449-462.

Loades, K.W., Bengough, A.G., Bransby, M.F., Hallett, P.D., 2015. Effect of root age on the biomechanics of seminal and nodal roots of barley (*Hordeum vulgare* L.) in contrasting soil environments. Plant Soil 395, 253-261.

Mao, Z., Roumet, C., Rossi, L.M.W., Merino-Martin, L., Nespoulous, J., Taugourdeau, O., Boukcim, H., Fourtier, S., Del Rey-Granado, M., Ramel, M., Ji, K., Zuo, J., Fromin, N., Stokes, A., Fort, F., 2023. Intra- and inter-specific variation in root mechanical traits for twelve herbaceous plants and their link with the root economics space. Oikos e09032.

Mao, Z., Wang, Y., McCormack, M. L., Rowe, N., Deng, X.B., Yang, X.D., Xia S.W., Nespoulous, J., Sidle, Roy.C., Guo, D.L., Stokes, A., 2018. Mechanical traits of fine roots as a function of topology and anatomy. Ann. Bot. 122, 1103-1116.

Mao, Z., Yang, M., Bourrier, F., Fourcaud, T., 2014. Evaluation of root reinforcement models using numerical modelling approaches. Plant Soil, 381, 249-270.

Marga, F., Gallo, A., Hasenstein, K.H., 2003. Cell wall components affect mechanical properties: studies with thistle flowers. Plant Physiol. Biochem. 41, 792-797.

Masuko, T., Minami, A., Iwasaki, N., Majima, T., Nishimura, S. I., Lee, Y. C., 2005. Carbohydrate analysis by a phenol–sulfuric acid method in microplate format.

Anal. Biochem. 339, 69-72.

McNear, D.H.Jr., 2013. The rhizosphere-roots, soil and everything in between. Nat. Educ. Knowl. 4, 1.

Mirzavand, J., Moradi-Talebbeigi, R., 2021. Relationships between field management, soil compaction, and crop productivity. Arch. Agron. Soil Sci. 67, 675-686.

Moradi, E., Rodrigo-Comino, J., Terol, E., Mora-Navarro, G., da Silva, A.M., Daliakopoulos, I.N., Khosravi, H., Fernandez, M.P., Cerda, A., 2020. Quantifying soil compaction in persimmon orchards using ISUM (Improved Stock Unearthing Method) and core sampling methods. Agriculture-Basel 10, 266.

More, S.S., Shinde, S.E., Kasture, M.C., 2020. Root exudates a key factor for soil and plant: An overview. Pharma Innov. J. 8, 449-459.

Naveed, M., Brown, L.K., Raffan, A.C., George, T.S., Bengough, A.G., Roose, T., Sinclair, I., Koebernick, N., Cooper, L., Hackett, C.A., Hallett, P.D., 2017. Plant exudates may stabilize or weaken soil depending on species, origin and time. Eur. J. Soil Sci. 68, 806-816.

Naveed, M., Brown, L.K., Raffan, A.C., George, T.S., Bengough, A.G., Roose, T., Sinclair, I., Koebernick, N., Cooper, L., Hallett, P.D., 2018. Rhizosphere-scale quantification of hydraulic and mechanical properties of soil impacted by root and seed exudates. Vadose Zone J. 17.

Nielsen, S.S., 2010. Phenol-sulfuric acid method for total carbohydrates. In Food analysis laboratory manual. Springer, 47-53, Boston, MA.

Oades, J.M., 1984. Soil organic matter and structural stability: mechanisms and implications for management. Plant Soil 76, 319-337.

Oleghe, E., Naveed, M., Baggs, E.M., Hallett, P.D., 2017. Plant exudates improve the mechanical conditions for root penetration through compacted soils. Plant Soil 421, 19-30.

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. Agriculture 11, 666.

731 Pearse, S.J., Veneklaas, E.J., Cawthray, G., Bolland, M.D., Lambers, H., 2007.
732 Carboxylate composition of root exudates does not relate consistently to a crop
733 species' ability to use phosphorus from aluminium, iron or calcium phosphate
734 sources. New Phytol. 173, 181-190.
735 Pearse, S.J., Veneklaas, E.J., Cawthray, G., Bolland, M.D., Lambers, H., 2006.
736 *Triticum aestivum* shows a greater biomass response to a supply of aluminium
737 phosphate than Lupinus albus, despite releasing fewer carboxylates into the
738 rhizosphere. New Phytol. 169, 515-524.
739 Peltonen-Sainio, P., Jauhiainen, L., Laitinen, P., Salopelto, J., Saastamoinen, M.,
740 Hannukkala, A., 2011. Identifying difficulties in rapeseed root penetration in
741 farmers' fields in northern European conditions. Soil Use Manage. 27, 229-237.
742 Pérez-Ramos, I.M., Volaire, F., Fattet, M., Blanchard, A., Roumet, C., 2013. Tradeoffs
743 between functional strategies for resource-use and drought-survival in
744 Mediterranean rangeland species. Environ. Exp. Bot. 87, 126-136.
745 Popova, L., van Dusschoten, D., Nagel, K.A., Fiorani, F., Mazzolai, B., 2016. Plant
746 root tortuosity: an indicator of root path formation in soil with different composition
747 and density. Ann. Bot. 118, 685-698.
748 Read, D.B., Gregory, J.P., 1997. Surface tension and viscosity of axenic maize and
749 lupin root mucilages. New Phytol. 137, 623–628.
750 Schneider, H.M., Strock, C.F., Hanlon, M.T., Vanhees, D.J., Perkins, A.C., Ajmera, I.B.,
751 Sidhu, J.S., Mooney, S.J., Brown, K.M., Lynch, J.P., 2021. Multiseriate cortical
752 sclerenchyma enhance root penetration in compacted soils. P. Natl. Acad. Sci.
753 USA 118, e2012087118.
754 Schwarz, M., Rist, A., Cohen, D., Giadrossich, F., Egorov, P., Büttner, D., Stolz, B.M.,
755 Thormann, J. J., 2015. Root reinforcement of soils under compression. J. Geopys.
756 Res-Earth 120, 2103-2120.
757 Semwal, T., Mali, N., Masakapalli, S.K., Uday, K.V., 2020. Effect of plant roots on
758 permeability of soil, In geotechnical characterization and modelling: Proceedings
759 of IGC 2018. Springer, Singapore, pp. 343-352.
760 Shah, A.N., Tanveer, M., Shahzad, B., Yang, G., Fahad, S., Ali, S., Bukhari, M.A.,

