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Enhancing spatial and temporal coordination of soil water and root growth to improve maize (*Zea mays* L.) yield

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ABSTRACT

Enhancing the spatial and temporal coordination between soil water and roots is very important for crop growth. The vertical distribution and relationship between soil water and root are however poorly understood during maize growth under different soil water conditions. In this study, two maize hybrids ZD958 and FM985 were treated with drip irrigation (DI), flood irrigation (FI), and rainfed (RF) in two–year field experiment as well as with irrigation at 0–30 (TI), 30–60 (MI), 60–90 (BI), 0–90 cm soil layers (AI) and no irrigation in three–year tube experiment. In field experiment, DI and FI both increased root dry weight, root length density (RLD), and the proportion of coarse root length at different soil layers relative to RF. DI increased grain yield by 10.0% in FM985 and by 10.8% in ZD958 compared with FI. Both total root and fine root length were greater in DI than in FI, which increased the nitrogen and water use efficiency and yield. In the tube experiment, irrigation at different soil layers increased root dry weight, RLD and the proportion of coarse root length compared with no irrigation, with AI increasing the most. FM985 distributed more roots at the 0–30 cm soil layer than ZD958. Grain yields were positively correlated with the RLD in each soil layer and coarse root proportion at the upper layer ($r=0.493^{**}$ in field experiment and $r=426^{**}$ in tube experiment) but negatively correlated with root–shoot ratio ($r=-0.793^{**}$ in field experiment and $r=-670^{**}$ in tube experiment) at maturity stage. In conclusion, there is a large potential to improve maize yield by enhancing the spatial coordination between root distribution and soil water movement.

1. Introduction

Maize (*Zea mays* L.) is an important staple crop in the world and its consumption is the highest among all grain crops (Ranum et al., 2014; FAO, 2021). In 2021, the total production of maize is 260.9 million tones in China, accounting for about 23% of global maize production (FAO, 2021). To date, the rapid growth of population has put great pressure on water resources (Turan et al., 2018). The use of large amounts of groundwater as an irrigation source for crop and feed production has depleted aquifers, causing severe water deficits (Turan et al., 2018; Fahad et al., 2019). Drought stress has been a key factor limiting maize production at different regions around the world, for which irrigation is becoming an important mitigation measure. Irrigation water accounts for more than 70% of the total water consumption (Boyer, 2017; Kebede et al., 2019), which is going to increase due to increased frequency and intensity of drought stress under climate change (Lobell et al., 2014; Wu et al., 2018). Irrigation is able to alleviate drought stress, but causes resource waste, land salinization, and greenhouse gas emission (Trost et al., 2016; Li et al., 2020,2020; Huang et al., 2021). How to synchronize root growth with water distribution is of particular importance to enhance crop productivity and water use efficiency.

Root morphology characteristics and distribution have an important impact on lodging resistance and water and nutrient uptake (Mi et al., 2016; Colombi et al., 2018). In general, maize roots are mainly distributed at the 0–30 cm soil layer and decrease with increased soil depth (Qin et al., 2018). The growth and development of maize roots show relative plasticity in heterogeneous environments, which is the physiological basis for maize to cope with drought stress (Yu et al., 2019; Liu et al., 2020). The genotypic differences in nutrient such as nitrogen and phosphorus uptake capacity of maize root system have been documented widely, and the ideal root architecture for high grain yield and high nutrient use efficiency has been proposed (Lynch, 2013; Mi et al.,

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2016). However, little is known about the response of root to the heterogeneous distribution of soil wate. The distribution of water is more variable and complex than that of nitrogen and phosphorus in the soil (Faloye et al., 2019; Musokwa et al., 2020; Duan et al., 2021). Developing deeper and broader root system is generally recognized as an effective strategy for alleviating drought stress. However, given the metabolic costs of extensive root growth, such mindless foraging is inefficient (Lynch, 2013; Mi et al., 2016). The deep, steep and fine roots promote grain yield of maize under limited resource availability, especially in intensive agricultural system (Lynch, 2013; Mi et al., 2016). The balance between water capture and metabolic costs of root is important for both grain yield increase and drought tolerance of maize (Wang et al., 2020; Vanhees et al., 2021). The spatial coordination of root growth and soil water movement should be the target of irrigation. Interestingly, gravity promotes root hydrotropism in the vertical direction, helps root to search for water in the vertical direction, and inhibits root hydrotropism in the horizontal direction (Li et al., 2020), Therefore, it is more meaningful to study the spatial coordination of soil water and root system in the vertical direction.

In the arid and semi–arid regions, rainfed farming is the most important option in maize production. However, rainfed agriculture is highly erratic and depends heavily on annual precipitation, which seriously threatens yield stability (Zipper et al., 2016; Mangani et al., 2018). With the development of farmland infrastructure and water conservancy project, more rainfed farmland is potentially irrigated. Moreover, flood irrigation increases greenhouse gas emission and global warming potential, in comparison with no irrigation and drip irrigation (Zhang et al., 2020; Wei et al., 2021). Our previous studies also prove that drip irrigation promoted grain yield and decreased greenhouse gas emission (Gao et al., 2021). Drip irrigation can increase water use efficiency and reduce water consumption by reducing evaporation through deeper water distribution and smaller soil surface wetness area (Umair et al., 2019; Zhang et al., 2019; Valentín et al., 2020). The economic and environmental benefits of different irrigation regimes have been extensively studied (Barakat et al., 2016; Surendran et al., 2016; Gao et al., 2021), while less is known about the effect of vertical distribution of soil water on maize root growth. On one hand, this information helps optimize irrigation regimes to match the root characteristics of current maize hybrids. On the other hand, genotypic differences in root characteristics provide possibilities for breeding and selecting new maize hybrids that adapts to different irrigation regimes.

The distribution of maize roots in the soil is important for crop growth, however, which is rarely reported. We hypothesize that a) the vertical distribution of soil water is a driver behind the effect of irrigation regime on grain yield of maize, b) irrigation depth regulates the distribution and diameter of maize roots, and c) spatial coordination of root system and soil water promote grain yield of maize. For this, field and tube experiments were conducted. Two maize hybrids with different tolerances to drought stress were used. Drip irrigation, flood irrigation, and no irrigation (rainfed) were performed in the field experiment; irrigations at different soil depths were performed in the tube experiment to achieve different water content at different soil layers.

2. Materials and methods

2.1. Experimental site

The field and tube experiments were conducted at the Wuqiao Experimental Station of China Agricultural University (37°41′N, 116°38′E, altitude 20 m above sea level), located in Hebei, China, from 2018 to 2020. The site featured silt loam soil and a temperate continental monsoon climate with a soil bulk density of 1.33 g cm^{-3}, a field capacity of 27.6 g g^{-1}, and a wilting point of 8.6 g g^{-1}. The average annual temperature was approximately 13.3 °C, and the annual precipitation was around 600 mm, with 38.6% occurring during the period from July to early August. The air temperature and precipitation information during the maize growing period are depicted in Fig. S1.

