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Effects of tillage methods on photosynthetic performance of different functional leaf groups of summer maize in coastal saline-alkali farmland

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Abstract

This study aims to determine the changes in the photosynthetic performance of leaves at different leaf positions and their correlation and to screen out the basic tillage methods suitable for improving the yield. The decrease in soil salt content significantly improved the PSII performance index and quantum yield for electron transport of the bottom leaf group, synergistically enhanced the photosynthetic performance of summer maize leaves (especially the bottom leaf group), and enhanced the correlation between the bottom, middle (including the ear leaf), and upper leaf groups. Under subsoiling tillage conditions, the bottom leaves could produce more carbohydrates to meet the normal growth of the root system, promote the photosynthesis of the middle leaf group at the ear position, and increase the nutrient output of the upper leaf group to the female ear in the middle and later stages of maize aging.

Keywords: leaf group; photosynthetic properties; saline-alkali farmland; summer maize; tillage methods.

Introduction

Farmland salinization is one factor restricting the increase in world food production (Liu *et al*. 2018). As an important reserve farmland resource in China, the coastal saline-alkali farmland has great production potential and economic value (Cui *et al*. 2021). Its rational development and utilization are an important way to alleviate the shortage of cultivated farmland resources and ensure food security in China (Cui *et al*. 2022a). The problems of shallow groundwater level, repeated changes in soil salinity in the cultivated layer, low irrigation rate, and mostly saline water available for irrigation in coastal saline-alkali farmland seriously affect the normal growth and development of crops (Xia *et al*.

Highlights

- Subsoiling tillage significantly reduced soil salt content
- The decrease in salt content enhanced the correlation between leaf groups of summer maize
- The decline in salt content increased the photosynthetic rate of the bottom leaf group

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Abbreviations: ABS/CS_0 – absorption flux per CS; B – bottom leaf group (leaf position 8–10); C_i – intercellular CO_2 concentration; DI_0/CS_0 – dissipated energy flux per CS; ET_0/CS_0 – electron transport flux per CS; FP – no-tillage; g_s – stomatal conductance; M – middle leaf group (leaf position 11–13); PI_{ABS} – PSII performance index; P_N – net photosynthetic rate; R1 – silking stage; R3 – milk maturity stage; R5 – maturity stage; R – rotary tillage; S – subsoiling tillage; TR_0/CS_0 – trapped energy flux per CS; U – upper leaf group (leaf position 14–16); Φ_{E0} – quantum yield for electron transport; Φ_{P0} – maximum quantum yield for primary photochemistry; Ψ_0 – probability that a trapped exciton moves an electron into the electron-transport chain beyond Q_A^-.

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2019). Therefore, reducing soil salt content in the tillage layer is an urgent problem that needs to be solved in coastal saline-alkali farmland improvement.

Farm salinization has recently become a growing threat to global food security (Hoa *et al*. 2019, Hassani *et al*. 2021). Maize production accounts for one-third of global food production (Ali *et al*. 2021). Attention should be paid to the negative impact of soil salinization on maize yield. Previous studies have shown that with the increase of soil salinity, the yield of maize decreases significantly, which seriously restricts the exploitation in saline-alkali farmland (Farooq *et al*. 2015). The yield formation of maize mainly depends on the accumulation of photosynthetic products and their rational distribution (Yue *et al.* 2022). Among them, the material (mineral nutrient and photosynthetic assimilate) exchange and compensation between the aboveground and the underground part, and between different leaf groups in the aboveground part play an important role (Poorter *et al*. 2012). Dry matter accumulation is the basis for maize yield, especially after flowering, which is crucial in maize yield (Rossini *et al.* 2011). The leaf area, dry matter, and photosynthetic potential of the middle leaf group of maize are large and stable, and the functional period is long, which is the main 'supplier' of carbohydrates to the ear. The leaf area, dry matter, and photosynthetic potential of the upper leaf group of maize decrease gradually. The functional period is shortened, and the carbohydrates maize produces mainly provide grain growth and development. The leaf area, dry matter, and photosynthetic potential of the bottom leaf group of maize are all small, and the functional period is short. In the pre-growth and mid-growth periods, the leaves of the root group are senescent, and the bottom leaf group mainly provides the photosynthetic products required by the root system. In the late growth stage, after the decline of the bottom leaf group, the photosynthetic products required by the root system were provided by the upper leaf group. Some studies have shown that the senescence of the bottom leaf group affects the supply of carbohydrates to the root system, thereby affecting the nitrogen uptake of maize, which in turn may lead to a decrease in leaf area index, chlorophyll disintegration, the decline in leaf photosynthetic rate, and overall plant senescence (Pommel *et al*. 2006, Li *et al*. 2022).