761 Tung, S.A., Hafeez, A., Souliyanonh, B., 2017. Soil compaction effects on soil
762 health and cropproductivity: an overview. Environ. Sci. Pollut. Res. 24,
763 10056-10067.
764 Souty, N., Rode, C., 1987. Aspect mécanique de la croissance des racines. I.-Mesure
765 de la force de pénétration. Agronomie 7, 623-630.
766 Ström, L., Owen, A.G., Godbold, D.L., Jones, D.L., 2002. Organic acid mediated P
767 mobilization in the rhizosphere and uptake by maize roots. Soil Biol. Biochem. 34,
768 703-710.
769 Sullivan, D.M., Havlin, J.L., 1991. Flow injection analysis of urea nitrogen in soil
770 extracts. Soil Sci. Soc. Am. J. 55, 109-113.
771 Terzano, R., Cuccovillo, G., Gattullo, C.E., Medici, L., Tomasi, N., Pinton, R., Mimmo,
772 T., Cesco, S., 2015. Combined effect of organic acids and flavonoids on the
773 mobilization of major and trace elements from soil. Biol. Fertil. Soils 51, 685-695.
774 Tracy, S.R., Black, C.R., Roberts, J.A., Sturrock, C., Mairhofer, S., Craigon, J.,
775 Mooney, S.J., 2012. Quantifying the impact of soil compaction on root system
776 architecture in tomato (*Solanum lycopersicum*) by X-ray micro-computed
777 tomography. Ann. Bot. 110, 511-519.
778 Vanhees, D.J., Loades, K.W., Bengough, A.G., Mooney, S.J., Lynch, J.P., 2020. Root
779 anatomical traits contribute to deeper rooting of maize under compacted field
780 conditions. J. Exp. Bot. 71, 4243-4257.
781 Vergani, C., Schwarz, M., Cohen, D., Thormann, J.J., Bischetti, G.B., 2014. Effects of
782 root tensile force and diameter distribution variability on root reinforcement in the
783 Swiss and Italian Alps. Can. J. For. Res. 44, 1426-1440.
784 Wang, C.Y., Yan, Z.K., Wang, Z.K., Batool, M., El-Badri, A.M., Bai, F., Li, Z., Wang, B.,
785 Zhou, G.S., Kuai, J., 2021. Subsoil tillage promotes root and shoot growth of
786 rapeseed in paddy fields and dryland in Yangtze River Basin soils. Eur. J. Agron.
787 130, 126351.
788 Wang, H., Hao, J., Feng, R., Nan, Y., Yang, S., Nan, J., 2015. Microhole subsoiling
789 decreasing soil compaction, and improving yield and seed quality of cotton. Trans.
790 Chin. Soc. Agric. Eng. 31, 7-14.

Wang, M., Feng, W.Y., Shi, J.W., Zhang, F., Wang, B., Zhu, M.T., Li, B., Zhao, Y.L., Chai, Z.F., 2007. Development of a mild mercaptoethanol extraction method for determination of mercury species in biological samples by P-replete LC-ICP-MS. Talanta 71, 2034–2039.

Wang, M., He, D., Shen, F., Huang, J., Zhang, R., Liu, W., Zhou, Q., 2019. Effects of soil compaction on plant growth, nutrient absorption, and root respiration in soybean seedlings. Environ. Sci. Pollut. R. 26, 22835-22845.

Whiteley, G.M., Hewitt, J.S., Dexter, A.R., 1982. The buckling of plant roots. Physiol. Plant. 54, 333-342.

Wolkowski, R., Lowery, B., 2008. Soil compaction: causes, concerns, and cures. University of Wisconsin-Extension, Coop. Ext. A3367 Retrieved from http://www.soils.wisc.edu/extension/pubs/A3367.pdf

Wu, X., Li, H., Rengel, Z., Whalley, W. R., Li, H., Zhang, F., Shen, J., Jin, K., 2022. Localized nutrient supply can facilitate root proliferation and increase nitrogen-use efficiency in compacted soil. Soil Till. Res. 215, 105198.

Xi, C.F., 1998. Soils of China (in Chinese). Chinese Agriculture Press, 162-174, Beijing, China.

Xie, Y., Islam, S., Legesse, H. T., Kristensen, H.L., 2021. Deep root uptake of leachable nitrogen in two soil types is reduced by high availability of soil nitrogen in fodder radish grown as catch crop. Plant Soil 1-15.

Xu, H., Wang, X.Y., Liu, C.N., Chen, J.N., Zhang, C., 2021. A 3D root system morphological and mechanical model based on L-Systems and its application to estimate the shear strength of root-soil composites. Soil Till Res 212, 105074.

Yang, Y.J., Chen, L.H., Li, N., Zhang, Q.F., 2016. Effect of root moisture content and diameter on root tensile properties. Plos One 11, e0151791.