2.2. Field experiment

In 2019 and 2020, a randomized block design with three replicates was employed for the field experiment. The maize hybrids, ZD958 (Z58×C7–2, Henan Qiu Le seed industry technology Co., LTD) and FM985(M801×FM1101, Jilin Fumin seed industry Co., LTD), were used as experimental materials. ZD958 is one of the most popular hybrids in China over the past two decades, and FM985 is a newly released hybrids that performs well under drought conditions. The three treatments included drip irrigation (DI), flood irrigation (FI), and rainfed (RF). For the DI treatment, a 16 mm diameter drip tap with a wall thickness of 0.3 mm was used. The flow rate and pressure were 2.2 L h^{-1} and 0.1 MPa, respectively, in the dropper. Each emitter was 300 mm apart along the drip, and adjacent drips were 60 cm apart. DI achieved a wetted area of around 90%. A PVC pipe with a diameter of 100 mm was used for FI treatment. The total irrigation amount was 150 mm. Each experimental plot was 45 m^2 (3 m width by 15 m length) including five rows of maize spaced 0.6 m apart. A separation of 1.5 m between plots mitigated water and nutrient transfer. The planting density was 67,500 plant ha^{-1} across all treatments. In 2019 and 2020, maize was sown on April 30th and harvested on September 1st. The concentration of organic matter, total N, available P and available K were 16.8 g kg^{-1}, 0.7 g kg^{-1}, 14.4 mg kg^{-1}, and 25.4 mg kg^{-1}, respectively, at the 0–30 cm soil layer. The fertilization scheme and soil water content were shown in Table S1 and Fig. S2, respectively.

Soil water content was determined using the drying method (Gao et al., 2021; Cao et al., 2022). The soil samples of different depths were collected by soil auger at 0–20 cm, 20–40 cm, and 40–60 cm depth, respectively, and the initial wet weight was measured. Subsequently, the samples were dried at 105°C until constant weight. Evapotranspiration was calculated using soil water balance equation (Rana and Katerji, 2000).

At tasseling stage (VT), root sampling was conducted by using hand–held core sampling, with minimum damage to the plot (Böhm, 1979). Root samples were taken 10 cm away both from the maize plant parallel (inter–plant) and perpendicular to maize row (inter–row). Soil cores (10 cm diameter×10 cm height) were collected at 20 cm intervals to a maximum depth of 60 cm. In each plot, we collected 18 soil cores with 2 horizontal sites and 3 vertical sites across 3 plants. At physiological maturity (R6) in 2019 and 2020, three maize roots were sampled per plot using the modified soil profile method (Holanda et al., 1998). This method provided a more comprehensive representation of the root system compared to hand–held core sampling. In brief, the bulk centering maize dimensions were set at half of the row spacing, half of the plant spacing, and 20 cm for length, width, and height, respectively. were passed through a 0.5 mm sieve and washed, and subsequently stored at 4 °C for further analysis. The root samples collected from 0–60 cm soil depth, with a total of three layers. Roots collected from a soil layer under each treatment were scanned using an HP Scanjet 8200 scanner (Hewlett-Packard Co., Palo Alto, CA, USA). The scanning images were further analyzed using WinRHIZO Tron 2015 software (Regent Instruments Inc., Quebec, Canada) to determine the length and diameter of roots. A root diameter exceeding 0.9 mm is classified as a coarse root (Wang et al., 2021; Vanhees et al., 2021). The proportion of coarse root, calculated as the ratio of coarse root length to the total root length (Vanhees et al., 2021). After scanning, the root samples were oven–dried at 80 °C after at 105 °C for 30 min to a constant weight.

At R6 in 2019 and 2020, three maize plants were sampled per plot and were oven–dried as described above to measure shoot dry weight. The root–shoot ratio is defined as the ratio of root dry weight to shoot dry weight. At VT, the stem bleeding sap was collected from the cut surface of stem. At 18:00 during VT period, three maize plants per plot were cut at the basal stem to measure the stem bleeding sap. A rubber balloon containing absorbent cotton (roughly 4 g) was employed to seal

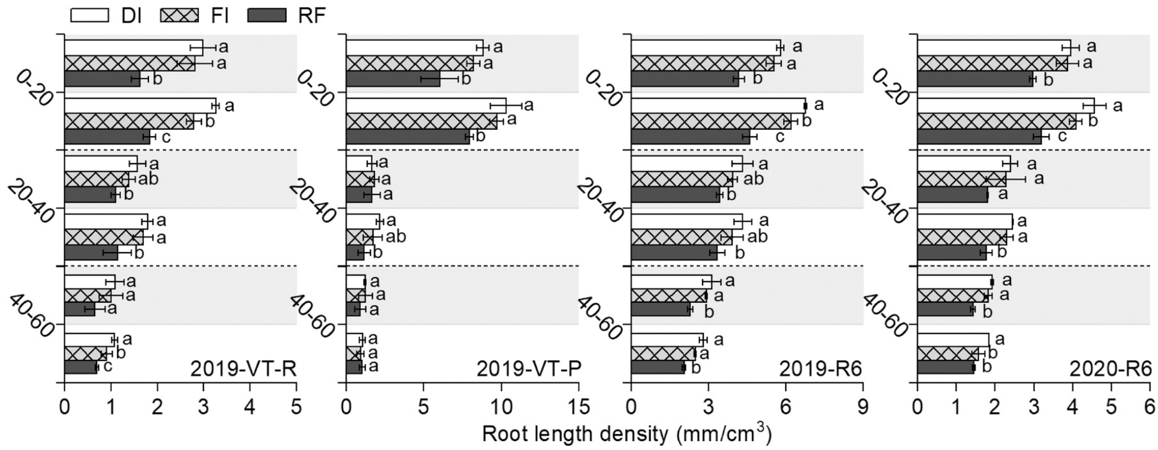

Fig. 1. Average root length density (mm cm^{-3}) of maize hybrids under rainfed (RF), flood irrigation (FI), and drip irrigation (DI) in the field experiment (2019 and 2020). Gray area indicates ZD958, and white area indicates FM985. Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). VT and R6 indicate tasseling stage and maturity stage, respectively. R and P represent interrow and interplant, respectively.

the incision. The rubber balloon was retrieved and weighted after 12 h.

At R6, grain yield was determined by harvesting three central rows from each plot. The calculation of grain yield was based on a basis of 14% of standard water content. The calculation formulas of agronomic nitrogen efficiency (AEN), nitrogen partial factor productivity (PFPN) and water use efficiency (WUE) refer to Ding et al. (2018) and Duan et al. (2021).

2.3. Tube experiment

The tube experiment was conducted under a rainproof shed in 2018, 2019, and 2020. The experimental materials were maize hybrid ZD958 and FM985. Five treatments including no irrigation (NI) and irrigations at the top soil layer (0–30 cm; TI), middle soil layer (30–60 cm; MI), bottom soil layer (60–90 cm; BI), and all the soil layers (0–90 cm; AI), respectively, as illustrated in Fig. S3. From the jointing stage to VT, irrigation was carried out to maintain soil water content at the designated soil layer. The experiment contained 160 tubes with 120 cm in height and 40 cm in diameter. These tubes were arranged in 8 rows with 16 replicates per treatment. Each tube was 1 cm apart. More details about the tubes were described in our previous study (Gao et al., 2021). The fertilization scheme is shown in Table S1. The soil water content was monitored using a soil moisture monitoring system (Caipos GmbH, Gleisdorf, Austria), and the results were listed in Fig. S4.

