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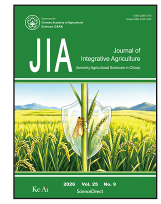

RESEARCH ARTICLE

Genotypic advantages of root–shoot growth alleviate the grain yield reduction of maize (*Zea mays* L.) under various soil compaction levels

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Highlights

- Heavy soil compaction reduced maize yield by 5.9–41.1%, while high compaction tolerance (H) hybrids had 12.0–30.3% greater yield advantages than the middle compaction tolerance (M) and low compaction tolerance (L) hybrids due to better root and shoot growth.
- Under heavy compaction, the selected H hybrid had greater root length, root surface area, and root weight, as well as root activity, absorption and antioxidant capacity, which increased leaf area index and dry matter accumulation, with increases of 5.6–27.2% and 8.3–23.2%, respectively.
- Root growth advantages were more obvious than shoot growth for the H hybrid under heavy compaction, leading to a greater root/shoot ratio.

Abstract

Soil compaction has become a serious limitation for further increasing the grain yield of maize (*Zea mays* L.) in the North China Plain (NCP). However, considerable variability exists among maize hybrids in their grain yield responses to soil compaction. To understand the physiological processes related to the variation of responses among maize hybrids to different soil compaction levels, a two-year field experiment was conducted with 17 maize hybrids and three soil compaction treatments (NC, no compaction with soil bulk density (SBD) of 1.0–1.3 g cm^{-3}; MC, moderate compaction with SBD of 1.4–1.5 g cm^{-3}, and HC, heavy compaction with SBD>1.6 g cm^{-3}) to examine the root and shoot morphological traits, dry matter accumulation, and grain yield. Compared to NC, MC and HC significantly reduced the maize yield by 0.9–26.7% and 5.9–41.1% across the hybrids and years, respectively. Hybrids with high compaction tolerance (H) had greater grain yield than those with middle compaction tolerance (M) and low compaction tolerance (L), particularly under HC. The yield benefits obtained from the H hybrid were enhanced due to better root and shoot growth under HC conditions. Greater root length, root surface area, and root weight, as well as root activity, absorption capacity, and antioxidant capacity for H hybrid was found under HC conditions, and it also showed increased leaf area index and dry matter accumulation. Moreover, the increases in root growth indices for the H hybrid were greater than that of shoot growth, particularly under HC conditions, leading to a greater root/shoot ratio. We conclude that soil compaction impacts maize root and shoot growth differently depending on genotype, and the root growth advantages of the H hybrid were more obvious than shoot growth, which enhanced the yield benefits from the H hybrid under heavy compaction conditions.

Keywords: maize hybrids, soil compaction, grain yield, root growth, shoot growth

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1. Introduction

The North China Plain (NCP) is one of the largest agricultural areas in China. It produces more than 31% of the nation's maize and plays an important role in ensuring the country's food security. The most common practice in this area involves a double-cropping system that integrates the planting of maize immediately following the wheat harvest every year. Under this intensive cropping system, long-term rotary tillage before wheat sowing promotes the formation of a hard plough pan at a soil depth about 15 cm (Latifmanesh *et al.* 2018; Nawaz *et al.* 2023), and continuous no-tillage direct stubble sowing for maize increases the soil bulk density of topsoil (0–15 cm) (Kan *et al.* 2020; Ding *et al.* 2023). In some areas of the NCP, the soil bulk density even reaches 1.6 g cm^{-3}, substantially exceeding the optimal range of 1.1–1.3 g cm^{-3} that is conducive to maize growth (Li *et al.* 2002) and leading to a reduction in grain yield of over 20% (Sun *et al.* 2023; Zhang *et al.* 2023).

Soil compaction exerts profound influences on the morphological and physiological development of the root system. The increased soil bulk density associated with compaction restricts the growth and distribution of roots, which leads to a reduction in root length and an increase in root diameter (Haling *et al.* 2013; Nosalewicz and Lipiec 2014; Vanhees *et al.* 2021). Consequently, the capacity of roots to penetrate soil is diminished and the root distribution density is increased in upper soil layers (Burr-Hersey *et al.* 2017), resulting in the reduced absorption of water and nutrients from the deep soil layers (Habibi *et al.* 2023; Tomobe *et al.* 2023). Root structural integrity and physiological functions are also significantly affected by soil compaction, which are manifested as alterations in the morphology of root cortex cells, secretion of organic acids and polysaccharides (Duan *et al.* 2023), root vigor, and antioxidant enzyme activities (Chimungu *et al.* 2014; Lynch and Wojciechowski 2015), which further impede the root uptake capabilities (Pfeifer *et al.* 2014). Furthermore, the impaired functionality of the root system directly diminishes the growth and photosynthesis of the above-ground plant parts, which leads to reductions in biomass and yield of the crops (Gregory and Wojciechowski 2020), as well as declines in stomatal conductance, photosynthetic rates, leaf number, stem dry weight, and leaf dry weight under high compaction treatments (Grzesiak *et al.* 2022). Soil compaction may also alter the signaling molecules produced by the roots, which influences the growth and responses of the aboveground plants (Lynch and Wojciechowski 2015; Noh *et al.* 2022). However, considerable variability exists among maize hybrids in their sensitivity and adaptation to soil compaction, with discernible differences observed in root system development (Xiong *et al.* 2020), aboveground plant growth (Grzesiak *et al.* 2021), and the coordination between these two aspects (Rut *et al.* 2022). Maize hybrids with enhanced resistance to soil compaction exhibit improved root growth and functionality under high soil compaction conditions (Rut *et al.* 2022), potentially due to their ability to modulate root penetration (Andersen *et al.* 2013) and alter growth trajectories (Konôpka *et al.* 2008; Atkinson *et al.* 2020). As a result, more resistant cultivars experience greater yields compared to those with greater sensitivity (Grzesiak *et al.* 2021).

Obviously, soil compaction can produce negative effects on both root development and aboveground growth. Meanwhile, the effect of soil compaction is different among various maize hybrids. However, how maize hybrids respond to different compacted soils by coordinating root and shoot growth remains poorly understood. In this study, 17 maize hybrids were used to evaluate the effects of three different soil compaction treatments (no soil compaction, moderate soil compaction, and heavy soil compaction) on the root morphological and physiological traits, shoot growth, and grain yield of maize. We also examined the physiological processes associated with root and shoot growth of the various maize hybrids in response to different soil compaction conditions.