Tillage can improve soil's physical structure (Xie *et al*. 2020), regulate root growth and development (Govaerts *et al*. 2006), and coordinate the relationship between aboveground and underground growth (Ren *et al*. 2018, Xu *et al*. 2018). The depth of rotary tillage is only 10–15 cm. Long-term no-tillage will increase the bulk density of soil and long-term rotary tillage will cause the bottom layer of the plow to be thickened, the topsoil to be loosened, and the soil water evaporation to be accelerated (Sang *et al*. 2016). Long-term no-tillage can cause an increase in soil bulk density, and limit crop root development and absorption and utilization of soil nutrients (Bengough *et al*. 2011, Blanco-Canqui and Ruis 2018). Compared with rotary tillage, subsoiling tillage can effectively increase soil deep-water infiltration. Compared with no-tillage, it can effectively reduce surface runoff, which is conducive to improving the gas exchange and growth of crop roots, and creating good soil conditions for the growth and development of crops (Tao *et al*. 2013). Tillage practices can cause changes in soil moisture, and salt movement is highly correlated with water movement. There is a significant positive correlation between water and salt movement in coastal saline-alkali farmland (Jiang *et al*. 2016, Yuan *et al.* 2021). Water is a good solvent for salt, and with rainfall or irrigation, the surface salt of the soil will dissolve with the water into the deep layers of the soil, thereby reducing the soil salinity content of the tillage layer (Qadir *et al*. 2001). Studies have shown that when the rainfall during the growing season exceeds 300 mm or a single rainfall exceeds 25 mm, it will produce a significant salt-leaching effect in the 0–40 cm soil layer (Liu *et al*. 2022). Under drought conditions, the salinity rises with the evaporation of soil water and accumulates on the surface of the soil, resulting in soil compaction and salinization in the tillage layer (Cucci *et al*. 2016, Walter *et al*. 2018).

Saline-alkali stress can significantly affect the root growth of crops (Cui *et al.* 2022b). In the early and middle stages of crop growth, the nutrients required for root growth are mainly supplied by the bottom leaf group (Rossini *et al.* 2011). We hypothesized that reducing crop salinity stress can improve the photosynthetic performance of the leaf group and jointly promote root growth and development, which in turn would promote the growth of the aboveground. Previous studies have been rich on the changes in photosynthetic properties of maize ear leaves and their effects on yield under saline-alkali stress, but it was obvious that leaves in different parts of maize contribute to yield formation. Therefore, the main objectives of this experiment were (*1*) to clarify the effects of different tillage methods on soil salinity content in the tillage layer of coastal saline-alkali farmland; (*2*) to elucidate the changes in photochemical and biochemical processes of photosynthesis and their synergistic effects in the upper, middle, and bottom leaf groups of summer maize based on three tillage methods (subsoiling tillage – S, rotary tillage – R, and no-tillage – FP); (*3*) to elucidate the contributions of upper, middle, and bottom leaf groups to the formation of summer maize yield. It has great significance for the rational use of farmland resources and improving grain production in coastal saline-alkali farmland.

Materials and methods

Study site: In 2021, a field test was conducted in Xiaobotou Town, Wudi County, Binzhou City, Shandong Province, China (38°02'N, 117°36'E). The region has a continental climate in the East Asian monsoon zone of the north temperate zone. The annual average temperature was 13.25°C, the monthly average rainfall was 38.65 mm, and the annual sunshine hours were 4,443.88 h. The average monthly temperature and precipitation from 2019 to 2021 are shown in Fig. 1S (*supplement*). The salt content was 1.74 g kg^{-1} and the pH was 8.12 in the 0–20 cm soil layer; the salt content was 1.63 g kg^{-1} and the pH was

8.25 in the 20–40 cm soil layer. The laboratory experiments were conducted from November to December 2021 in the Laboratory of Crop Water Physiology and Ecology of Shandong Agricultural University.

Experimental design: The medium and late maize (*Zea mays* L.) variety Wansheng 69 was used as the experimental material. Three types of tillage practice were used: subsoiling tillage, rotary tillage, and no-tillage. A randomized block design was adopted, with each test area being 50 m long and 15 m wide, and three replicates were set. We applied basal fertilizer (N-P_2O_5-K_2O, 25-12-5) of 750 kg ha^{-1}. Samples were taken at the silking stage (R1), milk maturity stage (R3), and maturity stage (R5) of maize. We divided summer maize leaves into bottom (8–10 leaves form roots), middle (11–13 leaves from roots, the 12th leaf is the ear leaf), and upper (14–16 leaves from roots) leaf groups.

Soil salinity: The soil samples were obtained by the five-point sampling method, which was carried out at the flowering stage, milk maturity stage, and maturity stage of maize. Five soil sampling points were selected in each plot to remove the vegetation on the surface layer of the soil, and soil samples of 0–40 cm soil layer were collected, with every 20 cm as a layer. Air-dried soil samples were weighed, and 1:5 soil leachate was prepared, shaken, allowed to stand, and filtered. The conductivity of soil samples was determined using a conductivity meter (*DDSJ-308*, *Shanghai Yidian Scientific Instrument Co.*, *Ltd.*, China). The conductivity regression equation between soil salinity and soil leachate was obtained using the residue-drying method.

Dry matter accumulation and leaf area index: Five representative maize plants with uniform growth were selected. We determined the average single-stem leaf area ($\bar{A}_{leaf}$) and the leaf area index (LAI) was calculated. The corn plant was divided into five parts: stems, leaves, female ears, male ears, and bracts, which were dried and weighed. The dry matter accumulation was calculated based on the number of spikes per hectare of each treatment.

$\bar{A}_{leaf}$ [m^2] = (leaf length [m] × leaf width [m] × 0.8)/number of measured samples

LAI = ($\bar{A}_{leaf}$ [m^2] × number of stems per unit area)/size of unit area [m^2]

Dry matter accumulation [kg ha^{-1}] = (five parts mass [kg] × total number of stems per unit area)/unit area [ha]

Chlorophyll content in leaves: The ear leaves of maize plants with representative and uniform growth were selected in each plot, and the chlorophyll (Chl) content was determined by the 80% acetone grinding method (Zhao *et al.* 2023):

$$C_a = 13.95 \times D_{665} - 6.88 \times D_{649}$$

$$C_b = 24.96 \times D_{649} - 7.32 \times D_{665}$$

$$C_t = C_a + C_b$$

where D_{649} and D_{665} are the absorbances of 649 and 665 nm, respectively; C_a and C_b are the content of Chl *a* and Chl *b*, respectively [mg L^{-1}]; C_t represents the total Chl content [mg L^{-1}].