Yu, P., Li, X., White, P.J., Li, C., 2015. A large and deep root system underlies high nitrogen-use efficiency in maize production. Plos One 10, e0126293.

Zhang, C. B., Chen, L. H., Jiang, J., 2014. Why fine tree roots are stronger than thicker roots: The role of cellulose and lignin in relation to slope stability. Geomorphology 206, 196-202.

821 Zhang, C.B., Zhou, X., Jiang, J., Wei, Y., Ma, J.J., Hallett, P.D., 2019. Root moisture
822 content influence on root tensile tests of herbaceous plants. Catena 172,
823 140-147.
824 Zhang, S., Grip, H., Lövdahl, L., 2006. Effect of soil compaction on hydraulic
825 properties of two loess soils in China. Soil Till. Res. 90, 117-125.
826 Zhang, Y., Culhaoglu, T., Pollet, B., Melin, C., Denoue, D., Barriere, Y., Méchin, V.,
827 2011. Impact of lignin structure and cell wall reticulation on maize cell wall
828 degradability. J. Agric. Food Chem. 59, 10129-10135.
829 Zhang, Z.B., Yan, L., Wang, Y.K., Ruan, R.J., Xiong, P., Peng, X.H., 2022. Bio-tillage
830 improves soil physical properties and maize growth in a compacted Vertisol by
831 cover crops. Soil Sci. Soc. Am. J. 86, 324-337.
832 Zhu, J.Q., Wang, Y.Q., Wang, Y.J., Mao, Z., Langendoen, E.J., 2020. How does root
833 biodegradation after plant felling change root reinforcement to soil? Plant Soil
834 446, 211-227.
835 Zwicke, M., Picon-Cochard, C., Morvan-Bertrand, A., Prud'homme, M.P., Volaire, F.,
836 2015. What functional strategies drive drought survival and recovery of perennial
837 species from upland grassland? Ann. Bot. 116, 1001–1015.

838 Figure Captions

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

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

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

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

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

862 **Fig. 6.** Principal component analysis of root morphological traits (TRL, CRL, FRL,
863 RSA, SRL, ARD and MRD) and root biochemical traits (UAC, GC, XC and OAC) of six
864 *Brassica napus* cultivars (LRM1, LRM2, LRM3, SRM1, SRM2 and SRM3) in
865 non-compacted (a) and compacted (b) treatments, respectively. TRL, total root length;
866 CRL, coarse root length; FRL, fine root length; RSA, root surface area; SRL, specific
867 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.

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.

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.

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.

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.

Table Captions

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

Table 2 The effects of soil compaction on the root morphological and biochemical

traits of six *Brassica napus* cultivars.

Supplementary information

Supplementary Fig. S1. A schematic representation of the root growth system (a) and root collection system (b).

Supplementary Fig. S2. Correlation between root tensile force (a), tensile strength (b) and modulus of elasticity (c) and root diameter of LRM and SRM cultivars in non-compacted treatment. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits.

Supplementary Fig. S3. Correlations between root tensile strain and root diameter of LRM and SRM cultivars in non-compacted (a) and compacted (b) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits.

Supplementary Fig. S4. Root cellulose (a) and lignin (b) concentrations of *Brassica napus* cultivars with LRM and SRM 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.

Supplementary Fig. S5. Correlations between maximum root depth (a), coarse root length (b) and average root diameter, and correlations between fine root length (c), root surface area (d) and coarse root length of six *Brassica napus* cultivars in non-compacted treatment.

Supplementary Fig. S6. Correlations between glucose (a), organic acid (b), uronic acid (c) and xylose (d) concentrations and specific root length of six *Brassica napus* cultivars in compacted treatments. The shaded areas indicate the 95% confidence range, derived from the models. $*P < 0.05$, $**P < 0.01$.

Supplementary Fig. S7. The concentrations of nitrogen (N), phosphorus (P) and potassium (K) in shoot (a-c) and root (d-e) 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

928 difference among four treatments at P <0.05.

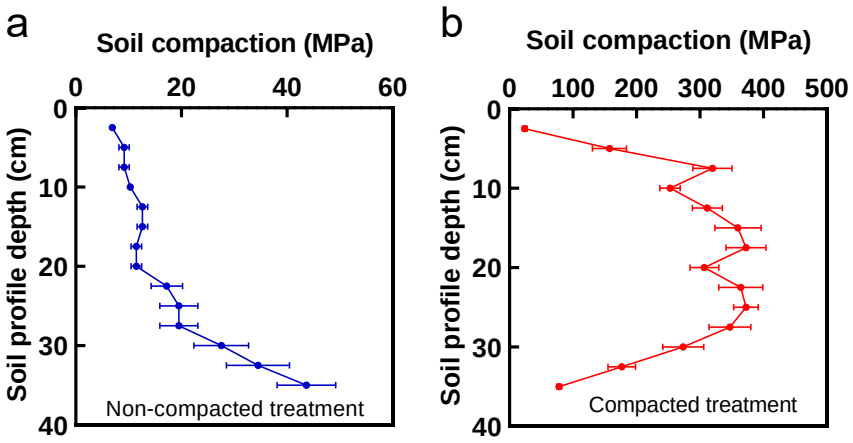
929 **Table S1** *Brassica napus* cultivars used in this study.

930 **Table S2** Particle density of sand in non-compacted and compacted treatments in this
931 study.

932 **Table S3** Fitting equations of root tensile force, root tensile strength and modulus of
933 elasticity with root diameter of LRM and SRM cultivars in non-compacted and
934 compacted treatments, respectively.

935 **Table S4** The compositions and amounts of organic acids in the rhizosphere of six
936 *Brassica napus* cultivars in non-compacted and compacted treatments.

