RESEARCH ARTICLE

Root growth, root senescence and root system architecture in maize under conservative strip tillage system

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Abstract

Aims Root system architecture (RSA) is important for nutrient and water acquisition efficiency. The adaptation of root growth and RSA to soil structure under conservative strip tillage (ST) system warrants further investigation.

Methods A three-year field experimentation was conducted in Northeast China to investigate the RSA and dynamic root growth of rain-fed maize under ST system by comparison with the conventional tillage (CT).

Results Grain yield in ST and CT was not signifcantly diferent, but their yield components difered. Compared to CT, grain number per ear was reduced

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by 4.4%, while 1000-grain weight was increased by 6.6% in ST. Root growth in ST plants was inhibited in the vegetative stage, as indicated by the reduced total root length (by 27.7–40.1%) compared to CT. During post-silking stage, the total root length was not different between ST and CT plants but the root xylem bleeding rate in ST plants was 70.7%-449.9% greater than that in CT. The uneven horizontal distribution of soil bulk density and soil temperature made the RSA of ST plants steeper compared to CT. Moreover, the D_{95} of root distribution in ST plant roots was greater. *Conclusions* In ST system, colder, more compacted soil in the inter-row soil likely caused the lower root growth and consequently lower shoot dry matter during the vegetative stage. However, root senescence was delayed which was beneficial for water and nitrogen acquisition during grain flling. Strategies to improve early root growth may increase maize productivity in ST systems.

Keywords Strip-till · Maize · Soil heterogeneity · Root system architecture · Root distribution · Root senescence

Introduction

Plant root system architecture (RSA), including root geometry and its spatial distribution characteristics, plays an important role in water and nutrient absorption (Lynch et al. [1995](#page-15-0); Brady et al. [1995;](#page-13-0) Amato and Ritchie [2002](#page-13-1); Doussan et al. [2006;](#page-14-0) Dorlodot et al. [2007;](#page-14-1) Hammer et al. [2009](#page-14-2); Paez-Garcia et al. [2015](#page-15-1); Maqbool et al. [2022\)](#page-15-2). RSA is dynamic and is afected by external environmental conditions including soil temperature, moisture, nutrients, pH, and microbial communities (Bengough et al. [2006;](#page-13-2) Mi et al. [2010](#page-15-3); Bao et al. [2014](#page-13-3); Robbins and Dinneny [2015\)](#page-15-4). Soil conditions in the feld is locally diferent (Jackson and Caldwell [1993\)](#page-14-3). Plants can sense the variation of soil environmental factors and make corresponding responses. For example, soil temperature can infuence the direction of root growth (Mosher and Miller [1972\)](#page-15-5). Low temperature induces smaller branching angles between primary and lateral roots, reduces root elongation, and reduces the volume that roots access (Nagel et al. [2009](#page-15-6)). In feld conditions, roots are continuously exposed to mechanical resistance caused by soil compaction. In response to soil compaction, the total root length is reduced, root diameter and root hair number are increased, and root angle becomes steeper (Correa et al. [2019\)](#page-14-4). Due to the soil heterogeneity, compensatory root growth may happen in the unimpeded soil and the total root length may not be altered (Unger and Kaspar [1994\)](#page-16-0).