Gas-exchange parameters of upper, middle, and bottom leaf groups: Ten representative maize plants with uniform growth were selected in each treatment. Measurements were done using the *CIRAS-III* (*PP System*, USA) gasometric system. The gas-exchange parameters, such as net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) in the upper, middle, and bottom leaf groups were determined. The measurement position was the central part (the widest) of the leaf. During the measurement, the natural light intensity [1,600 ± 50 μmol(photon) m^{-2} s^{-1}] and CO_2 concentration of 380 μmol mol^{-1} were maintained by the automatic control device of the *CIRAS-III*.

Fast Chl fluorescence-induced kinetic curves (OJIP): Representative and uniform maize plants (n = 15) were selected for each treatment. The dark-adaptation clamp was placed in the middle of the leaf for 20 min. The rapid Chl fluorescence-induced kinetic curve (OJIP) of leaves in the upper, middle, and bottom leaf groups was determined using a continuous excitation fluorescence meter (*Handy PEA*, *Hansatech*, UK), and the relevant parameters were calculated.

Yield and yield components: The first ears were harvested in 5 × 1.2 m^2 plots; the first panicle was collected, threshed, and dried after indoor seed examination. The data of yield components (ears number, kernels per ear, and 1,000-grain mass) were measured.

Data analysis: To process raw data, we used *Excel 2016* (*Microsoft Inc*., Redmond, Washington, USA). We performed a one-way analysis of variance (*ANOVA*) using *SPSS 26.0* software (*SPSS Inc*., Chicago, IL, USA) to assess the effects of treatments on experimental variables and crop yields. We performed a correlation analysis to determine the correlation between each pair of variables. In cases, where significant correlations were detected in the trial data, we performed regression analyses for the variables involved. To determine the differences between the results of the correlation analysis included in our study, we performed a structural equation analysis (SEM) using the *SPSS 26.0* software plug-in *Amos Graphics CLI* (*SPSS Inc*., Chicago, IL, USA). The images were created by *Origin 2022* (*Origin Lab Inc*., Northampton, MA, USA).

Results

Changes in soil salinity content under different tillage methods: With the advancement of the growth process, the salt content of the three tillage methods decreased to varying degrees in the 0–40 cm soil layer of maize season (Table 1). The salt content of 0–40 cm soil in S, R, and FP decreased by 4.1, 2.3, and 4.4%, respectively, and decreased by 4.6, 4.6, and 2.5% in 0–40 cm soil from milk maturity to maturity stage, respectively. Summer rainfall had a positive effect on the downward leaching of soil salinity. Compared with the pre-sowing stage, the salt content of 0–20 cm and 20–40 cm of corn in subsoiling tillage decreased by 49.7% and 31.3%, respectively. The salt content of 0–20 cm and 20–40 cm decreased by 38.8% and 23.3%, respectively. The salt content of no-tillage decreased by 29.6% at 0–20 cm and 12.5% at 20–40 cm. Among them, the salt reduction effect of subsoiling tillage was better. From the silking stage to the milk maturity stage, the salt content of no-tillage decreased more proportionally, which may be related to its initially higher salt content. After the soil salt content decreased to a certain extent, the leaching effect of rainfall on salt gradually weakened. Among them, the salt content of subsoiling tillage decreased more during the growth period of maize, which may be related to the fact that breaking the bottom layer of the plow promoted the infiltration of precipitation, and the salt content of the topsoil sank with the rainwater.

Leaf area index: The leaf area index of summer maize under different treatments and at various stages was as follows: S > R > FP (Fig. 1). The leaf area index of subsoiling tillage was significantly higher than that of rotary tillage and no-tillage at the silking stage, which was 7.8 and 34.7% higher, respectively. At the milk maturity stage, the subsoiling and rotary tillage were significantly higher than those of no-tillage, which were 9. and 39.4% higher, respectively, but there was no significant difference between them. The subsoiling tillage was significantly higher than that of rotary tillage and no-tillage at the maturity stage, which were 12.2 and 40.5% higher, respectively. The maximum leaf area index was reached at the silking stage, and then the leaf area gradually decreased.

Chlorophyll content: The Chl content of the ear positions of maize at different stages and treatments was as follows: S > R > FP (Table 2). Compared with rotary tillage and no-tillage, the total Chl content of subsoiling tillage at the silking stage was 8.2 and 18.3% higher. Compared with rotary tillage and no-tillage, the total Chl content of the subsoiling tillage at the milk maturity stage was 6.5 and 16.5% higher. Compared with rotary tillage and no-tillage, the total Chl content of subsoiling tillage at the maturity stage was 10.6 and 25.0% higher than that of rotary tillage and no-tillage. With the increase of the difference in leaf

Table 1. Effects of different tillage methods on soil salinity [g kg^{-1}] during different growth stages of summer maize in saline-alkali farmland. S – subsoiling tillage; R – rotary tillage; FP – no-tillage (farmer pattern); R1 – silking stage; R3 – milky stage; R5 – maturity stage; 0–20 and 20–40 means different soil depth [cm]. Values are means, *n* = 3. *Letters* (a, b, c) indicate statistical differences by LSD test (P<0.05) between different treatments in R1, R3, and R5.