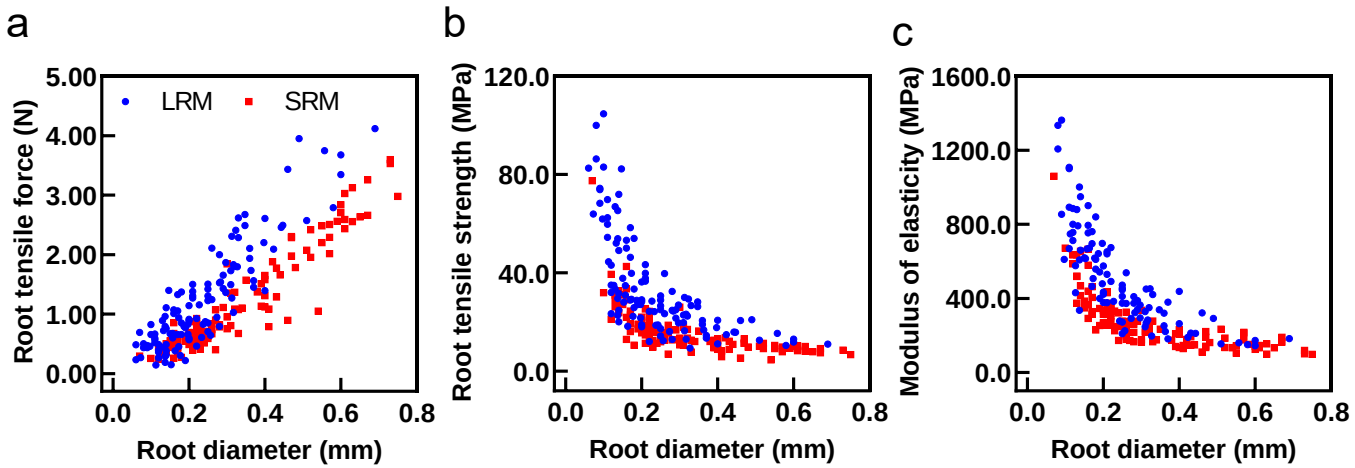
937 **Table S5** The loading scores of eleven root-related traits in the principal component
938 analysis among six *Brassica napus* cultivars.



939

940 Fig. 1. Penetration resistance at different soil profile depth in non-compacted (a) and

941 compacted (b) treatment, respectively.

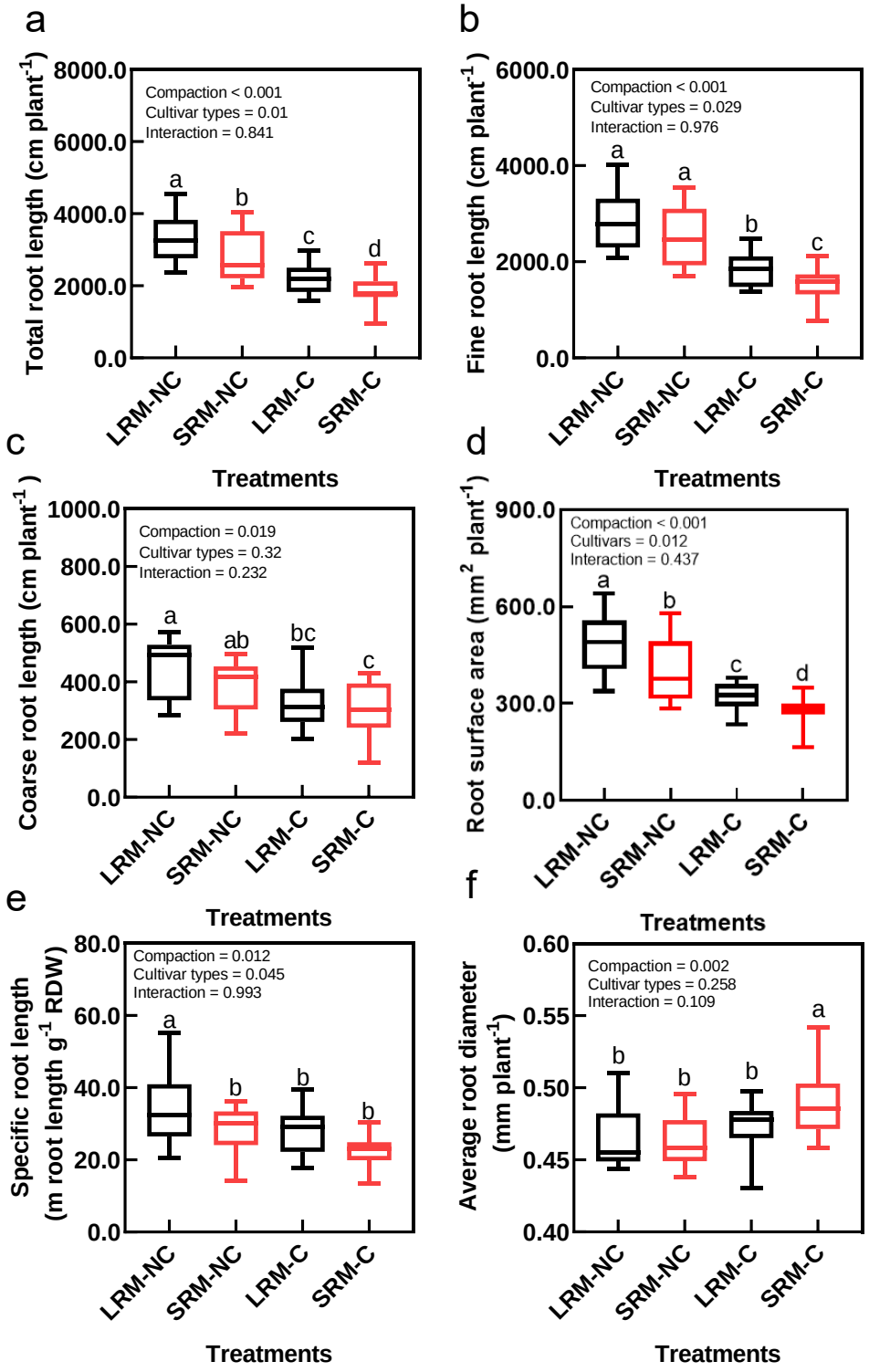


942

943 Fig. 2. Correlations between root tensile force (a), root tensile strength (b), modulus of elasticity (c) and root diameter of LRM or SRM

944 cultivars in compacted treatment. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with

945 small root mechanical traits.