2. Materials and methods

2.1. Site description

Field experiments were conducted at the Xinxiang Experiment Station of the Chinese Academy of Agricultural Sciences, Henan Province, China (35°18´N, 113°54´E), from 2022 to 2023. The average annual temperature, growing degree days and annual sunshine duration were 14°C, 4,647.2°C and 1,928.5 h. Mean annual precipitation was 656.3 mm, with most of the rain in July and August. The daily precipitation, average temperature and solar radiation in the maize growing seasons in 2022 and 2023 are shown in Fig. 1. The soil texture of this region is clay loam. The soil organic matter, available N, available P, available K and pH were 12.8 g kg^{-1}, 63.6 mg kg^{-1}, 17.5 mg kg^{-1}, 112.3 mg kg^{-1} and 8.1, respectively, in the topsoil layer (0–20 cm).

2.2. Experimental design and field management

The experiment was arranged in a split-plot experimental design with three replications. The main plots were subjected to three soil compaction treatments, including no compaction (NC, with soil bulk density at the 10–20 cm depth of 1.0–1.3 g cm^{-3}), moderate compaction (MC, with soil bulk density of 1.4–1.5 g cm^{-3}), and heavy compaction (HC, with soil bulk density of >1.6 g cm^{-3}). Before maize planting, deep ploughing and rotary tillage were conducted, and then the three soil compaction level treatments were laid out by repeated rolling using a tractor (JOHN DEERE 5–754; 4,476 kg) either 0, 5, or 15 times in 2022 and 0, 3, or 12 times in 2023. Data for the soil bulk density, penetration resistance, and porosity of the three soil compaction treatments in 2022 and 2023 are shown in Table 1. The subplots consisted of 17 maize hybrids from different maize-growing agro-ecological regions of China. The hybrid names, years and locations of introduction are shown in Appendix A. Each subplot was 48 m^2 (10.0 m long and 4.8 m wide) and consisted of eight rows.

Before sowing, a basal dose of fertilizers (150 kg ha^{-1} N, 120 kg ha^{-1} P_2O_5, and 90 kg ha^{-1} K_2O) was applied using a no-till planter with a depth of 5 cm. Another 120 kg ha^{-1} of N fertilizer was given as side dressing at the 8-leaf stage. Maize was planted on June 21 in 2022 and June 25 in 2023, and on October 29 in 2022 and October 16 in 2023. Seeds were sown by hand after a 3-cm-deep trench was made with a hand hoe for proper seed placement. The planting density was 67,500 plants ha^{-1}, and the row spacing was 60 cm. Maize

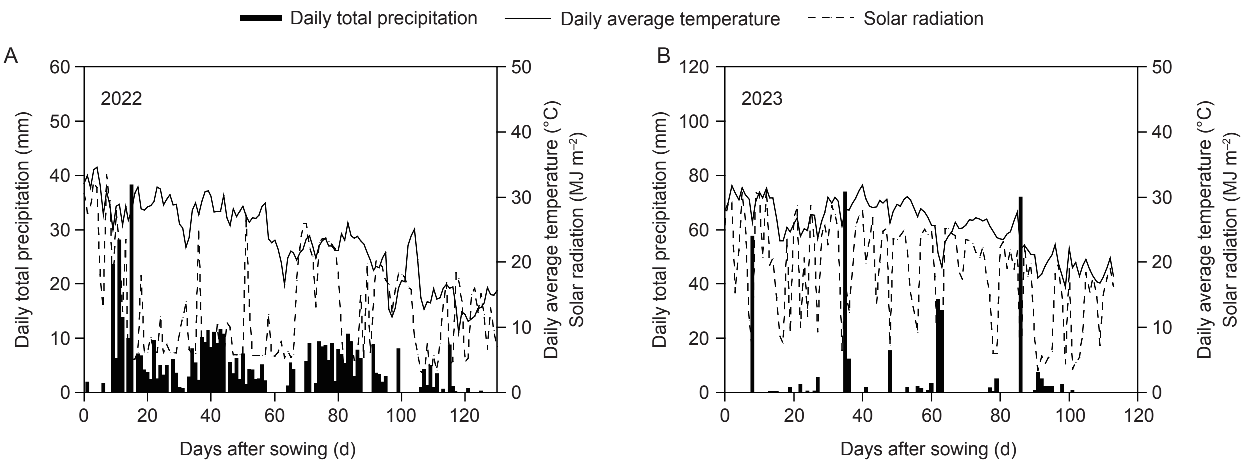

Fig. 1 Daily precipitation, average temperature, and solar radiation during the maize growing seasons in 2022 and 2023.

Table 1 Soil bulk density, penetration resistance, and porosity under different soil compaction treatments

Year	Compaction treatment[1)]	Bulk density (g cm^{-3})			Penetration resistance (kPa)			Porosity (%)		
		0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm
2022	NC	1.36 c	1.35 c	1.60 bc	345.6 cd	678.7 c	1,380.7 bc	44.4 a	41.6 b	36.9 b
	MC	1.50 bc	1.52 b	1.64 ab	456.0 cd	905.4 bc	1,551.6 abc	41.7 ab	37.9 cd	35.2 bc
	HC	1.56 ab	1.59 ab	1.67 a	643.2 c	1,325.0 a	1,702.5 ab	39.7 b	37.1 cd	35.1 bc
2023	NC	1.08 d	1.07 d	1.22 d	175.0 d	192.5 d	1,252.0 c	43.9 a	46.1 a	46.2 a
	MC	1.64 ab	1.53 b	1.54 c	1,395.3 b	965.0 b	1,228.3 c	35.7 c	38.2 c	35.4 bc
	HC	1.66 a	1.65 a	1.60 bc	2,499.4 a	1,467.2 a	1,895.6 a	31.2 d	35.9 d	34.7 c
Source of variation										
Year (Y)		ns	*	**	**	ns	ns	**	ns	**
Compaction (C)		**	**	**	**	**	**	**	**	**
Y×C		**	**	**	**	**	ns	**	**	**

1) NC, no compaction; MC, medium compaction; HC, heavy compaction.
Different lower-case letters in a column denote significant pairwise differences between means (P<0.05). *, P<0.05; **, P<0.01; ns, not significant.

was harvested at physiological maturity. For all the plots, the water, weeds, pests, and diseases were well controlled during the maize growing seasons in 2022 and 2023.