Tillage can change soil porosity, aggregate structure, bulk density and other characteristics, and afect soil respiration, temperature and humidity (Guan et al. [2014\)](#page-14-5). These biological and non-biological processes can afect plant root growth (Lipiec and Stepniewski [1995;](#page-14-6) Mosaddeghi et al. [2009;](#page-15-7) Ioanna et al. [2019](#page-14-7)). No-till (NT) is a major form of conservation tillage system. Compared with conventional tillage (CT), NT reduces soil erosion and increases soil water content, but reduces soil temperature and increase soil bulk density (Cannell [1985](#page-13-4); Dwyer et al. [1996](#page-14-8); Munkholm et al. [2012;](#page-15-8) Muñoz-Romero et al. [2012;](#page-15-9) Soane et al. [2012\)](#page-15-10), although long-term NT may reduce soil bulk density (Fiorini et al. [2018\)](#page-14-9). To reduce the disadvantageous efect of NT on soil temperature, strip-till (ST) has been gradually developed as a major form of conservative tillage in maize production (Morrison [2002;](#page-15-11) Licht and Al-Kaisi [2005a](#page-14-10); Trevini et al. [2013](#page-16-1); Fernández et al. [2015](#page-14-11); Sha et al. [2023\)](#page-15-12). ST combines the benefts of CT and NT by cultivating the intrarow soil to form a planting strip and leaving the interrow covered with crop residue through the whole maize growth period (Vyn and Raimbault [1992](#page-16-2)). By this way, soil temperature is increased and soil bulk density is reduced in the planting strip (Licht and Al-Kaisi [2005b\)](#page-14-12). As a result, root growth is improved, and maize yield is guaranteed to the similar level of NT (Morrison [2002;](#page-15-11) Potratz et al. [2020](#page-15-13)). However, compared with CT, the low temperature and high soil compaction in the inter-row soil is still a disadvantage (Lipiec and Hatano [2003](#page-14-13); Ren et al. [2019](#page-15-14)), which can cause maize yield fuctuation according to diferent soil types and climatic conditions. For example, in dry years or on sandy soils, the efect of ST on water and soil conservation is more obvious, and has yield advantages compared with CT (Temesgen et al. [2012\)](#page-15-15). In rainy years or in clayey soils, maize yield can be lower in ST compared to CT (Vyn and Raimbault [1992](#page-16-2); Licht and Al-Kaisi [2005a](#page-14-10)).

The adaptation of root growth and RSA to soil conditions greatly affect maize yield by affecting water and nutrient acquisition efficiency (Lynch [1995,](#page-15-0) [2013\)](#page-15-16). In addition, root senescence, as indicated by root xylem bleeding sap (Fageria [2004](#page-14-14); Doussan et al. [2006](#page-14-0)), also strongly afect nutrient and water absorption, especially during grain flling stage when grains become the main sink for assimilates (Wu et al. [2022a](#page-16-3), [b](#page-16-4)). A higher root xylem bleeding sap rate indicates greater water and nutrient absorption capacity (Guan et al. [2014](#page-14-5); Wu et al. [2022a](#page-16-3), [b\)](#page-16-4). Therefore, to understand the factors afecting maize yield formation and fgure out the corresponding solutions to increase maize productivity under ST system, a full understanding of root growth and senescence, as well as RSA under ST system is crucial. Ren et al. ([2019\)](#page-15-14) has showed that the root distribution of maize in ST plants was restricted to the planting rows compared with intensive tillage. Nevertheless, the adaptation of root characteristics in relation to yield formation in ST is largely unclear. In this study, we made a systemic comparison of maize root growth dynamics and the 3-D spatial root distribution between ST and CT, and explored their relationship with yield formation.

Materials and methods

Experimental location

This research was conducted in a long-term positioning experimental feld commenced in 2018, in San-Ke-Shu Village, Lishu County (Northeast China Plain), Jilin Province, China (43°2′ N, 123°5′ E). Plant samples were collected in 2019 and 2020, and in 2022. The typical cropping system in this region is rain-fed continuous spring maize. In the maize growing season from 1992 to 2022 (late April to early October), the average air temperature was 18.3 ℃, the rainfall was 513 mm, about 75% of which occurred during June—August (Table 1S). Rainfall was similar but unevenly distributed in 2019 and 2020, and relatively large in 2022, especially in June and July, but it had no destructive efect on maize growth (Fig. [1](#page-2-0) and Table 1S). The spring of 2020 was cooler than 2019 and 2022. The soil texture was meadow black soil (Soil Survey Staff 1998). The soil (0-20 cm layer) was high in clay (45.6%) and silt (41.6%), and low in sand (12.8%). The initial soil properties before sowing in 2019 were pH 5.9 (1:2.5 g/v soil:water ratio), organic carbon 27.3 g kg⁻¹, total N 1.4 g kg⁻¹, Olsen-P 36.9 mg kg^{-1} , available K 159 mg kg^{-1} in the 0—20 cm soil layer (measurement methods refer to Toth et al. [1948;](#page-16-5) Olsen [1954;](#page-15-18) Bremner and Tabatabai [1972](#page-13-5); Nelson and Sommers [1983](#page-15-19); Van Zwieten et al. [2010\)](#page-16-6).