946

947 Fig. 4. Root morphological traits of LRM and SRM cultivars in non-compacted (NC)
948 and compacted (C) treatments. Total root length (a), fine root length (b), coarse root
949 length (c), root surface area (d), specific root length (e) and average root diameter (f).
950 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.

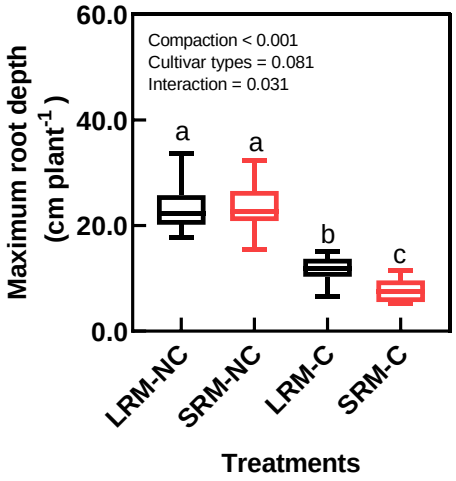
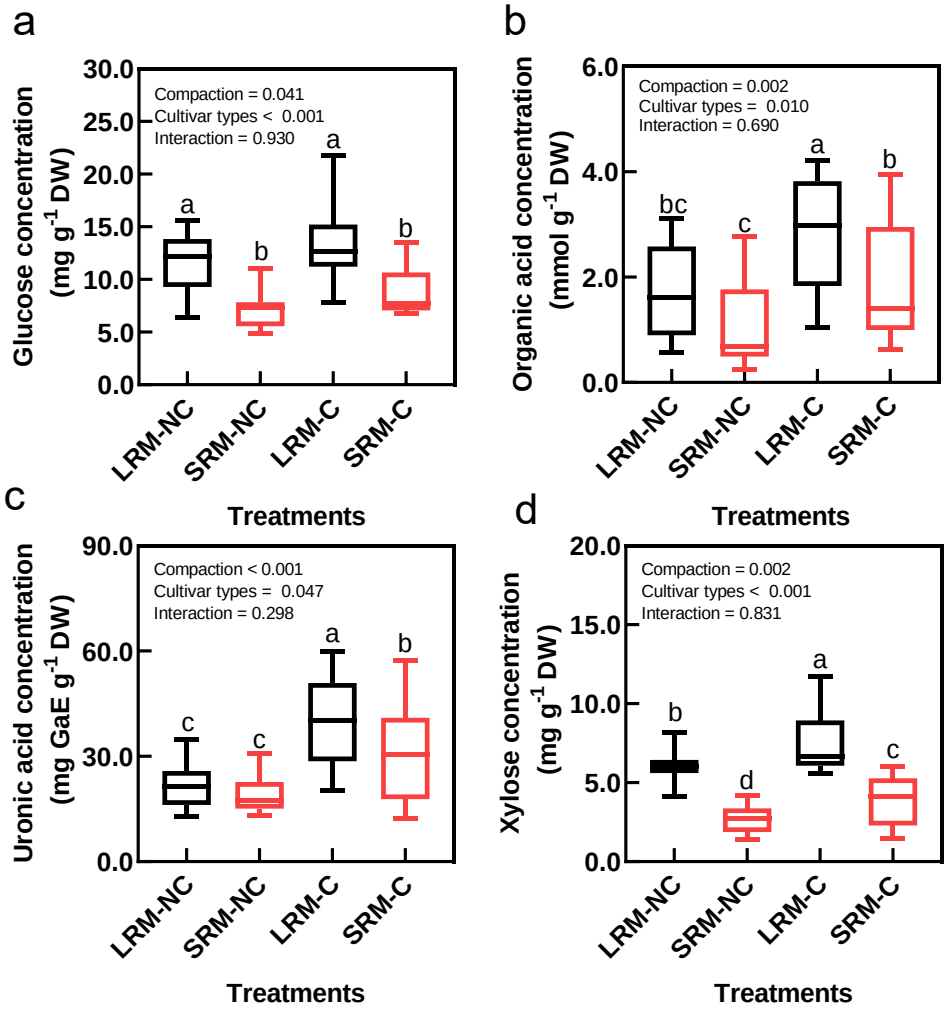
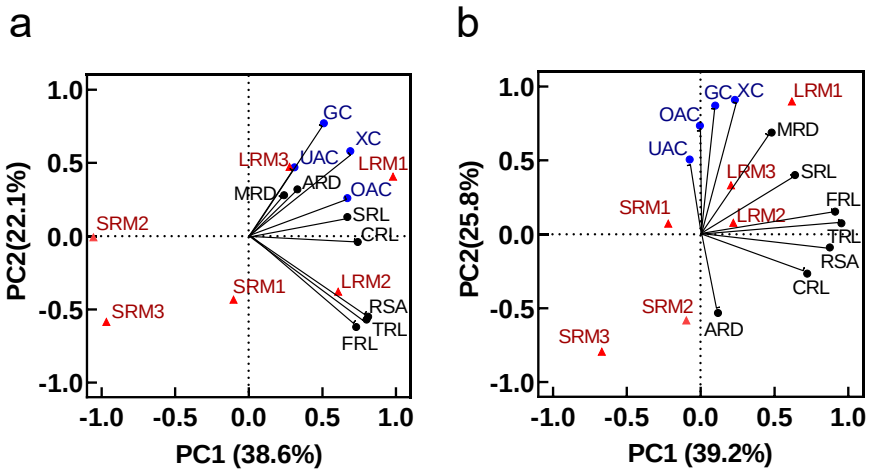