2.3. Sampling and measurements

The leaf area index (LAI) and dry matter (DM) of 17 maize hybrids were determined at the six-leaf stage (V6), the 12-leaf stage (V12), the silking stage (R1), the milking stage (R3), and the physiological maturity stage (R6). Three successive plants in the middle rows of each plot were collected randomly. The length and maximum width of each green leaf were measured. The LAI was calculated using the following formulas:

Fully unfolded leaf area=Length×Maximum width×0.75

Not fully unfolded leaf area=Length×Maximum width×0.50

LAI=Leaf area per plant (m^2)×Plant density (plants ha^{-1})/10,000 (m^2 ha^{-1})

After the measurement of leaf area, the sampled plants were dried at 105°C for 30 min and then at 75°C to a constant moisture content before being weighed.

Root morphological indices of the 17 maize hybrids were determined at the V6 and R1 stages. Root samples of three successive plants in each plot were taken after stalk sampling. Centered on each plant, a soil volume of 24 cm (intra-row direction)×30 cm (inter-row direction)×50 cm (depth) was excavated using a shovel. After washing free of soil, the root samples were scanned into images to calculate the root length, root surface area, and root volume using a root analysis system (GXY-B, China). Then, the root samples were oven-dried to measure their dry weight.

Hybrids DK517, ZD958, and DH605, representing high soil compaction tolerance (H), middle soil compaction tolerance (M), and low soil compaction tolerance (L), respectively, were selected for measuring root activity, root absorption area, root anatomical structures, and root antioxidant indices. Root samples of three successive plants in each plot were taken at the V6 and R1 stages. Centered on each plant, a soil volume of 24 cm (intra-row direction)×30 cm (inter-row direction)×50 cm (depth) was excavated using a shovel. After cleaning the roots with running water, the isolated roots of nodes 3 and 4 were collected to measure root activity, root absorption area, and antioxidant indices.

Root activity was represented by the activity of dehydrogenase, which was calculated by the reduction of triphenyl tetrazolium chloride (TTC). Fresh root tissues (0.2 g) were soaked in 5 mL of 0.4% TTC and 5 mL sodium phosphate buffer (1/15 mol L^{-1}, pH 7.0) in the dark at 37°C for 1 h, and then 2 mL H_2SO_4 (1 mol L^{-1}) was added to stop the reaction. Then, the samples were ground with 4 mL ethyl acetate, and ethyl acetate was added to the supernatant up to a final volume of 10 mL. The absorbance of that solution was measured at 485 nm, and the root activity was calculated by a standard curve (Li *et al.* 2023).

Root absorption area was measured using the methylene blue adsorption assay (Yan *et al.* 2016). Methylene blue at 0.0002 mol L^{-1} was diluted into three beakers, with volumes 10 times that of the root system. Roots were gently blotted dry and immersed in the solution within each beaker for 1.5 min, followed by the careful recovery of the solution. A total of 1 mL of solution from each beaker was then diluted tenfold and the absorbance was measured at 660 nm. The residual methylene blue content was ascertained from a previously established standard curve.

Root anatomical structures were measured at the R1 stage. Specifically, 2–3 cm segments of roots were selected at 2–3 cm from the crown base (Vanhees *et al.* 2020). Specimens were fixed using FAA (formaldehyde–acetic acid–ethanol, 1:1:18, v/v) solution. The paraffin embedding technique was employed for tissue clarification, wax impregnation, and embedding. Sections were prepared using a manual hand-cranked slicer, stained with safranin and fast green, and then examined and documented under a microscope, as previously reported by Yin *et al.* (2015). Structural measurements of the samples were conducted using ImageJ (National Institutes of Health, 1.8.0, 2023). The indices for root cross-sectional assessment, including root cross-diameter, cortex thickness, and central column diameter, were measured, in addition to root xylem vessel diameter and cortex thin-walled cell diameter.

The activities of antioxidant enzymes and the content of malondialdehyde (MDA) were measured in roots at V6 and R1. Fresh root samples were homogenized with a pH 7.0 phosphate buffer in an ice bath and then subjected to refrigerated centrifugation to obtain a crude enzyme solution. The superoxide dismutase (SOD) activity was recorded at 560 nm and defined as the amount of SOD required to produce a 50% inhibition of the reduction of nitroblue tetrazolium (NBT). The peroxidase (POD) activity was defined as the increase in absorbance every 30 s at 470 nm. The catalase (CAT) activity was assayed as the reduction in absorbance at 240 nm for 1 min following the decomposition of H_2O_2. MDA was measured with thiobarbituric acid (TBA).

At maturity, the grain yields of the 17 maize hybrids were determined. Ears were harvested from the central rows of each plot (24 m^2, 5.0 m long and 4.8 m wide). Grain moisture content was assessed using a PM8818 meter, and yields were standardized to a 14% moisture content. Twenty ears were selected randomly from the harvested maize for measuring the kernel number and 1,000-kernel weight.

2.4. Statistical analysis

The data were organized with Microsoft Excel 2016, while Duncan's multiple range test and multiple comparisons (α=0.05) were performed with SPSS 21.0. Pearson's correlation analysis was applied to assess the relationships between variables, and graphical representations were produced with Origin 2018. Cluster analysis was employed to group the different varieties based on their yields under HC conditions, by using the system clustering method available in SPSS 21.0.

3. Results

3.1. Grain yield of maize hybrids

Soil compaction led to significant yield reductions for all 17 maize hybrids, with greater reductions under HC than under MC (Table 2). Compared with NC, MC and HC reduced the grain yields of maize hybrids by 14.3 and 25.2% in 2022, and by 10.5 and 23.5% in 2023, respectively. Moreover, the yield reductions due to soil compaction differed among the 17 hybrids, ranging from 0.9–26.7% under MC and 5.9–41.1% under HC compared to NC.