Experimental design and feld management

The experiment was a single-factor completely random design with three replications. Two tillage treatments were set up: strip tillage (ST) and conventional tillage (CT). The size of each plot was 547 m^2 (76 m) long×7.2 m wide), with 12 rows spaced 0.6 m apart. According to the local maize yield level and soil-test based fertilizer recommendation (Feng et al. [2017](#page-14-15); Wang et al. [2018\)](#page-16-7), the following fertilizers were applied: 180 kg N ha⁻¹ (as urea), 75 kg P₂O₅ ha⁻¹ (as superphosphate), 90 kg K₂O ha⁻¹ (as potassium

chloride). All fertilizers were broadcasted before planting and no topdressing was applied during maize growth.

Maize was mechanically harvested and the residues remained in the feld. The feld was covered with the residues overwinter. For ST treatment (Table 2S), strip tillage was conducted using a strip-tiller (Yetter-2984, Illinois, USA) in 27 April 2019, 2 May 2020 and 8 May 2022, respectively. A clean soil strip about 12—15 cm in depth and 22—25 cm in width was created for planting and the residues were allocated to the inter-row area and were not disturbed through maize growth period. For CT treatment, the residues were removed from the feld and then the soil was tilled using a rotary tiller to a depth around 15 cm. Maize (Zea mays L. cv. De-Mei-Ya 3) was sown with a row spacing of 0.6 m on 9 May 2019, 6 May 2020 and 10 May 2022, respectively. Plant density was controlled at 70,000 plant ha^{-1} . Herbicides and pesticides were used to control weeds and pests, respectively. No irrigation was applied. Maize was harvested in 30 September 2019, 27 September 2020 and 29 September 2022, respectively.

Plant sampling and measurement

Shoot sampling, dry matter weight and grain yield

Plants were sampled in 2019 (2020) on 41 (41), 56 (53), 73 (76), and 87 (90) days after sowing (DAS), which were corresponding to seedling, jointing, silking and grain flling stage, respectively (Shen and Mao 2011), respectively. The GDD and the total rainfall for each growth stage were shown in Table 3S. For each sampling, three successive plants of each

Fig. 1 Mean air temperature and precipitation during maize growing season in 2019 and 2020. The arrow in the fgure represents the sowing time

plot were cut on the soil surface to determine shoot biomass (g plant⁻¹). All samples were oven-dried (DHG-9420A; Bilon Instruments Co. Ltd., Shanghai, China) at 80 ± 5 °C until constant weight (three or four days for seedling, four or fve days for jointing, six or seven days for silking, more than seven days for grain flling stage) after heating at 105 °C for 30 min. Then the dry weight was measured. At maturity, the two center rows (10 m length and 1.2 m width) of each plot were harvested by hand. The number of ears was counted and was calculated into the ear number per ha (EN). From the harvested ears, 20 were chosen to measure the grain number per ear (GN). Grains were threshed by a grain thresher, and three 100-grain samples were weighted to determine the 1000-grain weight (TGW).

Root sampling, root distribution and root morphological traits

In 2019 and 2020, a modifed monolith method was applied to fgure out the spatial distribution characteristics of the root system (Böhm [1979\)](#page-13-6). After the shoot was removed in each sampling, a soil volume centered on the plant root of 24 cm \times 60 cm \times 60 cm (distance between intra-row×distance between inter $row \times depth$) was excavated using a shovel. Three successive plant roots were sampled in each plot.

To analyze the vertical root distribution during maize seedling to grain flling stage, the soil volume was divided into 6 cm increments to the depth of 60 cm (Fig. 1S-A). To analyze the horizontal root distribution from the location of the plant to the middle of the inter-row, root growth at depth of 30 cm (5 layers with 6 cm deep in each layer) was also investigated at silking stage by reference to Shao et al. [\(2018](#page-15-21)) (Fig. 1S-B). In the inter-row direction, from the location of the plant, soil cubes were taken each 6 cm in the size of 24 cm \times 6 cm \times 6 cm cubes (distance between intra-row×distance between interrow \times depth). The soil cube size was 24 cm \times 3 cm \times 6 cm cube at the border, and totally 11 cubes were sampled between the neighboring rows in each layer. The soil cubes were crushed by hand and sieved through a 3 mm sieve. All visible selected living roots was temporarily stored in a self-sealing bag (numbered in advance), and then rinsed and frozen at—20 ℃ for further analysis.