Fig. 3. Maximum root depth of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The different small letters above the column indicate significant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



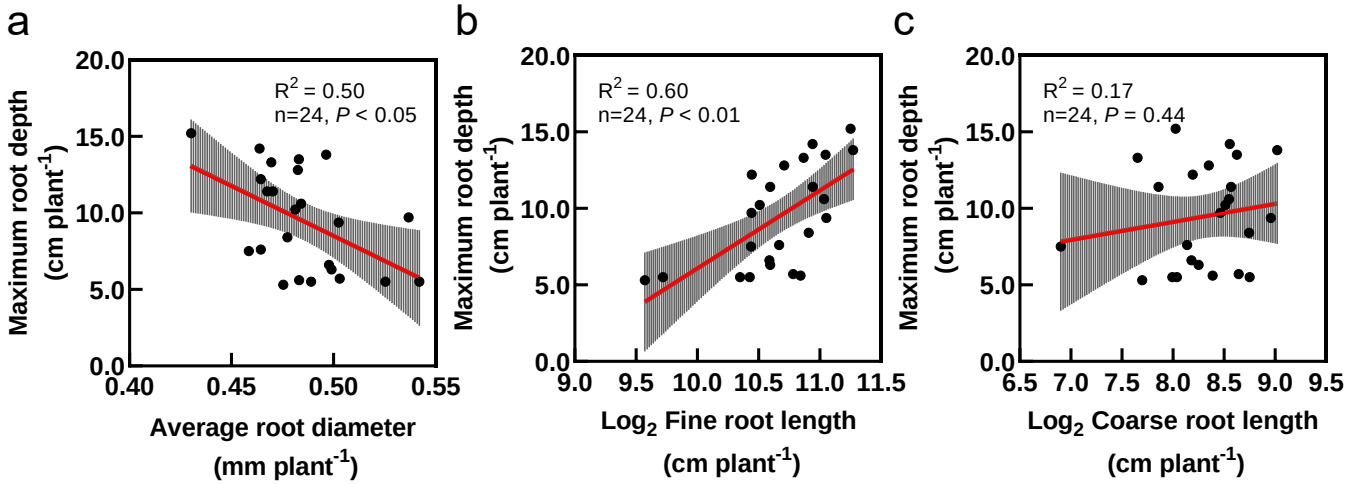
961

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



968

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



978

979 Fig. 7. Correlations between maximum root depth and average root diameter (a), fine root length (b) and coarse root length (c) of six *Brassica*

980 *napus* cultivars in compacted treatment. The shaded areas indicate the 95% confidence range, derived from the models