Hierarchical clustering was conducted based on the yields of the 17 maize hybrids under HC treatment over two years, and the hybrids fell into three groups, namely H, M, and L (Appendix B). No significant differences in yield were observed among the H, M, and L hybrids under NC conditions over consecutive years, while the H hybrids had greater yields than M and L under HC conditions, with increases of 12.9–23.3% and 12.0–30.3% in 2022 and 2023, respectively (Table 2). This indicates that H hybrids have obvious yield advantages compared to the other two hybrid groups, particularly under HC conditions.

3.2. Aboveground DM and LAI

Soil compaction significantly reduced the aboveground DM of each maize hybrid at each growth stage, and the DM differed for hybrids H, M, and L under both MC and HC (Fig. 2).

Table 2 Grain yield (Mg ha^{-1}) of 17 maize hybrids under different soil compaction treatments

Genotype[1)]	Hybrids	2022[2)]			2023[2)]		
		NC	MC	HC	NC	MC	HC
H	KW8901	8.9 b	8.3 a	8.0 a	11.3 b	10.8 b	10.7 a
	ZND787	9.0 b	8.2 a	7.5 a	12.2 a	11.0 a	10.5 a
	DK517	9.1 b	8.3 a	7.5 a	11.6 ab	10.9 ab	10.0 a
M	LC839	8.7 bc	7.9 ab	7.0 b	11.3 b	9.8 c	9.4 b
	ZD958	8.6 c	8.4 a	6.8 b	11.6 ab	11.0 a	9.5 b
	DK688	9.3 b	7.8 ab	6.9 b	11.1 b	11.0 a	9.3 b
	YN743	9.0 b	7.5 b	6.7 b	11.8 ab	9.8 c	9.3 b
	ZY013	8.7 c	7.8 ab	6.7 b	11.5 ab	10.6 b	9.2 b
	KW1	9.1 b	8.4 a	6.7 b	11.8 ab	10.5 b	9.0 b
L	XY335	8.8 bc	7.7 b	6.5 c	12.0 a	10.2 b	7.5 c
	ZY186	9.0 b	7.8 ab	6.5 c	11.2 b	10.6 b	8.2 c
	ND372	8.7 c	7.4 b	6.4 c	11.0 b	9.5 c	8.1 c
	XD1618	8.3 d	7.6 b	6.3 c	11.3 b	9.6 c	8.1 c
	YN211	8.7 c	7.1 b	6.2 c	11.5 ab	9.8 c	8.0 c
	ZY303	10.3 a	7.6 b	6.1 c	11.5 ab	10.6 ab	7.9 c
	LD771	9.3 b	7.9 ab	5.9 c	12.2 a	9.7 c	8.0 c
	DH605	8.8 c	7.8 ab	5.8 c	11.8 ab	10.8 ab	8.0 c
Source of variation							
Compaction (C)			**			**	
Genotype (G)			**			**	
C×G			**			**	

1) H, high compaction tolerance hybrid; M, medium compaction tolerance hybrid; L, low compaction tolerance hybrid.
2) NC, no compaction; MC, medium compaction; HC, heavy compaction.
Different lower-case letters in a column denote significant pairwise differences between means (P<0.05). **, P<0.01.

Under MC, H hybrids exhibited non-significant differences in aboveground DM at each growth stage compared to M, whereas it was markedly superior to L. Under HC, the aboveground DM of H hybrids at each growth stage were greater than those of M and L, and the total DM of H at maturity was greater than those of M and L by 8.3 and 22.9% in 2022, and by 10.1 and 23.2% in 2023, respectively.

Soil compaction significantly reduced the LAI of each maize hybrid at each growth stage, while the LAI differed for the H, M, and L hybrids under both MC and HC (Fig. 3).

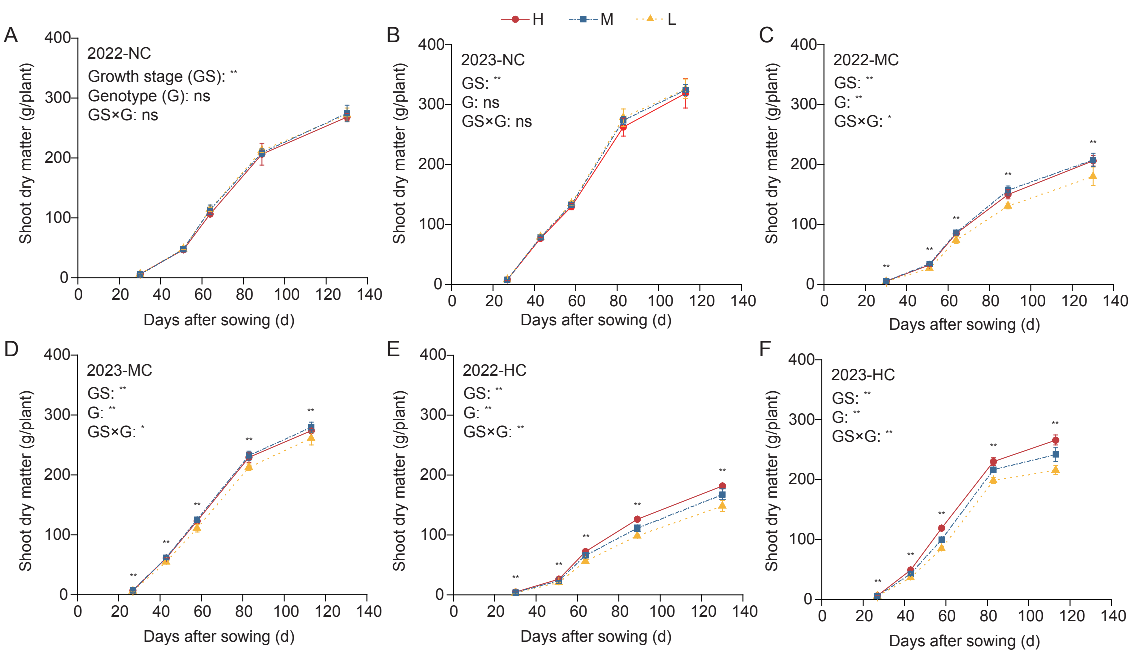

Fig. 2 Dry matter accumulation of maize under different soil compaction treatments. NC, no compaction; MC, medium compaction; HC, heavy compaction. H, high compaction tolerance hybrid; M, medium compaction tolerance hybrid; L, low compaction tolerance hybrid. Bars mean SD (n=9 (H), 18 (M) and 24 (L)). Different lower-case letters adjacent to the error bars denote significant pairwise differences between means (*, P<0.05; **, P<0.01; ns, non significant).