Tillage method	Growth stage					
	R1		R3		R5	
	0–20 cm	20–40 cm	0–20 cm	20–40 cm	0–20 cm	20–40 cm
S	1.89 ± 0.04^{c}	1.93 ± 0.01^{c}	1.77 ± 0.06^{b}	1.90 ± 0.02^{c}	1.70 ± 0.06^{c}	1.81 ± 0.04^{c}
R	1.99 ± 0.01^{b}	1.99 ± 0.02^{b}	1.89 ± 0.01^{a}	2.00 ± 0.03^{b}	1.81 ± 0.04^{b}	1.91 ± 0.02^{b}
FP	2.12 ± 0.01^{a}	2.16 ± 0.02^{a}	1.97 ± 0.05^{a}	2.13 ± 0.01^{a}	1.94 ± 0.02^{a}	2.06 ± 0.01^{a}

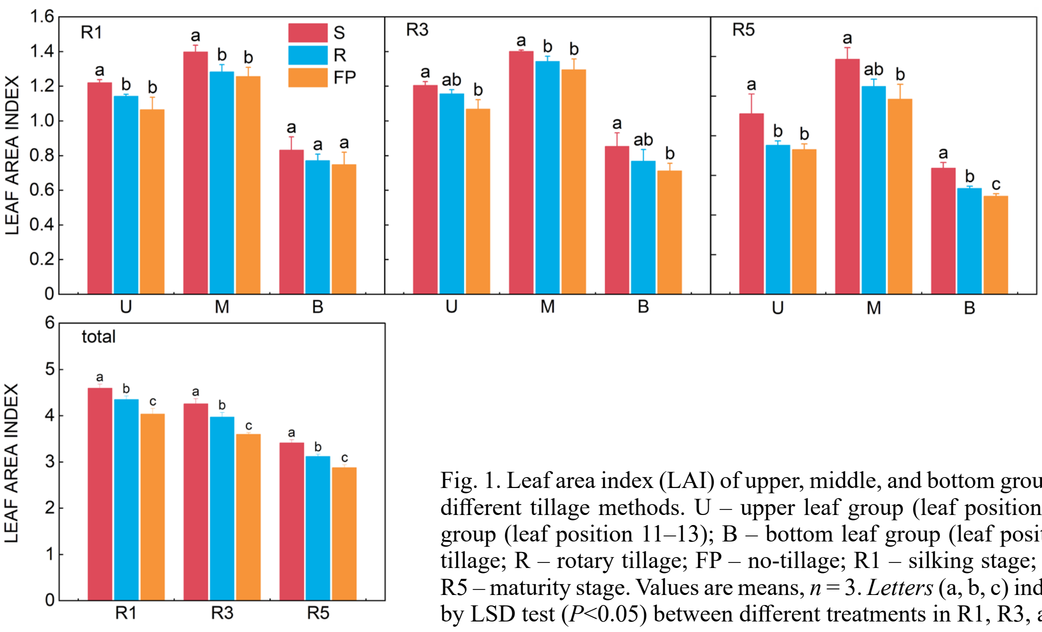

Fig. 1. Leaf area index (LAI) of upper, middle, and bottom groups of summer maize under different tillage methods. U – upper leaf group (leaf position 14–16); M – middle leaf group (leaf position 11–13); B – bottom leaf group (leaf position 8–10); S – subsoiling tillage; R – rotary tillage; FP – no-tillage; R1 – silking stage; R3 – milk maturity stage; R5 – maturity stage. Values are means, *n* = 3. *Letters* (a, b, c) indicate statistical differences by LSD test (P<0.05) between different treatments in R1, R3, and R5.

Table 2. Chlorophyll content of ear leaf of summer maize at different stages. S – subsoiling tillage; R – rotary tillage; FP – no-tillage; R1 – silking stage; R3 – milky stage; R5 – maturity stage. Values are means, $n = 3$. *Letters* (a, b, c) indicate statistical differences by LSD test ($P<0.05$) between different treatments in R1, R3, and R5.

Chlorophyll content	Growth stage	Tillage method		
		S	R	FP
Chl *a* [mg L^{-1}]	R1	33.36 ± 0.85[a]	31.73 ± 0.49[b]	28.53 ± 1.19[c]
	R3	33.10 ± 0.52[a]	30.83 ± 0.48[b]	27.54 ± 0.76[c]
	R5	27.31 ± 1.44[a]	24.17 ± 0.69[b]	21.03 ± 0.98[c]
Chl *b* [mg L^{-1}]	R1	12.04 ± 0.50[a]	10.58 ± 0.84[b]	9.53 ± 0.71[c]
	R3	11.03 ± 0.55[a]	10.28 ± 0.69[b]	8.91 ± 0.58[c]
	R5	9.10 ± 0.61[a]	8.32 ± 0.64[b]	7.01 ± 0.97[c]
Total Chl [mg L^{-1}]	R1	47.40 ± 1.70[a]	43.83 ± 0.97[b]	40.06 ± 2.37[c]
	R3	45.33 ± 1.03[a]	42.57 ± 0.96[b]	38.92 ± 1.52[c]
	R5	37.39 ± 1.17[a]	33.82 ± 0.37[b]	29.91 ± 1.05[c]

area index and Chl content in the middle and upper leaf groups during the growth period, the large and stable leaf area and photosynthetic potential of the middle and upper leaf groups in the subsoiling tillage laid the foundation for the high photosynthetic performance.