Another three successive plant roots were sampled to investigate the root morphological traits in each plot. A soil volume centered the maize root of 24 $\text{cm} \times 60$ $\text{cm} \times 30$ cm (distance between intrarow×distance between inter-row×depth) was excavated using a shovel after cutting off the shoots. The soil volume was put into a pool and immersed in water for 12 h, then the roots were cleaned manually. Using a protractor, the expansion angle of the nodal roots from the upmost whorl to the $1st$ whorl was measured (Fig. 0.2S). Randomly three roots were measured in each whorl and the average value was used to represent the nodal roots angle (°). The nodal roots were cut off after measurement, and the number of nodal roots in each whorl was recorded.

In 2022, the same method was used to investigate root senescence from silking stage to the physiological maturity. After the collection of root xylem bleeding sap at 72, 82, 97,112, 127 DAS (see below), the successive soil cube (24 cm \times 60 cm \times 30 cm) per plot were excavated and the cleaned roots were cleaned for investigation of total root length using the same procedure as above.

Root xylem bleeding sap

Root xylem bleeding sap was collected from silking stage to physiological maturity in 2022 at 72, 82, 97,112, 127 DAS according to Yang et al. ([2002\)](#page-16-8). In brief, fve evenly growing plants were selected from each plot, and their stems were cut at 10 cm above the soil surface at 18:00 on the frst day. The residual stem was put into a plastic container containing pre-weighted degreasing cotton and the interface was tied tightly with a rubber band to prevent the sap from flowing out. The degreasing cotton was collected at 6:00 am the next day. The weight of the bleeding sap was calculated using the subtraction method.

Determination of root length and root biomass

All the root samples were scanned using a scanner at 600 dpi resolution (Epson, Perfection V800 Photo Scanner, Los Alamitos, USA) and analyzed using WinRhizo software (R´egent Instruments Inc., Qu´ebec, Canada) to determine the total root length (m plant⁻¹). Root length density (cm cm⁻³) was calculated by dividing root length with the soil volume. After scanning, the roots were oven-dried at 80 ± 5 °C for a constant weight to obtain the root biomass (g plant⁻¹). The rooting depth (D₉₅), at which 95% of the coarse root length can be found within the 60 cm deep soil core, was estimated by linear interpolation (Schenk and Jackson [2002\)](#page-15-22).

Soil sampling and measurements

After sowing (May 22, 2019 and May 24, 2020), soil samples were collected in 0—30 cm soil layer using a ring knife at two positions, the middle of neighboring plants in intra-row (0—9 cm from the center of the plants horizontally) and the middle of the interrow (9—30 cm from the center of the plants horizontally), to measure the soil bulk density (g cm^{-3}). The ring knife has a diameter of 5 cm and a volume of 100 cm³. Additional soil samples were collected to determine fresh weight as quickly as possible and ovendried at 105 °C for 24 h to obtain dry soil weight (g). Volumetric soil water content (cm cm^{-3}) was calculated by referring to Ren et al. [2019](#page-15-14). At the same position of 0—20 cm soil layer, a portable soil thermometer (TP—101, XinTai wei, China) was used to measure soil temperature (℃) at 5 cm, 10 cm, 15 cm and 20 cm below soil surface.

At silking stage in 2020, centered on the plant that was used for root sampling, three soil cubes per plot was used to investigate the spatial distribution of soil bulk density and soil moisture. Soil samples were collected using a ring knife every 6 cm layer to a depth of 0–30 cm at 11 positions, including three positions in the intra-row direction: 0—3 cm (close to the plant), 3—9 cm at both sides from the plant, and eight positions in the inter-row direction: 9—15 cm, 15—21 cm, 21—27 cm, 27—30 cm, at both sides from the plant, respectively. The same soil samples for soil bulk density measurement were used for determining soil moisture.

Statistical analysis

All data were analyzed with analysis of variance using SPSS 19.0 (SPSS Inc., Chicago, IL, USA) to examine the efects of tillage methods on grain yield and its components, shoot growth, root distribution, root morphological traits and soil physical properties. The statistical signifcance of diferences among means was assessed by the Tukey HSD test ($P \le 0.05$). Linear regression model was used to analyze the relationship between soil bulk density and root length density. All the graphics were made using OriginPro 2022 (OriginLab., CA, USA).