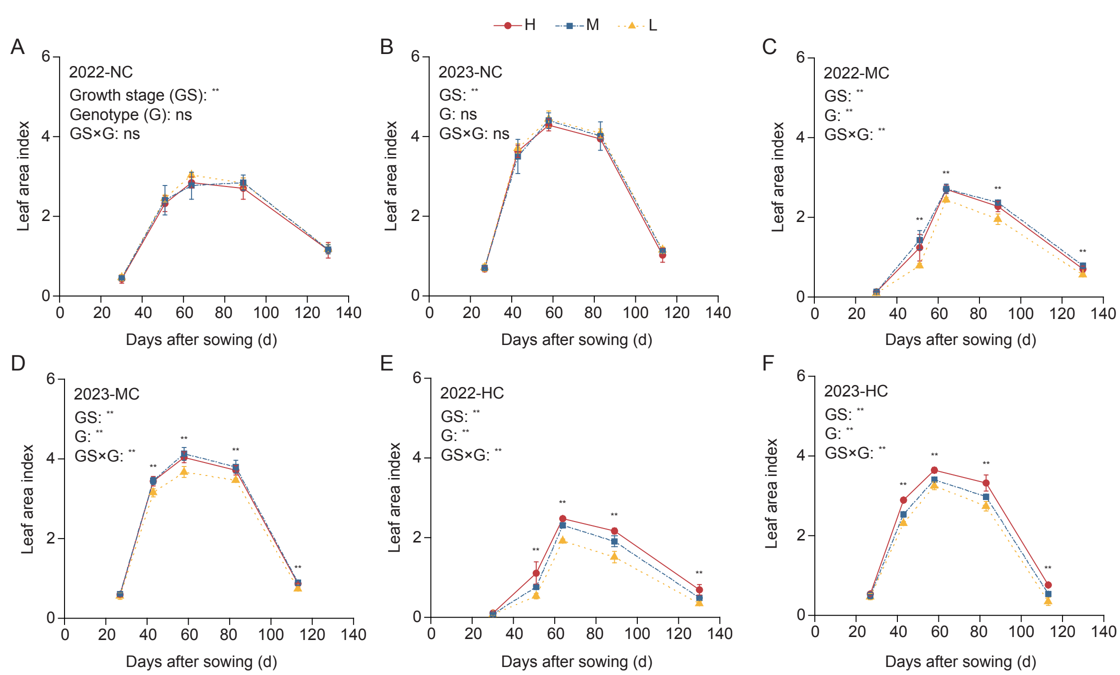

Fig. 3 Leaf area index (LAI) of maize under different soil compaction treatments. NC, no compaction; MC, medium compaction; HC, heavy compaction. H, high compaction tolerance hybrid; M, medium compaction tolerance hybrid; L, low compaction tolerance hybrid. Bars mean SD (n=9 (H), 18 (M) and 24 (L)). Different lower-case letters adjacent to the error bars denote significant pairwise differences between means (**, P<0.01; ns, non significant).

Under MC, the LAI of H hybrids at each stage were significantly greater than those of L, but did not differ from M. Under HC, the LAI of H at each stage was significantly higher than those of M and L, and the maximum LAI of H at silking was greater than those of M and L by 5.6 and 27.2% in 2022, and by 7.1 and 12.0% in 2023, respectively.

3.3. Root morphological traits

Soil compaction significantly reduced the root length, surface area, volume, and dry weight of maize during the V6 and R1 stages, while these impacts strengthened with soil compaction intensity and exhibited differences among the hybrids (Fig. 4). The H hybrid consistently exhibited superior root morphological