At the 12–leaf stage (V12), VT and R6 in 2019 and at R6 in 2020, the soil tube was cut into three 30 cm–sections. Roots from each section

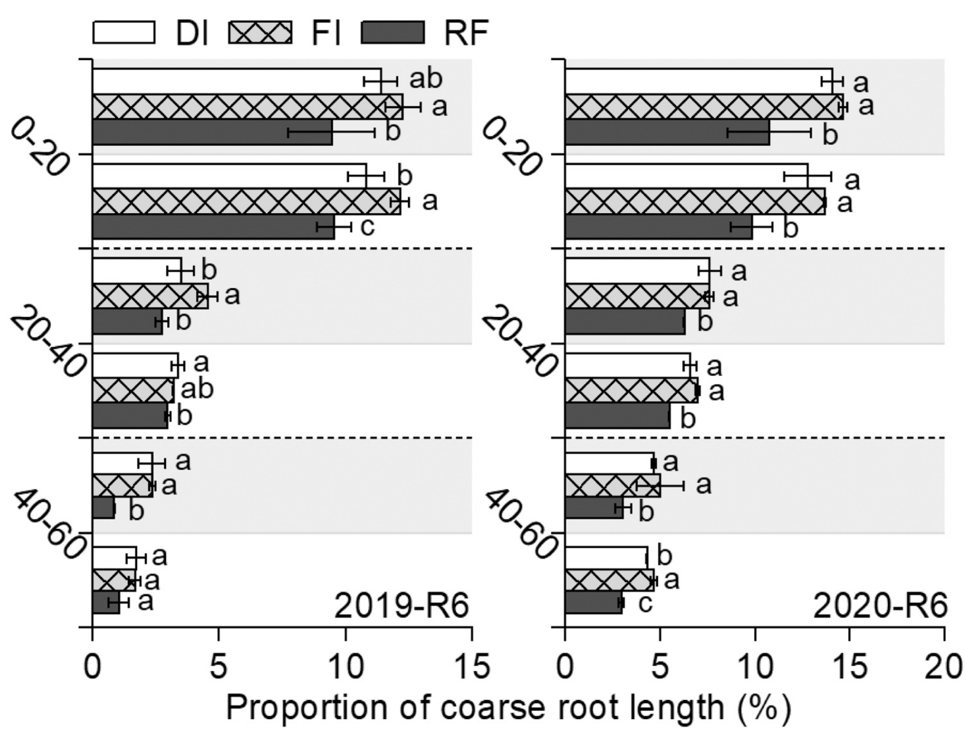

Fig. 2. Proportions of coarse root length (%) of maize hybrids under rainfed (RF), flood irrigation (FI), and drip irrigation (DI) in the field experiment (2019 and 2020). Gray area indicates ZD958, and white area indicates FM985. Values are means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). R6 indicate tasseling stage and maturity stage, respectively.

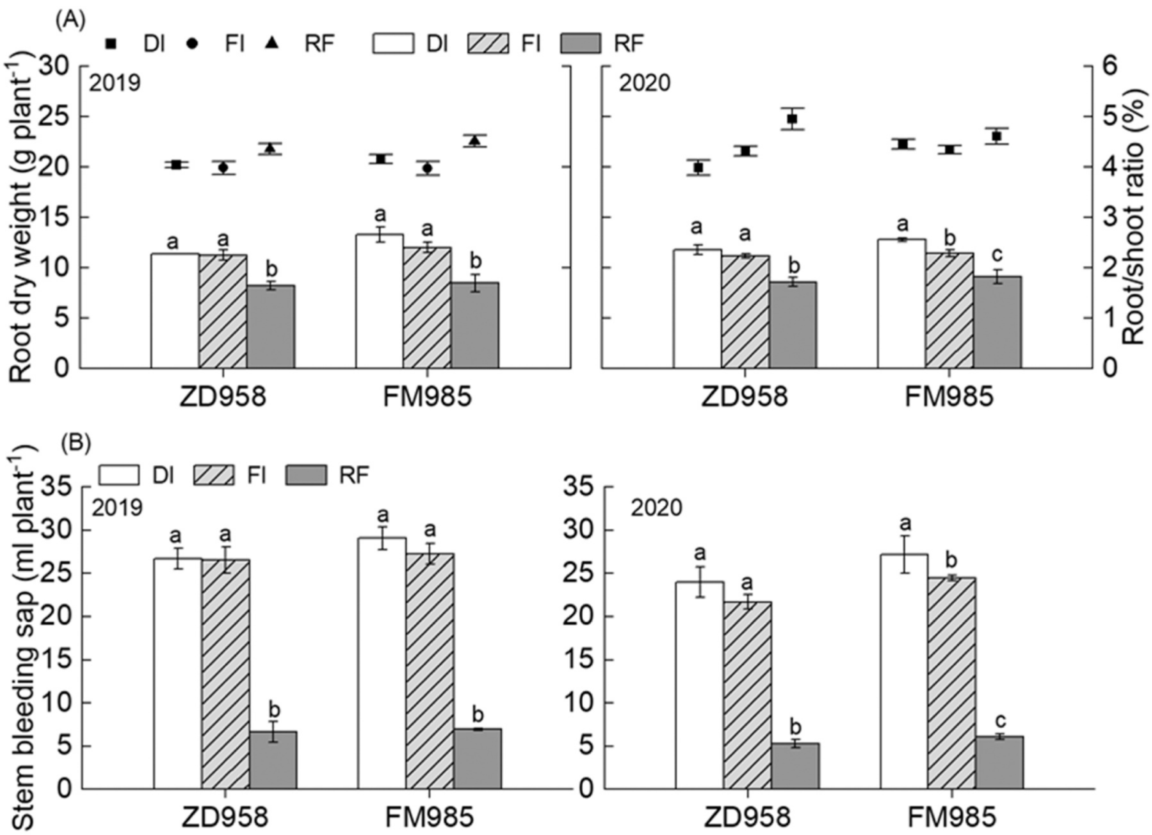

Fig. 3. Root dry weight (g plant^{-1}), root dry weight/shoot dry weight (%), and stem bleeding sap volume (ml plant^{-1}) of maize hybrids under rainfed (RF), flood irrigation (FI), and drip irrigation (DI) in the field experiment (2019 and 2020). Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$).

were collected, washed, and scanned to measure root length and root diameter. Root length density and the proportion of coarse root length were calculated. The root dry weight was measured based on oven–dried samples.

At VT in 2019 and 2020, four maize plants were sampled to measure dry weight after oven–drying. The root–shoot ratio was calculated as the ratio of root dry weight to shoot dry weight. The stem bleeding sap was collected in the same ways as the field experiment.

At R6, all ears were harvested to determine grain yield on a basis of plant. The grain yield was estimated on 14% standard water content.