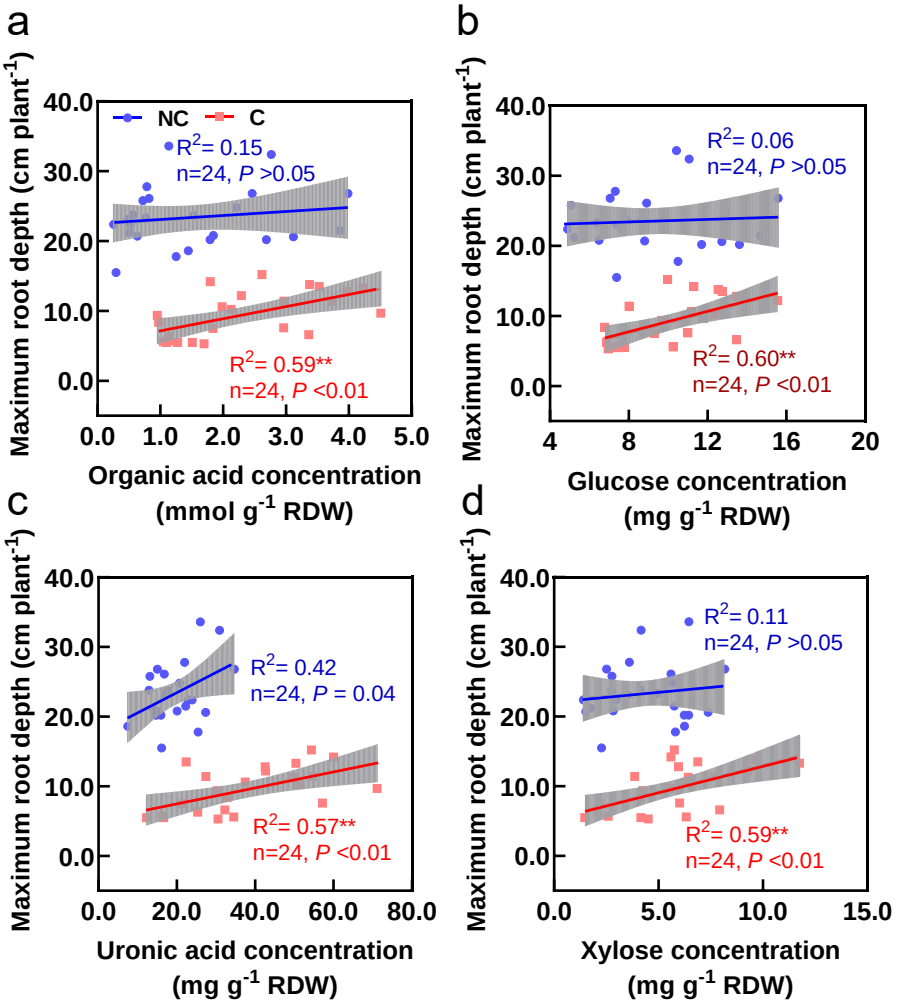
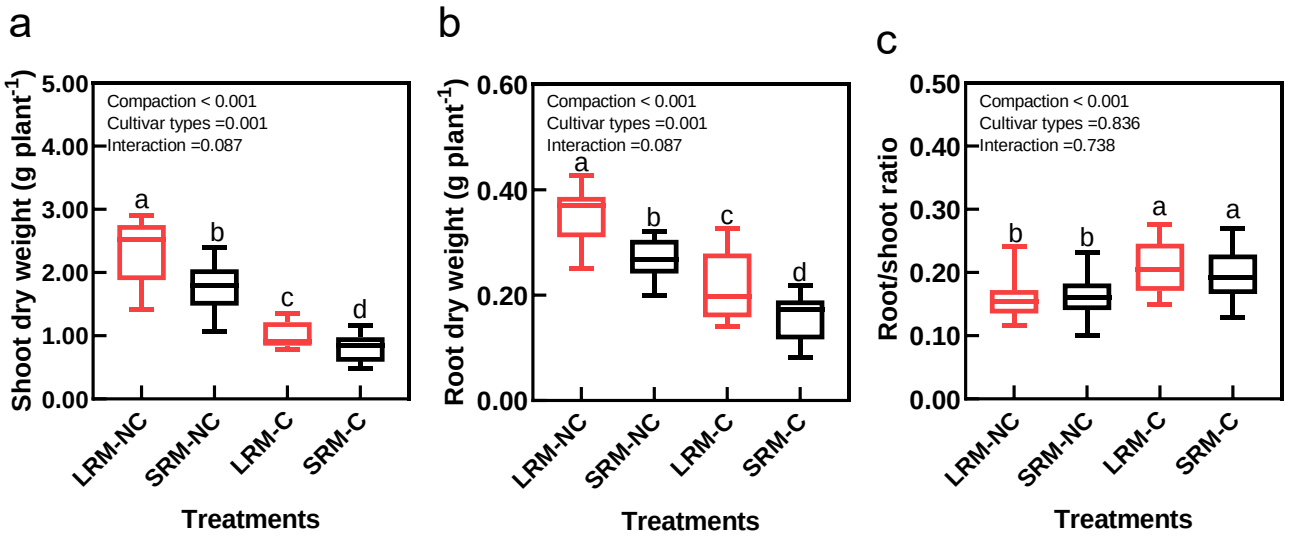


Fig. 8. Correlations between maximum root depth and organic acids (a), glucose (b), uronic acid (c) and xylose (d) concentrations of six *Brassica napus* cultivars in both non-compacted (NC) and compacted (C) treatments. The shaded areas indicate the 95% confidence range, derived from the models. $^{*}P$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



986

987 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)
988 treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical traits. The
989 different small letters above the column indicate significant difference among four treatments at P <0.05.