Photosynthetic gas-exchange parameters: The photosynthetic data of the three leaves in the upper, middle, and bottom leaf groups were averaged (Fig. 2). The net photosynthetic rate (P_N) of summer maize subsoiling tillage at the silking stage was higher than that of other treatments, and the P_N of subsoiling tillage in the upper, middle, and bottom leaf groups was 10.1, 12.9, and 17.2% higher than that of rotary tillage, respectively. It was 19.9, 30.3, and 64.3% higher than that of no-tillage. The P_N of subsoiling tillage at the milk maturity stage was higher than that of other treatments, and the P_N of subsoiling tillage in the upper, middle, and bottom leaf groups was 14.3, 18.0, and 8.5% higher than that of rotary tillage, respectively. It was 28.4, 22.0, and 54.4% higher than that of no-tillage. The P_N the subsoiling tillage at the maturity stage was also higher than that of the other treatments, and the P_N of the subsoiling in the upper, middle, and bottom leaf groups was 16.3, 18.2, and 13.9% higher than that of the rotary tillage, respectively. It was 23.6, 27.8, and 86.5% higher than that of no-tillage. The photosynthetic performance of leaves in the upper, middle, and bottom groups was significantly improved by subsoiling. The stomatal conductance (g_s) of summer maize subsoiling tillage was significantly higher than that of other treatments, and the g_s of subsoiling tillage in the upper, middle, and bottom leaf groups were 9.5, 6.8, and 27.2% higher than that of rotary tillage, respectively. It was 22.7, 16.9, and 49.5% higher than that of no-tillage. The g_s of the subsoiling at the milk maturity stage was higher than that of other treatments, and the g_s of the subsoiling tillage in the upper, middle, and bottom leaf groups was 18.2, 16.9, and 10.9% higher than that of the rotary tillage, respectively. It was 37.4, 32.6, and 16.2% higher than that of no-tillage. The g_s of the subsoiling tillage at the maturity stage was also higher than that of the other treatments, and the g_s of the subsoiling tillage in the upper, middle, and bottom leaf groups was 5.7, 25.8, and 8.6% higher than that of the rotary tillage, respectively. It was 11.4, 50.0, and 34.6% higher than that of no-tillage. The intercellular CO_2 concentration (C_i) of summer maize was FP > R > S at different growth stages, and no-tillage in the upper, middle, and bottom leaf groups at the silking stage was 11.7, 29.7, and 8.2% higher than that of subsoiling tillage. Compared with rotary tillage, it was 12.5, 19.5, and 3.2% higher. Compared with the subsoiling tillage, no-tillage in the upper, middle, and bottom leaf groups at the milk maturity stage was 7.5, 5.4, and 18.0% higher than that of the subsoiling. Compared with rotary tillage, it was 3.2, 0.8, and 8.2% higher. Compared with the subsoiling tillage, no-tillage in the upper, middle, and bottom leaf groups at the maturity stage was 13.3, 20.7, and 16.6% higher than that of the subsoiling tillage. Compared with rotary tillage, it was 5.1, 2.5, and 9.2% higher.

Compared with no-tillage and rotary tillage, subsoiling tillage increased the net photosynthetic rate and stomatal conductance, and reduced the intercellular CO_2 concentration of summer maize after flowering (Fig. 2). The trend of intercellular CO_2 concentration was not consistent with the photosynthetic rate and stomatal conductance, indicating that the factors affecting the photosynthetic rate were mainly nonstomatal. The results indicated that the factors affecting photosynthesis in each stage after flowering of summer maize were nonstomatal, and one of the reasons for the high photosynthetic rate of subsoiling tillage in each growth stage was that it reduced the limitation of photosynthesis by nonstomatal factors. Except for the bottom leaf group at the silking stage, the P_N of subsoiling tillage in all leaf groups at other stages was significantly higher than that of other treatments. Except for the bottom leaf group at the milk maturity stage, the g_s of subsoiling tillage in each leaf group at different stages was significantly higher than that of other treatments. The P_N of each treatment was the highest in the middle leaf group, followed by the upper leaf group. The higher P_N of the bottom leaf group in the later subsoiling tillage compared with other treatments ensured the nutrient