2.4. Statistical analysis

The two–way ANOVA was conducted with hybrid and irrigation as fixed factors using General Linear Model after Shapiro–Wilk's Test for normality and Levene's Test for homogeneity of variance using SPSS 17.0 software (SPSS Inc., Chicago, IL, USA). Comparisons among different irrigation treatments were performed with Duncan's multiple range test only when the ANOVA indicated significant difference. A P–value $\leq$ 0.05 was considered significant. The correlation coefficient analysis was performed with linear stepwise regression model.

3. Results

3.1. Field experiment

3.1.1. Root length

Drip irrigation (DI) increased root length density (RLD) compared to rainfed (RF) and flood irrigation (FI) (Fig. 1). At VT, DI increased RLD between rows by 6.2% in ZD958 and by 16.8% in FM985 compared to FI, and by 83.6% and 77.5% compared to RF at the 0–20 cm soil depth. The similar patterns were detected at the deeper soil layers. Irrigation had a great influence on interplant RLD at the 0–20 cm depth. DI increased interplant RLD by 7.7% in ZD958 and by 6.3% in FM985, respectively, compared to FI, and by 46.5% and 29.9% compared to RF. At R6, DI increased RLD by 9.1% in ZD958 and by 4.7% in FM985 compared to FI, and by 38.5% and 46.7% compared to RF, respectively, at the 0–20 cm depth. The similar patterns were detected at the other soil layers over two years. Compared to the ZD958, FM985 significantly increased the RLD at 0–20 cm depth regardless of irrigation treatments.

Hybrid and irrigation had significant effect on the proportion of coarse root length to total root length (CRP), except that hybrid had no significant effect on CRP at the 0–20 cm depth (Fig. 2; Table S2). There was no significant difference between DI and FI on CRP at 0–20 cm depth of ZD958, which was higher than that of RF. FI increased the CRP of FM985 by 9.8% and 33.3%, respectively, compared to DI and RF. At the 20–40 cm soil layer, DI increased CRP of FM985 by 17.2% compared to RF. At the 40–60 cm soil layer, DI increased CRP by 113.5% in ZD958 and by 56.2% in FM985, and FI increased by 118.8% and 59.7%, compared to RF.

FI and DI had no significant difference in the total fine root length density (FRLD) of ZD958 at different soil layers, which was higher than that of RF (Fig. S5). DI increased the FRLD of FM985 by 11.9% at 0–20 cm soil layer and by 15.0% at 40–60 cm soil layer compared with FI. There was no significant difference in FRLD at 20–40 cm soil layer between DI and FI.

3.1.2. Root dry weight, root–shoot ratio and stem bleeding sap

The root dry weight of ZD958 and FM985 did not differ between DI and FI, which was higher than that of RF (Fig. 3A). DI increased the root

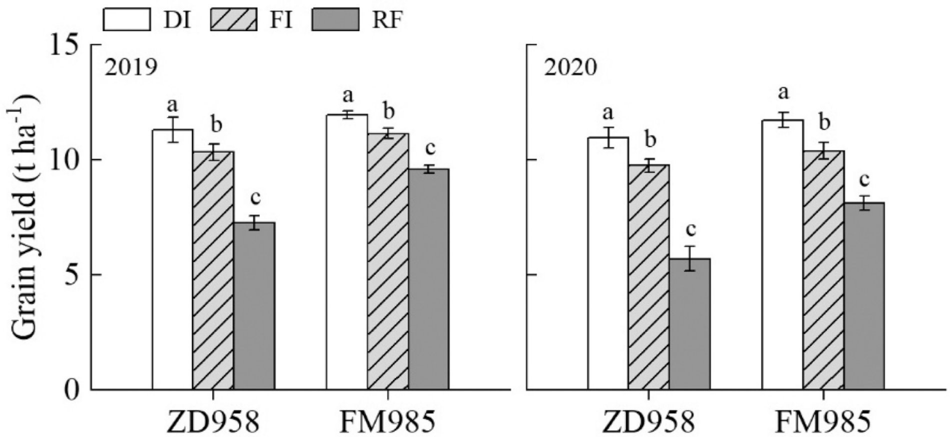

Fig. 4. Grain yield (kg ha^{-1}) of maize hybrids under rainfed (RF), flood irrigation (FI), and drip irrigation (DI) in the field experiment (2019 and 2020). Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$).

Table 1
The agronomic efficiency of nitrogen (AEN), partial factor productivity of nitrogen (PFPN) and water use efficiency (WUE) of maize hybrids under rainfed (RF), flood irrigation (FI), and drip irrigation (DI) in the field experiment (2020).

Hybrid	Treatment	AEN (kg kg^{-1})	PFPN (kg kg^{-1})	WUE (kg m^{-3})
ZD958	DI	9.00	60.88	2.21
	FI	7.87	54.19	2.02
	RF	5.52	31.64	1.86
FM985	DI	11.19	64.81	2.34
	FI	9.31	57.43	2.15
	RF	6.10	44.90	2.53
ANOVA				
Hybrid (H)		ns	**	ns
Irrigation (I)		**	**	**
H*I		ns	**	ns

dry weight by 37.7% in ZD958 and by 48.6% in FM985 compared to RF. The root dry weight of FM985 was higher than that of ZD958 regardless of irrigation treatments. The root–shoot ratio of RF was higher than that of DI and FI. There was no significant difference in stem bleeding sap between DI and FI, except for FM985 in 2020; DI and FI had significantly higher stem bleeding sap than RF (Fig. 3B). The stem bleeding sap of FM985 was 10.9% higher under DI than under FI.

3.1.3. Grain yield, nitrogen and water use efficiency

The grain yield of ZD958 under DI was 10.8% and 74.0% higher than that under FI and RF, respectively (Fig. 4). The grain yield of FM985 under DI was 10.0% and 34.5% higher than that under FI and RF, respectively. Under RF, the grain yield of FM985 was 36.6% higher than that of ZD958.

Irrigation had positive effects on nitrogen use efficiency (Table 1). DI increased the agronomic efficiency of nitrogen (AEN) by 20.2% in FM985 and by 14.4% in ZD958 compared with FI, which was higher than that of RF. Similarly, DI increased partial factor productivity of nitrogen (PFPN) by 12.9% in FM985 and by 12.3% in ZD958 compared with FI. The water use efficiency (WUE) of ZD958 was 9.4% and 18.8% higher under DI than under FI and RF, respectively. However, the WUE of FM985 was 8.1% and 17.7% higher under RF than under DI and FI, respectively.