Results

Grain yield, shoot and root biomass and root to shoot ratio

The interaction effect of tillage \times year was not signifcant for grain yield and its components (Table [1](#page-4-0)). Across 2019, 2020 and 2022, there was not signifcant diference in grain yield between ST and CT. Grain number (GN) per ear of ST was 4.4% less compared to that of CT. In contrast, the thousand-grain weight (TGW) of ST was 6.6% higher than that of CT. Ear number (EN) per hectare was not afected by tillage systems.

Shoot and root biomass were reduced signifcantly in ST plants compared with CT in the vegetative stage. Shoot biomass in ST plants decreased by 12.3—15.1% at seedling, 8.3—16.8% at jointing, and root biomass in ST plants decreased by 8.7—31.3% at seedling, 16.0—17.7% at jointing (Table [2](#page-5-0)). The difference was gradually reduced during the late growth stage. During silking and post-silking stage, there was

no signifcant diference in the shoot and root biomass between the ST and CT plants (Table [2\)](#page-5-0). Root to shoot ratio was not diferent between ST and CT at any growth stage in two years (Table [2](#page-5-0)).

Soil properties

After sowing, soil bulk density (Fig. [2A](#page-6-0)), moisture (Fig. [2B](#page-6-0)) and temperature (Fig. [2C](#page-6-0)) were measured in the intra-row (0—9 cm from the center of the plants horizontally) and inter-row (9—30 cm from the center of the plants horizontally). Overall, the basic physical conditions of ST were similar to CT in the intra-row soil, but diferent from CT in inter-row soil, especially in the 0—15 cm soil layer. In 2019 and 2020, the soil bulk density and volumetric soil water content in the inter-row of ST were increased by 4.3%—17.9%, 20.8%—79.4%, respectively, in the 0—15 cm soil layer compared with CT. On the contrary, the soil temperature in the inter-row of ST was reduced by 6.9%—18.7% compared with CT. The efect of tillage on the soil temperature was highly signifcant in 2019.

At silking, compared with CT with uniform soil bulk density, the soil bulk density under ST had greater heterogeneity. The bulk density of ST was similar to that of CT in the intra-row soil, but significantly larger than CT in the inter-row soil (Fig. [3](#page-7-0)A). In 0—12 cm soil layer, the average soil bulk density of ST in the inter-row was 1.53 cm cm^{-3} , which was 23.4% lager than that of CT (Table 4S). The bulk density in the two treatments did not difer signifcantly in deeper soil. ST practice increased the volumetric soil water content in inter-row soil (Fig. [3B](#page-7-0)). On average, the soil water content of ST in the inter-row was 59.5% lager than that of CT in 0—12 cm soil layer, but this signifcant diference did not extend to the 12–30 cm soil layer (Table 5S).

Root length and nodal root angle

Compared with CT, root growth in ST plants was signifcantly inhibited, especially in the vegetative stage. The total root length in ST plants decreased by 38.5—41.6% at seedling stage, 27.6—27.8% at jointing stage and 13.1—16.2% at silking stage. However, there was no signifcant diference between ST and CT at two weeks after silking (Fig. [4\)](#page-7-1).

The size of maize root system was determined by the growth of each nodal root in each whorl. The total number of the nodal roots of ST plants was similar as that of CT (Table [3](#page-8-0)). The growth angle of the nodal roots was changed by ST (Fig. [5A](#page-8-1), 2S).

Fig. 2 Efects of tillage methods on soil bulk density (g cm−3) (**A**), soil volumetric water content $(cm cm⁻³)$ (**B**) and soil temperature (℃) (**C**) after sowing (May 22, 2019 and May 24, 2020). ST: striptill, CT: conventional-till. Each value is the mean of three replicates $(\pm SE)$

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Fig. 3 Spatial distribution of soil bulk density (g cm−3) (**A**) and volumetric soil water content (cm cm−3) (**B**) in the soil profle (0—30 cm depth) at silking stage as infuenced by strip-till (ST) and conventional-till (CT) in 2020. The specifc soil sampling and measurement methods are in *Soil sampling and measurements*

Fig. 4 Efects of tillage methods on total root length (m plant−1) in 2019 and 2020. The sampling volume for the roots is 24 $\text{cm} \times 60 \text{ cm} \times 60 \text{ cm}$ (distance between intra-row \times distance between inter-row×depth). ST: strip-till, CT: conven-

tional-till. Each value is the mean of three replicates $(\pm SE)$. The asterisks denote signifcant diference among diferent tillage treatments. * $P \le 0.05$, ** $P \le 0.01$. ns denote no significant diference

Root length (m plant Root length (m plant⁻¹)

That is, the nodal roots from node 5 and node 6 of the ST plants had a signifcantly smaller root extension angle than that of CT (decreased by 6.9—18.5% and 10.8—20.0% for the nodal roots from node 5 and node 6, respectively) (Fig. [5B](#page-8-1)). That is, the top nodal roots became steeper.