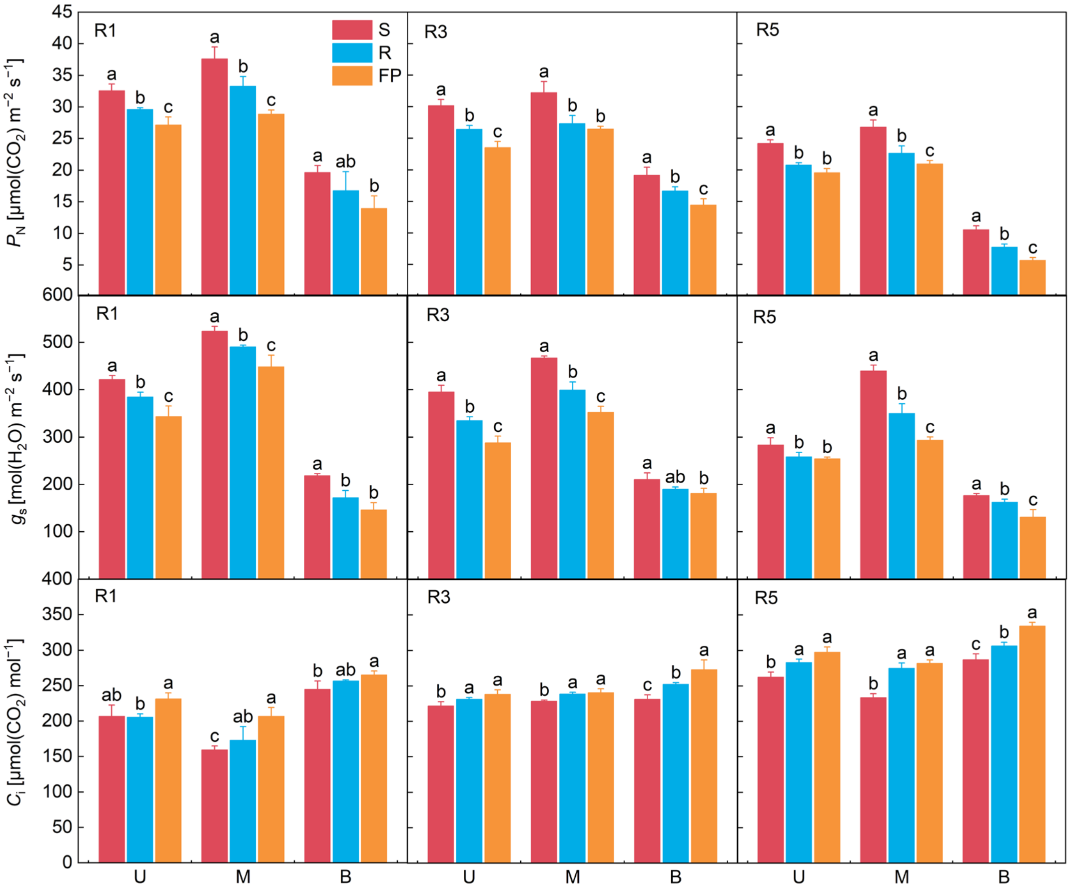

Fig. 2. Photosynthetic gas-exchange parameters of summer maize. U – upper leaf group (leaf position 14–16); M – middle leaf group (leaf position 11–13); B – bottom leaf group (leaf position 8–10); S – subsoiling tillage; R – rotary tillage; FP – no-tillage; R1 – silking stage; R3 – milk maturity stage; R5 – maturity stage; P_N – net photosynthetic rate; g_s – stomatal conductance; C_i – intercellular CO_2 concentration. Values are means, $n = 3$. *Letters* (a, b, c) indicate statistical differences by LSD test (P<0.05) between different treatments in R1, R3, and R5.

uptake and supply of roots and sufficient nutrient supply to the middle and upper leaf groups, maintaining its high photosynthetic duration and high photosynthetic rate.

Analysis of fluorescence parameters: The fluorescence produced by chloroplasts in plant cells when they are just exposed to light shows a rapid transition from the lowest (O point) to the highest peak (P point), which is called OJIP fluorescence kinetics (Tsimilli-Michael 2020). The trend of FP > R > S were all found in the upper, middle, and bottom leaf groups at different stages, and W_k and V_J increased significantly with the advancement of fertility (Fig. 3, Appendix 1). The W_k and V_J of each leaf group in each stage of subsoiling tillage were significantly lower than those of rotary tillage and no-tillage. The PI_{ABS}, Ψ_0, Φ_{P0}, and Φ_{E0} of the upper, middle, and lower leaf groups after flowering in deep tillage were significantly higher than those in rotary tillage and no tillage (except for the upper leaf groups Φ_{P0} in the R1 and R5 and except for the upper and lower leaf groups Ψ_0 in the R3).

From the initial to the maximum value of fluorescence measurement, the energy flux absorption, capture and transfer per leaf section (ABS/CS_0, ABS/CS_m, TR_0/CS_0, TR_0/CS_m, ET_0/CS_0, and ET_0/CS_m) of different leaf groups in different treatments was S > R > FP, while the heat dissipation per unit leaf section (DI_0/CS_0 and DI_0/CS_m) was S < R < FP (Fig. 4, Appendix 1). Compared with rotary tillage and no-tillage, the ABS/CS_0 of subsoiling tillage increased by 10.8 and 19.6% on average. ABS/CS_m increased by 10.2 and 16.8% on average. Compared with rotary tillage and no-tillage, the TR_0/CS_0 of subsoiling tillage increased by 16.4 and 32.0% on average. TR_0/CS_m increased by 15.8 and 28.8% on average. Compared with rotary tillage and no-tillage, the ET_0/CS_0 of subsoiling increased by 21.2 and 41.4% on average. ET_0/CS_m increased by 20.7 and 30.5% on average. Compared with rotary tillage and no-tillage, the DI_0/CS_0 of subsoiling tillage was reduced by 8.9 and 15.7% on average. The average decrease in DI_0/CS_m was 9.4 and 17.3%. The results showed that the overall leaf performance of maize improved significantly with the decreasing soil salt content. With the advancement of the growth period, the energy absorption, conversion, and transfer per unit blade section of each treatment leaf group decreased, and the heat dissipation increased. However, compared with the subsoiling tillage, rotary tillage, and no-tillage, the energy absorption, transformation, and transfer per unit leaf section of the upper, middle, and bottom leaf groups decreased more, and the heat dissipation