3.2. Tube experiment

3.2.1. Root length

Different soil depth irrigations (NI, TI, MI, BI, and AI) had significant effects on RLD and CRP (Table S3). The maximum and minimum RLD occurred under AI and NI, respectively, regardless of hybrid and growth stage (Fig. 5). FM985 had a higher RLD at the 0–30 cm depth compared to ZD958 in different irrigation treatments. Compared with MI and BI, TI

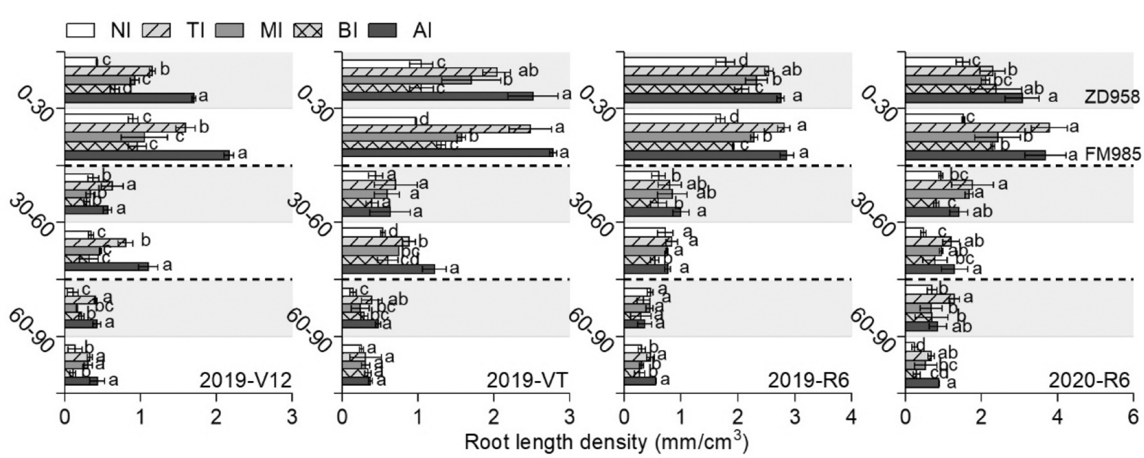

Fig. 5. Average root length density (mm cm^{-3}) of maize hybrids under different irrigation treatments in the tube experiment (2019 and 2020). Gray area indicates ZD958, and white area indicates FM985. Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). NI, TI, MI, BI, and AI indicate no irrigation, irrigation at 0–30, 30–60, 60–90, and 0–90 cm soil layer, respectively. V12, VT, and R6 indicate twelve-leaf stage, tasseling stage, and maturity stage, respectively.

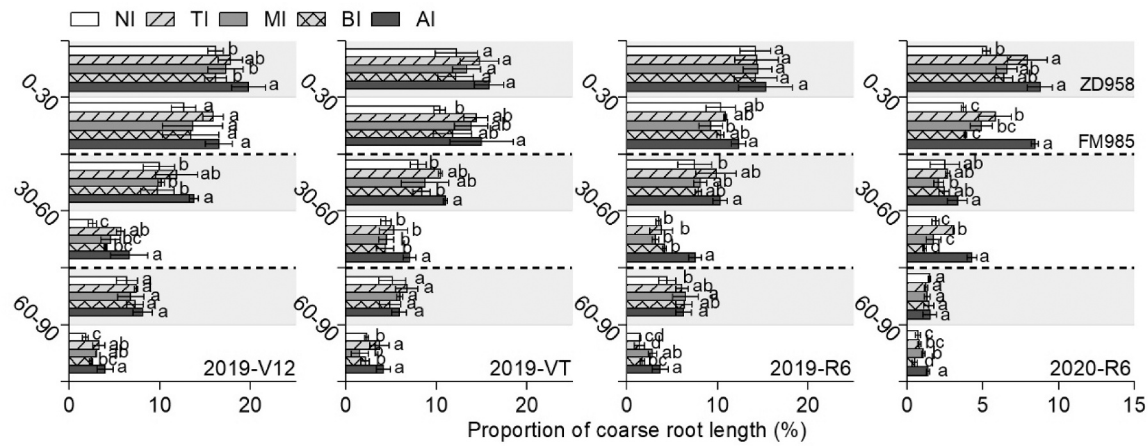

Fig. 6. Proportions of coarse root length (%) of maize hybrids under different irrigation treatments in the tube experiment (2019 and 2020). Gray area indicates ZD958, and white area indicates FM985. Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). NI, TI, MI, BI, and AI indicate no irrigation, irrigation at 0–30, 30–60, 60–90, and 0–90 cm soil layer, respectively. V12, VT, and R6 indicate twelve-leaf stage, tasseling stage, and maturity stage, respectively.

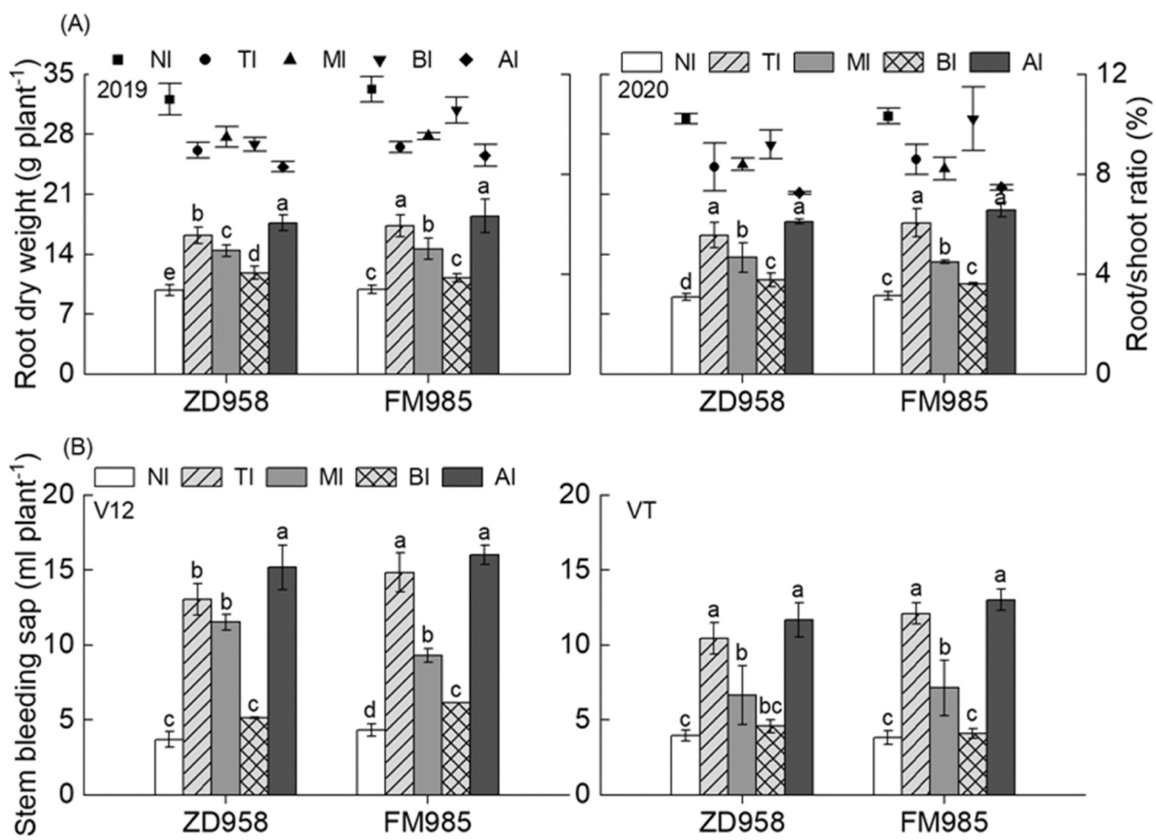

Fig. 7. Root dry weight (g plant^{-1}), root dry weight/shoot dry weight (%), and stem bleeding sap volume (ml plant^{-1}) of maize hybrids under different irrigation treatments in the tube experiment (2019 and 2020). Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). NI, TI, MI, BI, and AI indicate no irrigation, irrigation at 0–30, 30–60, 60–90, and 0–90 cm soil layer, respectively. V12 and VT indicate twelve-leaf stage and tasseling stage, respectively.