Fig. 5 Efect of tillage methods on RSA. A, the representative RSA of ST and CT plant; B, nodal root angle (°) under ST and CT in 2019 and 2020. ST: strip-till, CT: conventional-till.

Each value is the mean of three replicates $(\pm SE)$. The asterisks denote signifcant diference among diferent tillage treatments. **P*≤0.05, ***P*≤0.01. ns denote no signifcant diference

Root distribution

The root length density of ST plants in the topsoil $(0-12$ cm) was lower than that of CT (by 37.7-46.7% at seedling, by 26.0—38.2% at jointing, by 17.2—25.8% at silking, and by 5.7—22.8% at two weeks after silking) (Fig. [6](#page-9-0)A, B). For vertical root distribution, the average D_{95} of the vertical root distribution in ST plant were 3.3%, 6.0%, 7.0% and 3.5% higher than that of CT at seedling, jointing, silking and two weeks after silking, respectively (Table [4](#page-9-1)).

Compared with CT, the horizontal root distribution in ST plants was severely inhibited (Fig. [7](#page-10-0)), especially in the topsoil (0—12 cm) which was the cultivated layer. The proportion of the intra-row roots of ST was increased by 7.0%—12.7% in the 0—12 cm soil layer compared with CT (Fig. [8](#page-11-0)). In contrast, in inter-row soil, at 9—15 cm,

For each growth stage, diferent letters denote signifcant difference ($P \le 0.05$) among the tillage treatments. D₉₅ indicates the rooting depth of 95% of the root system in the 0—60 cm soil layer

15—21 cm, 21—27 cm, and 27—30 cm away from the plant, the average root length density of ST was reduced signifcantly by 23.2—32.0%, 24.3—35.6%,

Fig. 6 Efects of tillage methods on root length density (cm cm−3) at diferent maize growth stages in 2019 (**A**) and 2020 (**B**) in the soil profle (0—60 cm depth). The sampling volume for the roots is 24 cm \times 60 cm \times 60 cm (distance between intrarow×distance between inter-row×depth). ST: strip-till, CT:

conventional-till. Each value is the mean of three replicates $(\pm S$ E). The asterisks denote significant difference among different tillage treatments. **P*≤0.05, ***P*≤0.01. ns denote no signifcant diference

Fig. 7 Spatial distribution of root length (cm plant⁻¹) in the soil profile (0—30 cm depth) as infuenced by strip-till (ST) and conventional-till (CT) in 2019 and 2020. The specifc root sampling and measurement methods are in *Root sampling, root distribution and root morphological traits*

28.6—55.7%, and 43.3—54.1% compared with CT, respectively (Table 6S). At diferent position in the interrow soil, root length density was signifcantly negatively correlated with soil bulk density (Fig. [9\)](#page-11-1).

Root senescence

Root senescence during post-silking stage was studied in more detail in 2022 (Fig. [10](#page-12-0)). It was found that the total root length of ST plants was signifcantly less than CT until 97 days after sowing (early grain flling stage). This diference disappeared and the total root length of ST plants was signifcantly larger than that of CT at 112 days after sowing. This indicated that root senescence of ST plants was slower than CT. In accordance, at 112 and 127 days after sowing, the rate of root xylem bleeding sap of ST plants was 70.7% (P<0.01) and 449.9% (P<0.01) higher than that of CT plants, respectively.