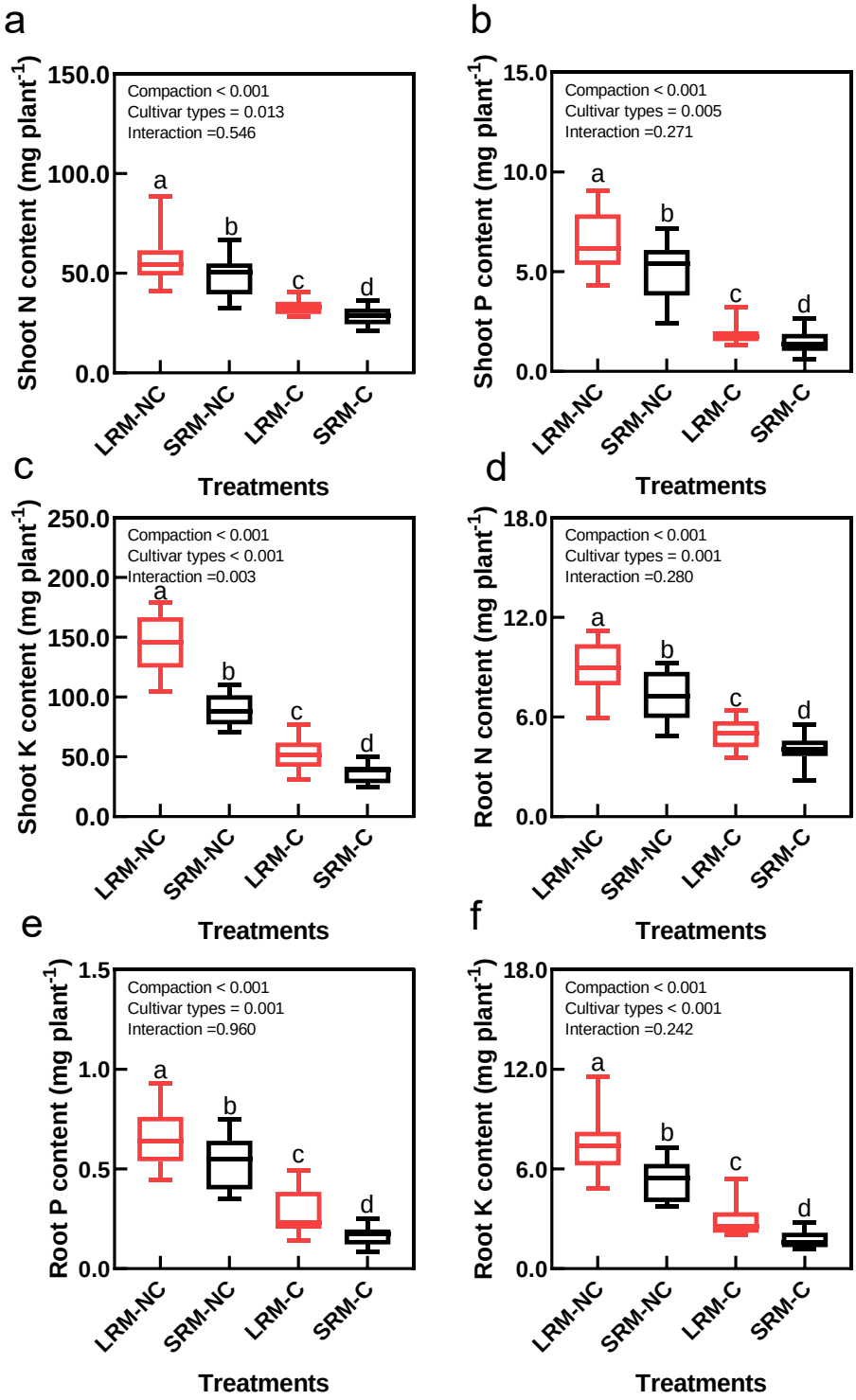
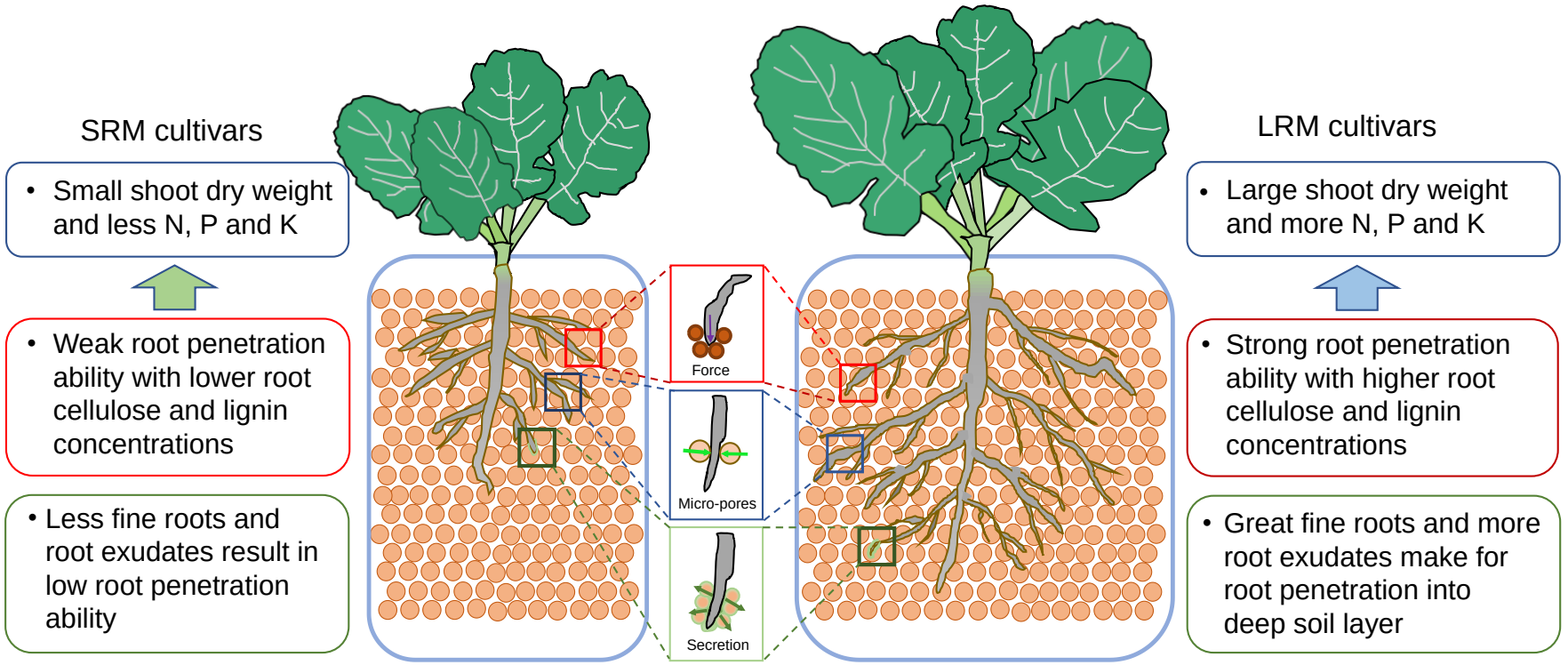


Fig. 10. The contents of nitrogen (N), phosphorus (P) and potassium (K) in shoot (a-c) and root (d-f) of LRM and SRM cultivars in non-compacted (NC) and compacted (C) treatments. LRM, *Brassica napus* cultivars with large root mechanical traits; SRM, *Brassica napus* cultivars with small root mechanical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



996

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

1000 Table 1 Soil bulk density and total porosity of soil in non-compacted and compacted
1001 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

1002 Note: [1] The total porosity of soil (%) was calculated with the formula by Hao et al.
1003 (2008).

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**	1.32ns	7.07*	1.01ns	3.63*	1.52ns	48.07***	75.73***	3.43*	7.35**
Compaction × Cultivars	0.93ns	4.21*	4.43*	0.04ns	1.47ns	0.07ns	2.71ns	0.71ns	0.05ns	1.11ns	0.16ns

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, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.