increased RLD at V12 by 51.6% and 66.7% in ZD958, and by 24.8% and 74.3% in FM985 at the 0–30 cm depth. Similarly, the maximum and minimum CRP occurred under AI and NI, respectively, regardless of hybrid and growth stage (Fig. 6). At V12, TI increased CRP by 3.0% and 10.2% in ZD958, and by 16.7% and 18.5% in FM985 at the 0–20 cm depth, compared with MI and BI.

3.2.2. Root dry weight, root–shoot ratio and stem bleeding sap

Irrigation at different soil depth had significant effects on root dry weight (Table S3). AI and NI had the highest and lowest root dry weight, respectively, across hybrid and year (Fig. 7A). TI increased root dry weight by 15.7% and 42.2% in ZD958, and by 26.6% and 60.6% in FM985, compared with MI and BI. At V12 and VT, the stem bleeding sap under AI and TI was significantly higher than that under the other treatments (Fig. 7B). TI increased stem bleeding sap at V12 by 13.2%

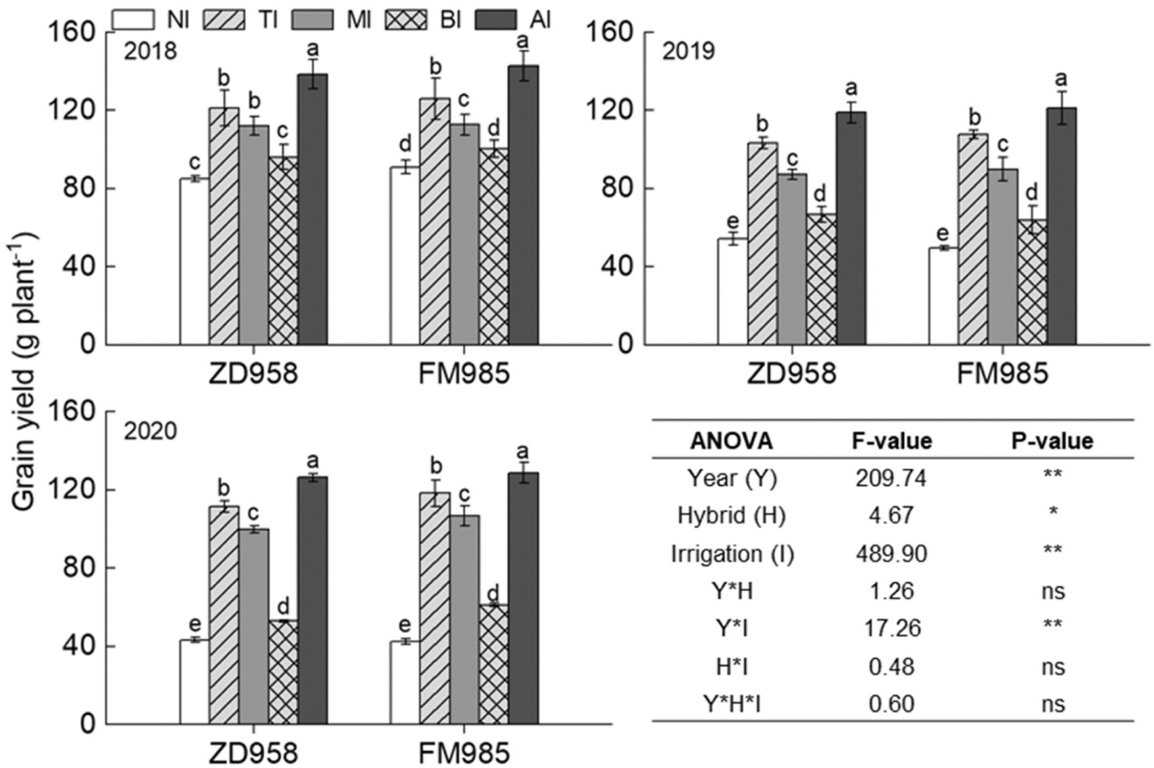

Fig. 8. Grain yield (g plant^{-1}) of maize hybrids under different irrigation treatments in the tube experiment (2019 and 2020). Values are measured as means with SD. Different letters on the bars indicate significant differences between different irrigation treatments ($p < 0.05$). NI, TI, MI, BI, and AI indicate no irrigation, irrigation at 0–30, 30–60, 60–90, and 0–90 cm soil layer, respectively.

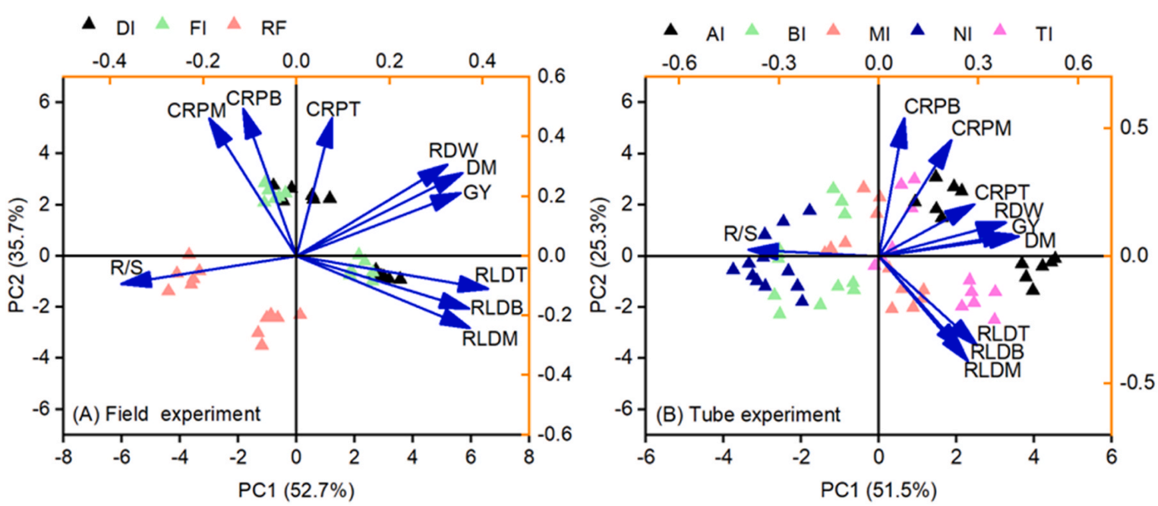

Fig. 9. Principal component analysis illustrates the relationship in grain yield, dry matter, and root variables of maize hybrids under different irrigation treatments in the field experiment and tube experiment. DI, FI, and RF indicate drip irrigation, flood irrigation, and rainfed, respectively. NI, TI, MI, BI, and AI indicate no irrigation, irrigation at 0–30, 30–60, 60–90, and 0–90 cm soil layer, respectively. GY, grain yield; RLDT, RLDM, and RLDB indicate root length density at the top, middle, and bottom soil layer; CRPT, CRPM, and CRPB indicate coarse root proportion at the top, middle, and bottom soil layer; DM, aboveground dry matter weight; RDW, root dry matter weight; R/S, root dry matter weight divided by aboveground dry matter weight.'.

and 153.1% in ZD958, and by 59.4% and 140.7% in FM985, compared with MI and BI. There was no significant difference in stem bleeding sap between TI and AI at VT.