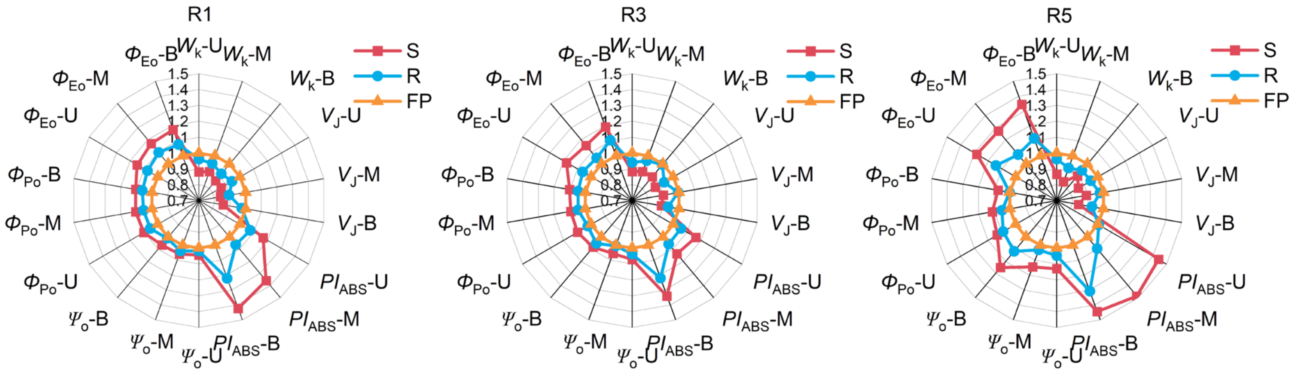

Fig. 3. Comparison of fluorescence induction dynamics curve parameter in upper, middle and bottom leaves of summer maize under different tillage methods. U – upper leaf group (leaf position 14–16); M – middle leaf group (leaf position 11–13); B – bottom leaf group (leaf position 8–10); S – subsoiling tillage; R – rotary tillage; FP – no-tillage; R1 – silking stage; R3 – milk maturity stage; R5 – maturity stage; W_k – relative variable fluorescence at K-step; V_J – relative variable fluorescence intensity at the J-step; PI_{ABS} – performance index on absorption basis; Ψ_0 – probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^- (at t = 0); Φ_{P0} – maximum quantum yield for primary photochemistry (at t = 0); Φ_{E0} – quantum yield for electron transport (at t = 0).