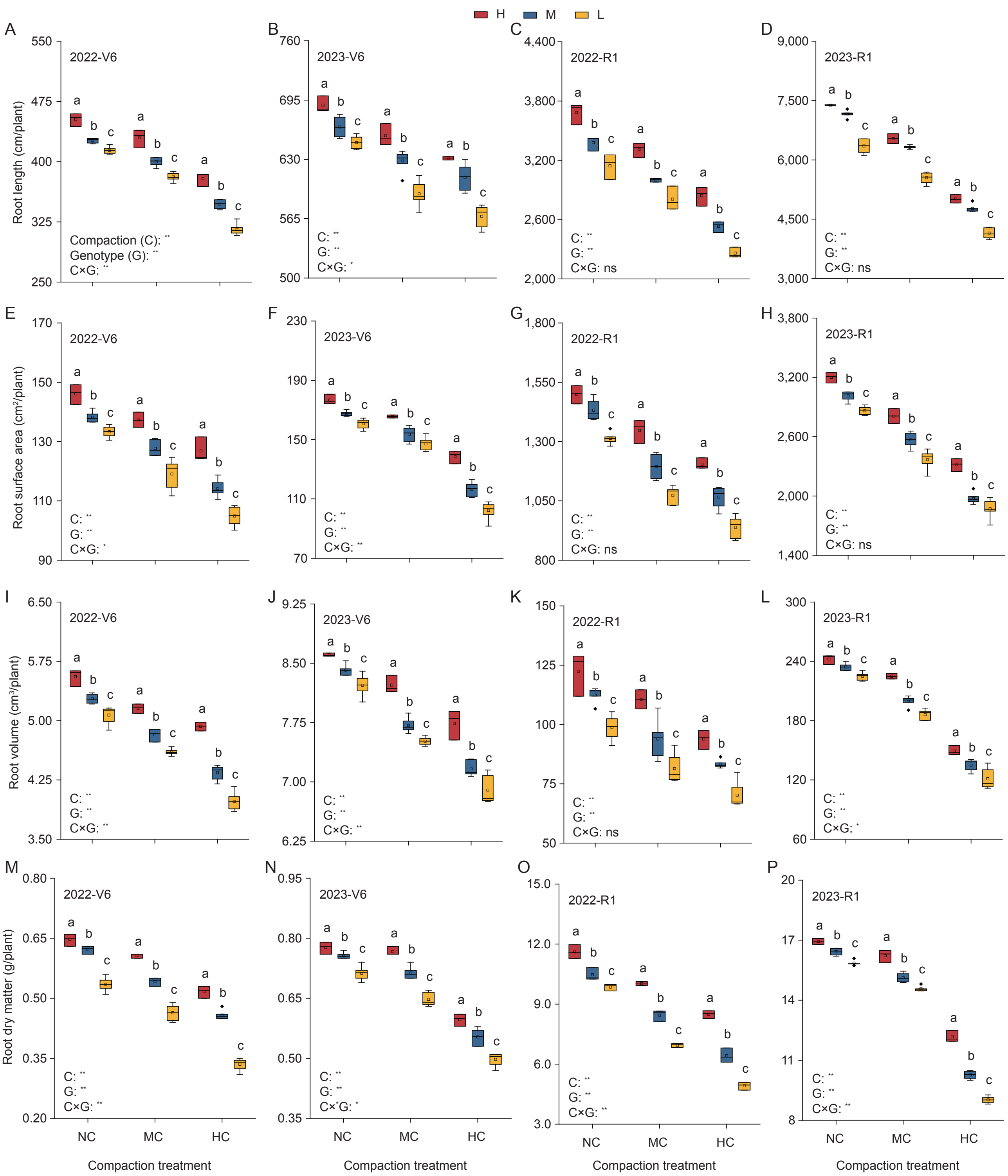

Fig. 4 Root morphological indices of maize under different soil compaction treatments. NC, no compaction; MC, medium compaction; HC, heavy compaction. H, high compaction tolerance hybrid; M, medium compaction tolerance hybrid; L, low compaction tolerance hybrid. Bars mean SD (n=9 (H), 18 (M) and 24 (L)). Different lower-case letters adjacent to the error bars denote significant pairwise differences between means (*, P<0.05; **, P<0.01; ns, non significant).

index values compared to M and L across the soil compaction treatments and years, particularly under HC conditions at the R1 stage. Under HC, the root length, root surface area, root volume, and root dry weight of the H hybrid were 8.7, 25.4, 15.1, and 11.6% greater than M, and 23.2, 53.7, 26.0, and 28.4% greater than L averaged for the two years, respectively.

3.4. Root activity and absorption capacity

Soil compaction exerted marked impacts on maize root activity (RA), the total absorption areas (TAA), and the active absorption areas (AAA) during the V6 and R1 stages, while the impacts strengthened with soil compaction intensity and exhibited differences among hybrids (Fig. 5). No significant differences were found among the three hybrids under NC, while DK517 (H) was superior in RA, TAA, and AAA compared to ZD958 (M) and DH605 (L) under compaction conditions, particularly under HC at the R1 stage. Under HC, the RA, TAA, and AAA of the H hybrid were 15.1, 1.7, and 0.7% greater than M, and 33.8, 2.6, and 2.2% greater than L averaged over the two years, respectively.

3.5. Root antioxidant capacity

Soil compaction significantly reduced the activities of SOD, POD, and CAT in the root system at the R1 stage, while these impacts strengthened with soil compaction intensity and exhibited differences among the hybrids (Fig. 6). DK517 (H) was superior in SOD, POD, and CAT activities compared to ZD958 (M) and DH605 (L) under compaction conditions, particularly under HC, while no significant differences were found among the three hybrids under NC. Under HC, the activities of SOD, POD, and CAT for DK517 (H) were 15.9, 7.4, and 58.6% greater than those of ZD958 (M), and 33.9, 35.3,

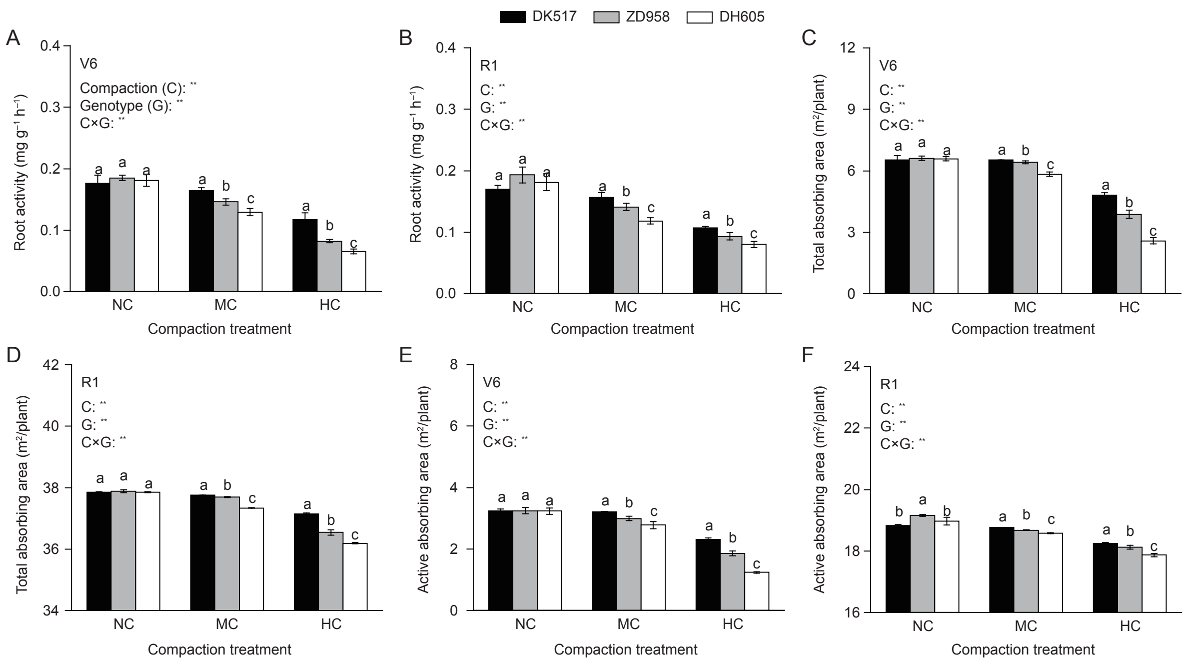

Fig. 5 Root physiological indices of maize under different soil compaction treatments. NC, no compaction; MC, medium compaction; HC, heavy compaction. DK517, Dika 517; ZD958, Zhengdan 958; DH605, Denghai 605. V6, six-leaf stage; R1, silking stage. Bars mean SD (n=6). Different lower-case letters adjacent to the error bars denote significant pairwise differences between means (**, P<0.01).