3.2.3. Grain yield

Irrigation at different soil depths significantly affected maize yield and the grain yield of AI was the highest across hybrid and year (Fig. 8). Compared with NI, MI and BI, TI increased grain yield by 96.8%, 12.8% and 63.9% in ZD958, and by 111.4%, 14.1% and 62.3% in FM985. The interaction effect between hybrid and irrigation was not significant on grain yield (Table S3).

3.3. Relationship between grain yield and root characteristics

The relationship between grain yield and root characteristics can be further explored by principal component analysis (PCA) plots (Fig. 9,

Table 2
Principal component analysis (PCA) factor loading plots of the root traits for field experiment and tube experiment.

Index	Field experiment		Tube experiment	
	PC1	PC2	PC1	PC2
GY	0.353	0.212	0.402	0.084
RLDT	0.412	-0.111	0.295	-0.349
CRPT	0.077	0.464	0.288	0.203
RLDM	0.373	-0.242	0.268	-0.411
CRPM	-0.188	0.461	0.219	0.455
RLDB	0.372	-0.179	0.253	-0.372
CRPB	-0.115	0.493	0.076	0.540
DM	0.357	0.279	0.421	0.078
RDW	0.325	0.308	0.384	0.133
R/S	-0.376	-0.095	-0.393	0.024

GY, grain yield; RLDT, RLDM, and RLDB indicate root length density at the top, middle, and bottom soil layer; CRPT, CRPM, and CRPB indicate coarse root proportion at the top, middle, and bottom soil layer; DM, aboveground dry matter weight; RDW, root dry matter weight; R/S, root dry matter weight divided by aboveground dry matter weight.

Table 2) and correlation plots (Fig. 10). The PC1 in field experiment therefore explains 52.7% of the variability, and the PC2 explains 35.7% (Fig. 9A). Similarly, the PC1 in tube experiment therefore explains 51.5% of the variability, and the PC2 explains 25.3% (Fig. 9B). In the field experiment and tube experiment, the root length density of different soil layers was significantly and positively correlated with yield. The coarse root proportion at the top layer and yield was significantly correlated (Figs. S3, and S4). Root length density of different soil layers was negatively correlated with the corresponding coarse root proportion in the field experiment. For both field experiment and tube experiment, the R/S was negatively related to the aboveground biomass and yield.

4. Discussion

Our previous studies demonstrate that there is a significant difference in the vertical distribution of soil water among different irrigation regimes (Gao et al., 2021). The difference in the vertical distribution of soil water partly explains the effects of irrigation regime on maize production. Given the plasticity and hydrotropism of roots (Yu et al., 2014; Liu et al., 2020), the present study is conducted to explore the effect of the vertical distribution of soil water on the maize roots as well as the spatial coordination of soil water and roots in the field and tube experiments.

4.1. The vertical distribution of soil water affected maize root morphology

Roots exhibit robust plasticity to various adverse soil conditions, including drought, flooding, nutrient deficiency, and soil compaction (Ahmed et al., 2018; Yu et al., 2019; Liu et al., 2020; Vanhees et al., 2021; Turan, 2022). Soil water content can alter root structure and distribution, shifting root distribution to water–rich layer (Lynch, 2013; Zhan et al., 2015). Plants with deeper roots are better able to cope with drought. The high plasticity of root distribution along the soil profile arises from fluctuations in soil water content (Wang et al., 2020; Cao et al., 2022). Moreover, gravity also promotes roots to search for water in the vertical direction (Li et al., 2020). Considering root hydrotropism, water deficit increases the proportion of deep roots, decreases root number and diameter, and increases root length and the proportion of fine roots, thereby expanding the water absorption area (Yu et al., 2014; Liu et al., 2020). Evidence also indicates that drought increases soil hardness and root penetration resistance, further limiting root access to deeper soil layers (Colombi et al., 2018). Similarly, RF and NI reduced the total root dry weight, root length, and coarse root proportions while increasing the proportions of deep–root biomass (Fig. 1 and Fig. 5). Soil water distribution was heterogeneous under different irrigation conditions, which affected the growth and root architecture of maize. Greater soil water at the upper soil layer (about 20 cm) was observed in flood irrigation versus rainfed, inhibiting root growing deeply. By contrast, soil water content in drip irrigation is evenly distributed across different soil layers. The proportion of coarse root and surface root in flood irrigation exceeds that of drip irrigation in both hybrids, potentially driven by the reduction of fine root length (Fig. 1 and Fig. S5). Furthermore, the influence of irrigation regimes on soil structure also indirectly affects root plasticity. The increase in coarse root proportion of flood irrigation may be due to soil compaction (Hossne et al., 2015; Yan et al., 2022), since root diameter generally increases in response to mechanical resistance (Vanhees et al., 2021). Drip irrigation improves soil structure by allowing water to penetrate slowly and evenly into the soil (Reyes–Cabrera et al., 2016).