Discussion

Root growth, root senescence and RSA in relation to soil environment under ST system

Maize shoot and root growth is often impeded by low root-zone temperature during early spring (Brouwer and Hoagland [1964;](#page-13-7) Knoll et al. [1964;](#page-14-16) Richner et al. [1996;](#page-15-23) Nagel et al. [2009](#page-15-6)). Mechanical resistance can also limit root growth and reduce total root length (Grzesiak et al. [2002](#page-14-17); Bingham et al. [2010;](#page-13-8) Pfeifer et al. [2014\)](#page-15-24). At seedlings stage, the inter-row soil in ST had a lower soil temperature and higher bulk density than CT, and this was associated with lower shoot and root biomass during the vegetative stage (Fig. [4](#page-7-1) and Table [2](#page-5-0)). Chassot et al. ([2001\)](#page-14-18) showed that, in NT compared to CT, the poorer root and shoot growth of maize seedlings was presumably caused by the lower

Fig. 8 Efect of tillage methods on the proportion of root length in intra-tow soil in 0—30 cm soil layer in 2019 and 2020. ST: strip-till, CT: conventional-till. Each value is the

mean of three replicates $(\pm SE)$. The asterisks denote significant diference among diferent tillage treatments. **P*≤0.05, ***P*≤0.01. ns denote no signifcant diference

Fig. 9 Linear regressions between root length density (cm cm−3) and soil bulk density (g cm−3) of the inter-row soil in 0—12 cm soil layer in 2020. Data from all sampling positions in inter-row soil of ST and CT treatment were pooled for the analysis

topsoil temperature rather than by mechanical impedance. Because low temperature can reduce the availability of soil nutrients, limit root absorption of nutrients, and thus have a negative impact on crop growth (Miedema [1982](#page-15-25)). The same explanation may be true in the present study. Although the diference in temperature between ST and CT was relatively small in 2020, the soil temperature in the inter-row of ST was about 3 ℃ lower than that of CT (Fig. [2\)](#page-6-0). Licht and Al-Kaisi [\(2005b](#page-14-12)) showed that a temperature decrease of only 1.2—1.4 ℃ delayed the emergence of maize. With the increase of air temperature, the diference in root size (as shown in total root length) became smaller at jointing stage.

When the soil environment is adverse to plant growth, plant roots tend to avoid the adverse environment and proliferate in the soil zones with favorable conditions, which is called a compensation adjustment (Bingham and Bengough [2003](#page-13-9)). RSA can adapt to the soil physical properties by changing root length density (Wu et al. [2022a](#page-16-3), [b\)](#page-16-4), nodal roots angle (Jin et al. [2013\)](#page-14-19), and root distribution

Fig. 10 Efect of tillage methods on total root length (m plant⁻¹) and rate of root bleeding sap (g h⁻¹ plant⁻¹) during post-silking growth stage in 2022. The broken line in the fgure shows the trend of total root length, and the bar chart shows the trend of root bleeding sap. 72 days after sowing is the sampling time of silking stage. The sampling volume for the roots is 24 cm \times 60 cm \times 30 cm (distance between intra-row \times distance between inter-row×depth). ST: strip-till, CT: conventional-till. Each value is the mean of three replicates $(\pm SE)$. The asterisks denote signifcant diference among diferent tillage treatments. **P*≤0.05, ***P*≤0.01. ns denote no signifcant diference

(Ren et al. 2019). Ren et al. (2019) showed maize plants under ST had smaller root number density than CT in the top 40 cm layer at inter-row positions. In this research, when the soil temperature is no longer a limiting factor in ST system at silking stage, we found that the heterogeneous soil compactness caused by ST practice shaped the RSA. The inter-row soil bulk density in the 0—12 cm soil layer was signifcantly greater under ST than that of CT (Fig. [3](#page-7-0) and Table [4](#page-9-1)S). The roots of ST plants tended to grow into the intra-row soil and avoided growing into the colder, more compacted inter-row soil, leading to a high proportion of root length in the intra-row in ST plants (Fig. [8\)](#page-11-0). This was demonstrated by the negative correlation between soil bulk density and root length density (Fig. [9\)](#page-11-1). Less root growth in the inter-row soil was associated with steeper root angles and, consequently, proportionately more roots at depth (Table [4](#page-9-1)). A deeper root system may help compensate for lack of soil exploration in the surface soil. Reducing root distribution in the top soil is believed to benefcial for drought tolerance (Wasson et al [2012\)](#page-16-9).