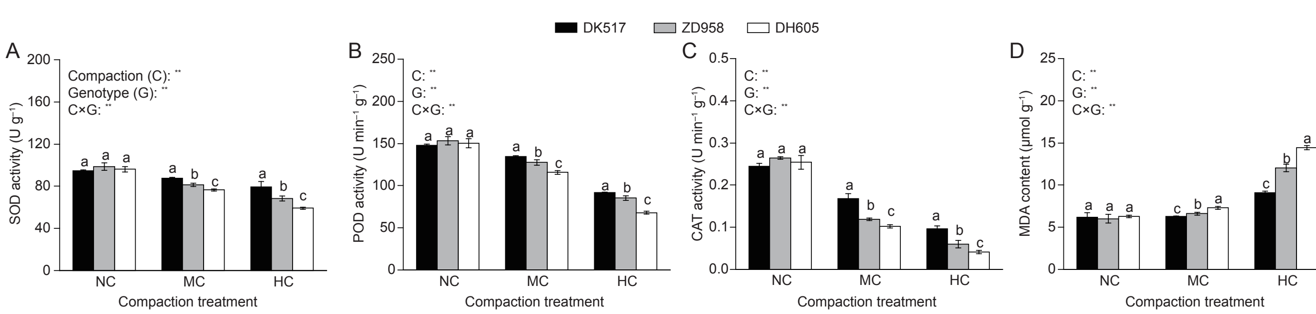

Fig. 6 Antioxidant enzyme activities and malondialdehyde (MDA) content in the roots of maize under different soil compaction treatments. NC, no compaction; MC, medium compaction; HC, heavy compaction. DK517, Dika 517; ZD958, Zhengdan 958; DH605, Denghai 605. SOD, superoxide dismutase; POD, peroxidase; CAT, catalase; MDA, malondialdehyde. Bars mean SD (n=6). Different lower-case letters adjacent to the error bars denote significant pairwise differences between means (**, P<0.01).

and 134.5% greater than those of DH605 (L), respectively.

Soil compaction significantly increased the content of MDA in maize root at the R1 stage, while this impact strengthened with soil compaction intensity and exhibited differences among the hybrids (Fig. 6). No significant differences were found among the three hybrids under NC, while DK517 (H) exhibited an inferior MDA content compared to ZD958 (M) and DH605 (L) under compaction conditions, particularly under HC. The MDA content for DK517 (H) was 24.4 and 37.0% less than those of ZD958 (M) and DH605 (L) under HC, respectively.

3.6. Root anatomical traits

Soil compaction induced the lateral expansion of the root system at the R1 stage, with greater expansion under higher compaction levels, as indicated in Table 3. This response was compaction-dependent rather than genotype-specific. Despite an observable trend toward enlargement, there were no significant differences in the cross-sectional diameter, cortex diameter, or stele diameter among the hybrids subjected to the soil compaction treatments. When assessed against NC, the MC treatment resulted in respective expansions of 38.5 and 16.6%, 37.5 and 16.6%, and 34.5 and 17.9% in the vessel and cortex cell diameters of hybrids DK517 (H), ZD958 (M), and DH605 (L), respectively. Under HC, these enhancements were markedly greater, with increases of 96.2 and 89.2%, 90.3 and 94.6%, and 42.7 and 87.6%, respectively.

Table 3 Root anatomical structure of maize under different soil compaction treatments

Treatment[1)]	Cross-sectional diameter (mm)	Cortex diameter (mm)	Stele diameter (mm)	Vessel diameter (mm)	Cortex cell diameter (μm)
Compaction					
NC	4.08 b	0.65 c	2.55 b	0.10 c	35.29 c
MC	4.16 b	0.68 b	2.75 a	0.11 b	48.39 b
HC	5.05 a	1.28 a	2.83 a	0.18 a	58.82 a
Genotype					
DK517	4.52 a	0.90 a	2.77 a	0.12 a	45.17 a
ZD958	4.42 a	0.87 a	2.71 a	0.14 a	45.35 a
DH605	4.40 a	0.90 a	2.66 a	0.13 a	44.96 a
Source of variation					
Compaction (C)	**	**	*	**	**
Genotype (G)	ns	ns	ns	**	**
C×G	ns	**	ns	**	**

1) NC, no compaction; MC, medium compaction; HC, heavy compaction. DK517, Dika 517; ZD958, Zhengdan 958; DH605, Denghai 605.
Different lower-case letters in a column denote significant pairwise differences between means (P<0.05). *, P<0.05; **, P<0.01; ns, not significant.

3.7. Relationship between shoot and root growth

The correlation analysis between shoot and root parameters of maize under soil compaction treatments (Table 4) revealed that yield, shoot dry matter, and LAI at the V6 and R1 stages were significantly positively correlated with the root morphology indicators (root length, root surface area, root volume, and root dry weight), root activity, and antioxidant enzyme (SOD, POD, and CAT) activities (P<0.01). In contrast, they were negatively correlated with MDA content, CSD, CD, and VD.

4. Discussion

4.1. Soil compaction affects maize yield differently depending on genotype

Soil compaction produced by long-term minimal tillage or no tillage in the winter wheat–summer maize cropping system can strongly affect plant growth, development, and productivity (Kan *et al.* 2020; Han *et al.* 2022; Ding *et al.* 2023). In this study, repeated tractor rolling was used for designing different soil compaction treatments to examine the variation of responses to different levels of soil compaction among maize hybrids. Soil compaction reduced the grain yields of 17 maize hybrids by 11.3 and 27.9% under MC and HC averaged over the two years, respectively. H hybrids had an obvious yield advantage under soil compaction conditions compared to the other two types of hybrids (M and L), particularly under HC conditions. This result was consistent with previous studies which reported that differences between maize hybrids grown under non-stress and stress conditions were found to reduce the grain yield (Grzesiak *et al.* 2021). Moreover, the grain yield varied significantly between years and was probably related to the large amount of precipitation and high daily maximum air temperatures (35°C–38°C) encountered 1 wk before silking in 2022 (Fig. 1), which may have limited pollination and fertilization, eventually reducing the maize yields (Shao *et al.* 2021).