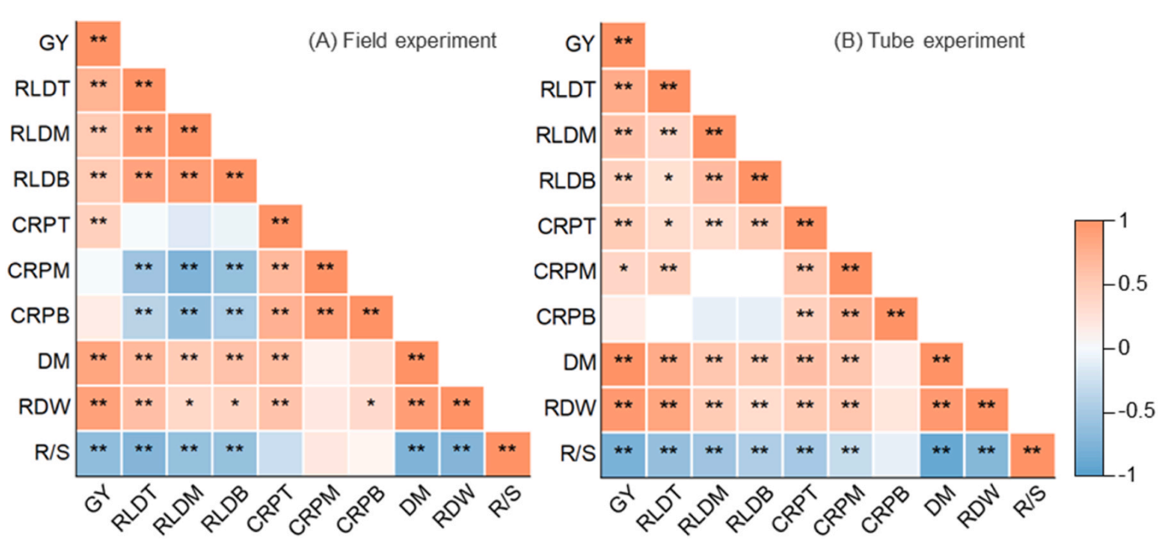

Fig. 10. Correlation plots showing the relationship in grain yield, dry matter, and root variables of maize hybrids under different irrigation treatments in the field experiment and tube experiment. The correlation coefficient is visualised by the scale bar, negative correlations are blue and positive correlations are orange. GY, grain yield; RLDT, RLDM, and RLDB indicate root length density at the top, middle, and bottom soil layer; CRPT, CRPM, and CRPB indicate coarse root proportion at the top, middle, and bottom soil layer; DM, aboveground dry matter weight; RDW, root dry matter weight; R/S, root dry matter weight divided by aboveground dry matter weight; * and ** indicate significant differences at 0.05 and 0.01 level, respectively.

4.2. Spatial coordination of root system and soil water content

In arid environments, root spatial distribution is more important than root growth and development (Dunbabin et al., 2013). The distribution of roots in soil determines the range and potential for water and nutrient uptake (Dunbabin et al., 2013; Chilundo et al., 2017). Therefore, rainfed reduced root length and the space for nutrient uptake, which reduced nitrogen use efficiency and yield (Fig. 1, Fig. 3 and Table 1). It is generally believed that the morphology and distribution of deep roots are more important for drought resistance (Lynch, 2013). Zhan et al. (2015) also suggested that reducing lateral root branching density could increase root depth and improve drought resistance, consistent with the findings in wheat (*Triticum* spp., Lilley and Kirkegaard, 2016), rice (*Oryza* spp., Liao et al., 2019), and soybean (*Glycine max*. L., He et al., 2017). Root competition is more intense near the surface, especially in intensive agriculture (Mi et al., 2016; Gao et al., 2021). Gravity also inhibits root expansion in the horizontal direction (Li et al., 2020). Compared with drip irrigation, flood irrigation inhibited root growing deeply and increased root distribution at the surface soil layer (Fig. 1), which reduced water and nutrient uptake (Table 1, Zhang et al., 2017; Yan et al., 2022). Greater root length of drip irrigation can increase water and nutrient uptake and reduce the risk of drought stress (Lynch, 2018). Likewise, yield was significantly correlated with root length in each soil layer (Fig. 9, Fig. 10). Moreover, fine roots were more closely related to water and nutrient acquisition than coarse roots (McCormack et al., 2015; Roumet et al., 2016). Our results showed that total root length and total fine root length were greater in DI than in FI (Fig. 1 and Fig. S5), which increased water and nutrient uptake. The PCA and correlation results show that the coarse root proportion at the top layer was significantly correlated with yield in both field and test tube experiments (Fig. 9, Fig. 10). In addition, larger root increase metabolic costs and reduce aboveground biomass and kernel (Lynch, 2013; Mi et al., 2016). Such effects were observed in both the field experiment and tube experiment, that is the R/S was negatively related to the aboveground biomass and yield (Fig. 10). Therefore, regulating root growth and spatial distribution, while also enhancing the coordination between roots, water, and fertilizer, can improve maize yield under drought stress.

4.3. Interactive effects of hybrid and irrigation on maize root system

Irrigation shapes root morphology and distribution by altering the temporal and spatial availability of water (Gao et al., 2021; Wang et al., 2021). The temporal and spatial coordination between roots and water is expected to be the key in increasing yield and water use efficiency. Root plasticity in response to the vertical distribution of soil water is the basis for selecting and breeding suitable hybrids. FM985 exhibited a larger root system at the surface layer compared to ZD958. In the tube experiment, the larger decrease in the grain yield of TI were observed at ZD958 versus FM985, possibly due to the higher proportion of roots at the upper layer of FM985 (Fig. 5). In contrast, the BI in FM985 exhibited a greater yield reduction than in ZD958. Flooding irrigation increased the coarse roots proportion at the upper soil layer, especially in FM985. Apparently, the compaction and hypoxia environment created by flood irrigation is not conducive to fine root growth, resulting in a reduction in the fine root length. Fine roots are the most physiologically active part and are closely linked to water and nutrient uptake (Eissenstat, 1992; McCormack et al., 2015), which may explain the larger decline in yield of FM985. Conversely, FM985, characterized by more fine roots, exhibited higher yields under drip irrigation. Whether the field experiment or the tube experiment, a noteworthy correlation emerged between root length density in each soil layer and grain yield. This correlation underscores the positive influence of root length in each soil layer on facilitating nutrient and water absorption, ultimately contributing to an increase in yield. Grain yields were positively correlated with the coarse root proportion at the upper layer but not at the middle and bottom layers. In addition, grain yields were negatively correlated with root–shoot ratio. These findings indicated that a larger coarse root proportion at the upper layer was more favorable for improving yield, while a lower coarse root proportion at the middle and bottom layer could reduce the metabolic cost and energy consumption.

In summary, irrigation regimes influence the vertical distribution of soil water and the root distribution of maize. Under drip irrigation, soil water is evenly distributed in vertical direction, which promotes root growth and increases water and nitrogen use efficiency. Abundant soil water content at specific layers triggers root growth, and different maize hybrids have different growth responses in terms of root length density and root diameter. Maize hybrids with high root plasticity increase root length density in the wet soil layer, thereby improving the coordination between root growth and soil water movement.

5. Conclusions

Irrigation regimes affect maize root distribution by regulating the vertical distribution of soil water. Drip irrigation increases the total root length, especially the fine roots, and then increases nitrogen and water use efficiency as well as yield. Moreover, irrigation significantly increases root dry weight, root length density, and the proportion of coarse root length, especially at the shallow soil layer. Enhancing the spatial coordination between roots and soil water helps alleviate yield losses. Grain yields were positively correlated with the root length density in each soil layer and coarse root proportion at the upper layer, but were negatively correlated with root–shoot ratio. Future research can focus on investigating the balance between root systems and the absorption of nutrients and water, along with the associated metabolic costs with roots.

CRediT authorship contribution statement

Wang Pu: Funding acquisition, Writing – review & editing. **Lv Yanjie:** Supervision, Writing – review & editing. **Huang Shoubing:** Conceptualization, Supervision, Validation, Writing – review & editing. **Gao Jia:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. **Xu Chenchen:** Investigation, Software. **Zhang Yingjun:** Investigation, Software.

Declaration of Competing Interest

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

Data availability

The authors are unable or have chosen not to specify which data has been used.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2024.108728.

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