The signifcance of roots in resource acquisition depends not only on root size but also root activity (Chen et al. [2015](#page-14-20)). Normally, maize root size begins to decrease since silking due to more root senescence (Yan et al. 2011 ; Chen et al. 2015). At grain filling stage, fast root senescence is a disadvantage for water and nutrient uptake and therefore grain development (Li et al. 2022). In the present study, although root size of ST plants was smaller than CT at silking stage, there was not signifcant diference in total root length between ST and CT at grain flling stage (Fig. [4\)](#page-7-1), suggesting root senescence in ST plants was delayed in comparison to CT. In 2022, the total root length in ST plants was even signifcantly greater than that in CT plants at grain flling stage (Fig. [10\)](#page-12-0). The greater rate of root xylem bleeding in ST plants in 2022 supports that root senescence may have been delayed. The smaller root size and slower shoot growth at vegetative growth stage of ST plants may save some soil water for later plant growth. It was found that during post-silking stage, there is normally more soil moisture storage in ST compared to CT (Licht and Al-Kaisi [2005b\)](#page-14-12). Also, nutrients (especially nitrate) in the topsoil can gradually leach into deep soil (Thorup-Kristensen et al. [2009\)](#page-16-11) and promote local later root proliferation there (Drew et al. [1973](#page-14-22)), so as to maintain the activity of the whole root system. More evidence is needed to validate and explain the delayed root senescence in ST practice.

Relationship between root characteristics and yield formation of maize in ST system

The smaller root system in ST plants can reduce nutrient uptake (Sha et al. [2023\)](#page-15-12) and therefore restrict pre-silking dry matter accumulation. Presilking shoot growth has great effect on ear develop-ment (D'Andrea et al. [2008;](#page-14-23) Abendroth et al. [2011;](#page-13-10) Gonzalez et al. [2019](#page-14-24); Mueller et al. [2019;](#page-15-26) Liu et al. [2021\)](#page-15-27). Indeed, compared to CT, ST plants had few grains number per ear (Table [1\)](#page-4-0), which is a major reason limiting grain yield under ST system. Therefore, improving early root development may be crucial to increase maize yield under ST system. Qin et al. [\(2005](#page-15-28)) suggested that developing new type starter fertilizer can be a promising way to enhance early root growth in the conservative tillage.

During grain-flling stage, at which 35 to 55% of the grain N was accumulated, maize root size and activity may greatly afect grain N accumulation, grain development and fnal grain yield (Hirel et al.

[2007;](#page-14-25) Chen et al. [2015\)](#page-14-20). At this stage, the sustained root activity may contribute to the efficient postsilking N uptake in ST plants (Sha et al. [2023](#page-15-12)). As a result, grain weight in ST plants was higher than that in CT plants (Table [1](#page-4-0)), which contributed to the stability of grain yield. It should be mentioned that root senescence and leaf senescence is interacted (Liu et al. [2018\)](#page-14-26). Maize plants use a large amount of photosynthates to grow new roots and maintain the respiration of old roots during grain flling (Niu et al. [2010;](#page-15-29) Yan et al. [2011\)](#page-16-10). Indeed, it is found that leaf senescence is also delayed in ST plants during grain flling stage (Sha et al. [2023\)](#page-15-12).

It is well understood that plant root system architecture (RSA) is closely related to soil resource acquisition, and maize with steep, deeper RSA can increase water and nitrogen acquisition from the deeper soil (Mi et al. [2010](#page-15-3), [2016;](#page-15-30) Lynch [2013;](#page-15-16) Trachsel et al. [2013](#page-16-12)). Feng et al. ([2019](#page-14-27)) showed that more roots in deeper soil contribute to efficient N uptake and maize grain yield. In this study, although the growth of sallow roots in ST plants were restricted by the colder, more compacted inter-row soil environment, the deeper root growth was maintained (Fig. [7](#page-10-0) and Table [4](#page-9-1)). This change of RSA in ST plants can help to improve water and nitrogen acquisition efficiency at grain filling stage (King et al. [2003](#page-14-28); Wasson et al. [2012](#page-16-9)).

Conclusion

In conclusion, compared with CT, the colder and more compacted inter-row soil in ST was unfavorable to early root growth, resulting in restricted shoot growth and few grain per ear. The heterogeneous soil environment in ST modifed root distribution, resulting in proportionately more roots in the intra-row soil. While the shallow roots in ST plants was reduced, the deeper root growth was maintained. At grain flling stage, root senescence was delayed. The delayed root senescence and reshaped RSA may contribute to efficient resource acquisition at grain flling stage, contributing to greater grain weight and stabilized grain yield. It was suggested that improving early root growth may be crucial to increase maize productivity in ST system.

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Data availability Data will be made available on request.

Declarations

Conficts of interest The authors declare no competing interests.

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