4.2. Genotypic differences in the root growth response to soil compaction

Soil compaction can directly limit the morphological and physiological development of the maize root system (Li *et al.*

Table 4 Correlation analysis between the shoot and root parameters of maize[1)]

Item[2)]	RL	RS	RV	RD	RA	SOD	POD	CAT	MDA	CSD	CD	SD	VD	CCD
Yield	0.91**	0.92**	0.91**	0.95**	0.91**	0.94**	0.96**	0.87**	–0.97**	–0.85**	–0.86**	–0.69*	–0.87**	–0.64
Total biomass	0.90**	0.90**	0.81**	0.87**	0.90**	0.94**	0.90**	0.85**	–0.90**	–0.70*	–0.72*	–0.59	–0.75*	–0.56
Shoot dry matter at V6	0.84**	0.81**	0.86**	0.83**	0.92**	0.86**	0.91**	0.84**	–0.83**	–0.85**	–0.84**	–0.79*	–0.87**	–0.76*
Shoot dry matter at R1	0.93**	0.93**	0.90**	0.95**	0.92**	0.95**	0.96**	0.86**	–0.97**	–0.81**	–0.84**	–0.61	–0.84**	–0.61
LAI at V6	0.89**	0.86**	0.80**	0.83**	0.91**	0.91**	0.89**	0.84**	–0.85**	–0.70*	–0.71*	–0.60	–0.75*	–0.59
LAI at R1	0.90**	0.89**	0.86**	0.88**	0.93**	0.96**	0.94**	0.90**	–0.91**	–0.75*	–0.76*	–0.71*	–0.79*	–0.59

1) RL, root length; RS, root surface area; RV, root volume; RD, root dry matter; RA, root activity; SOD, superoxide dismutase; POD, peroxidase; CAT, catalase; MDA, content of malondialdehyde; CSD, cross-sectional diameter; CD, cortex diameter; SD, stele diameter; VD, vessel diameter; CCD, cortex cell diameter.
2) V6, six-leaf stage; R1, silking stage. LAI, leaf area index.
*, P<0.05; **, P<0.01.

2023; Zhang *et al.* 2023). In this study, root morphological indices and root physiological indices all significantly declined under the soil compaction treatments, with greater reductions under HC. However, there were genotypic differences in the maize root growth responses to soil compaction (Colombi and Walter 2017; Xiong *et al.* 2020). Although no significant differences in the cross-sectional diameter, cortex diameter, or stele diameter were found among H, M, and L hybrids, the H hybrid consistently exhibited superiority in root length, root surface area, root volume, and root dry weight, as well as in root activity, total absorption area, and active absorption area, particularly under heavy compaction conditions. This indicated that root length was not associated with thickening under soil compaction (Vanhees *et al.* 2020), so the hybrids with a root growth advantage can compensate for the limitation on root capacity to penetrate the soil by increasing root length. As a result, the enhanced root morphological and physiological indices can help to maintain a higher root absorption capacity (Pfeifer *et al.* 2014; Wang *et al*. 2025).

Moreover, ROS transcription and signaling responses in plant roots have a certain protective effect on the vitality and absorption capacity of the root system under adverse stresses (Jacobsen *et al.* 2021; Habibi *et al.* 2023). This study showed that the root system of the H hybrid (DK517) could maintain relatively higher activities of SOD, POD, and CAT and reduced MDA content, particularly under heavy compaction. The enhanced antioxidant capacity of the root system likely contributes to a more complete root cell membrane structure to maintain root vitality and root absorption, and thereby increase the adaptability to compaction stress (Ahmad and Li 2021).

4.3. Genotypic differences in shoot growth responses to soil compaction

Due to limitations in the morphological and physiological development of maize root systems under compaction, the root's absorption of water and nutrients from the soil decrease, especially from the deep soil layers (Habibi *et al.* 2023; Tomobe *et al.* 2023), which could limit maize shoot growth. In this study, soil compaction significantly reduced the DM and LAI among the hybrids. However, the H hybrids exhibited superiority in the aboveground DM and LAI due to better root growth, particularly under HC. The correlation analysis results confirmed that the variation in aboveground DM and LAI contributed to yield variation among the hybrids under compaction conditions. This result is consistent with previous findings that differences between maize hybrids grown under non-stress and stress conditions were found in reduced maize growth parameters, such as seedling dry matter, plant height, and leaf area, as well as grain yield, and the grain yield and DM in the hybrids sensitive to soil compaction were more strongly inhibited than in the resistant hybrids (Grzesiak *et al.* 2021).

4.4. Practical implications and future directions

Soil compaction led to significant reductions in the grain yield of maize, and the impact was strengthened with soil compaction intensity and exhibited differences among hybrids. The hybrids with obvious advantages of both root and shoot growth could achieve a relatively higher grain yield, particularly under heavy soil compaction. Moreover, the increases in root growth indices for the H hybrid were greater than that of shoot growth under heavy compaction, leading to an increased root/shoot ratio (Appendix C). Thus, unleashing the biological potential of varieties with advantageous root traits is an important strategy for breaking the limitations of soil compaction stress. Although breeding efforts have enhanced the compaction tolerance and yield stability of maize hybrids in recent years, further research should focus on identifying root/shoot regulatory measures that enhance compaction tolerance without compromising yield potential, which is essential for narrowing the yield gap in soil compaction environments.

5. Conclusion

Soil compaction led to significant reductions in the grain yield of maize, while the impact was strengthened with soil compaction intensity and exhibited differences among hybrids. The H hybrid had obvious yield advantages compared to the other hybrids due to better root and shoot growth under heavy compaction. The increases in root growth indices for the H hybrid were greater than that of shoot growth, particularly under heavy compaction conditions. Greater morphological and physiological indices for the H hybrids under compaction help to maintain the greater leaf area index and dry matter accumulation, ultimately improving the maize yield. These findings enhance our understanding of compaction tolerance and identified the genotypes and traits beneficial for breeding high-yielding and compaction-tolerant hybrids of maize.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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