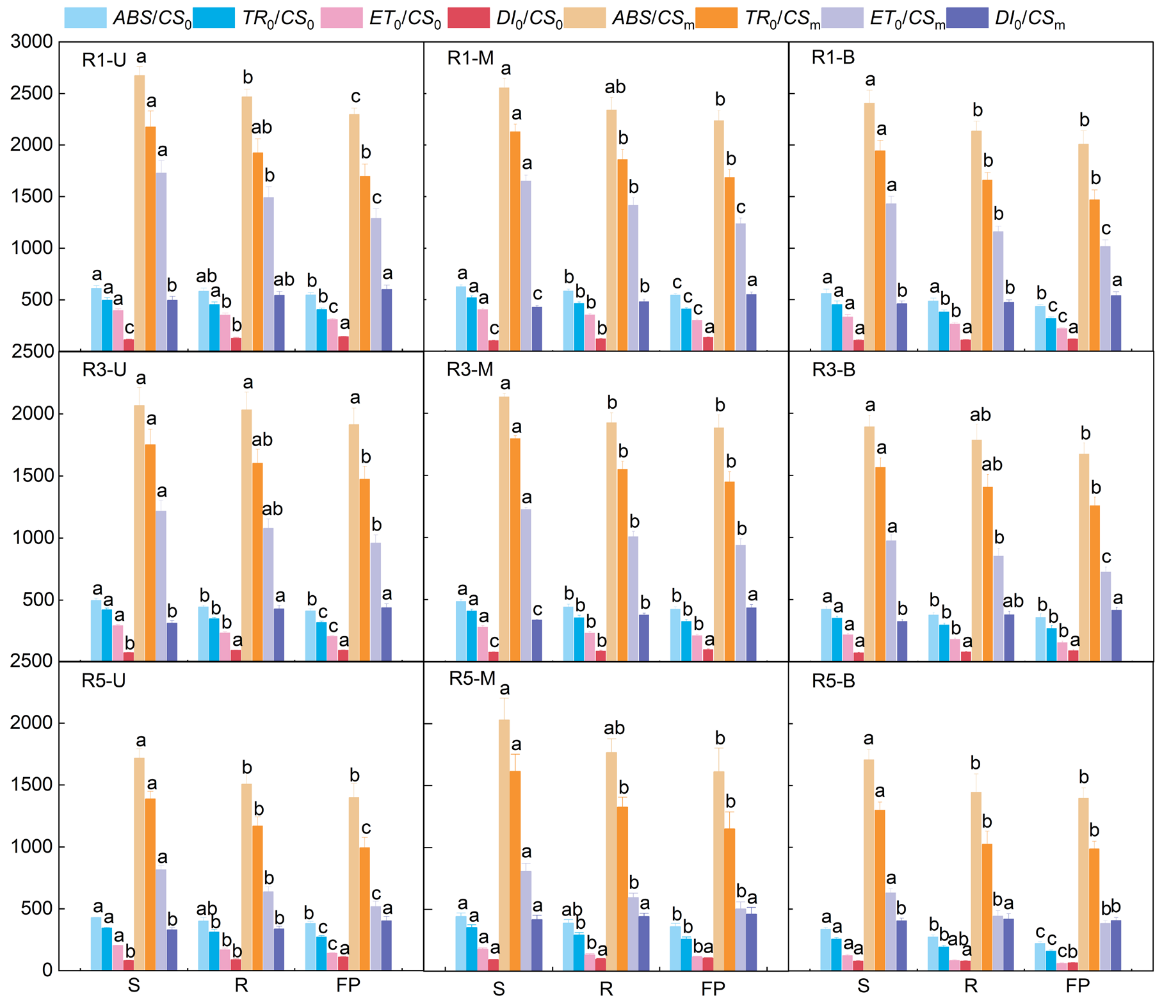

Fig. 4. Change of unit leaf section energy from initial to maximum fluorescence value in maize leaf group under three tillage methods. U – upper leaf group (leaf position 14–16); M – middle leaf group (leaf position 11–13); B – bottom leaf group (leaf position 8–10); S – subsoiling tillage; R – rotary tillage; FP – no-tillage; R1 – silking stage; R3 – milk maturity stage; R5 – maturity stage; ABS/CS_0 – absorption flux per CS (at t = 0); TR_0/CS_0 – trapped energy flux per CS (at t = 0); ET_0/CS_0 – electron transport flux per CS (at t = 0); DI_0/CS_0 – dissipated energy flux per CS (at t = 0). When $t = t_{Fm}$, CS_0 was replaced by CS_m. Values are means, *n* = 3. *Letters* (a, b, c) indicate statistical differences by LSD test ($P<0.05$) between different treatments in S, R, and FP.

increased more. With the advancement of the growth process, the differences in photosystem performance and photosynthetic rate in the bottom leaf groups under different treatments became larger. The subsoiling tillage effectively delayed the premature senescence of the bottom leaf group, ensured the normal root function, and laid the foundation for a timely supply of nutrients to the middle and upper leaf groups (Pommel *et al*. 2006, Li *et al*. 2022).

Yield and yield components: Under the same experimental conditions, subsoiling tillage could significantly increase maize yield compared to rotary tillage and no-tillage (Table 3). The measured yield of subsoiling tillage was 6.9 and 10.3% higher than that of rotary tillage and no-tillage, respectively. There was no significant difference in the spike number per acreage between the three tillage methods. There was no significant difference in the number of grains per panicle between subsoiling tillage and no-tillage, and the number of grains per panicle of subsoiling tillage was significantly higher than that of rotary tillage. The 1,000-grain mass of no-tillage was significantly lower than that of subsoiling and rotary tillage.

Discussion

The SEM analysis showed that the soil salinity content of summer maize in coastal saline-alkali farmland was significantly affected by tillage methods (Fig. 5; Fig. 5S, *supplement*). Subsoiling tillage with summer rainfall and sufficient irrigation has a better salt-leaching effect (Table 1) and the highest yield (Table 3). Therefore, we speculated that the decrease of soil salinity content in the tillage layer could alleviate the salinity stress of maize plants and improve the photosynthetic performance of summer maize (Fig. 2). As we all know, the light environment, respiratory substrate concentration, and leaf area of maize are different at different leaf positions (Li *et al*. 2022, Wu *et al*. 2022). Does the alleviation of salt stress improve the photosynthetic performance of leaves in different parts of maize? In the following part, we will discuss the changes in leaf photosynthetic performance and its correlation in the upper, middle, and bottom leaf groups of summer maize after anthesis as much as possible.

Tillage methods change the soil salinity content of the tillage layer in coastal saline-alkali farmland

Tillage methods directly affect the physical properties and water changes of the soil, thereby changing the growth and development of crops (Xie *et al*. 2020). Subsoiling tillage breaks the 'plow bottom' (Yin *et al*. 2021), it can effectively enhance the water permeability of the soil (Mohanty *et al*. 2007), promote rainwater infiltration, reduce shallow soil salinity, and alleviate salt stress on crop roots. In the subsoiling tillage, with the infiltration and pressure of rainfall, the soil salt content of the tillage layer was significantly reduced, and the ion toxicity of crops was alleviated (Sang *et al*. 2016, Liu *et al*. 2022). This study showed that the soil salt content of 0–40 cm soil layer after flowering of summer maize was significantly reduced. Compared with rotary tillage and no-tillage, the salt content of 0–40 cm soil in subsoiling tillage was reduced by 5.4 and 12.6% on average (Table 1). Under the experimental conditions, compared with rotary tillage or no-tillage, the subsoiling tillage significantly reduced the salt content of the tillage layer (Table 1). However, it is worth noting that compared to rotary tillage or no-tillage, subsoiling tillage increases the vertical migration of water and salt (Bengough *et al*. 2011, Bian *et al*. 2016, Blanco-Canqui and Ruis 2018). There was no significant decrease in soil salt content between different periods (Table 1). However, we do not know how soil water and salt dynamics change before, during, and after a major rainfall or irrigation. In the process of water evapotranspiration in the field, all tillage methods have the upward movement of water and salt, and the subsoiling tillage had higher water evapotranspiration compared with no-tillage (Blanco-Canqui and Ruis 2018). We hypothesized that the reduction of soil salt content in each treatment after farmland water input was higher than the difference in soil salt content during the sampling period. The reduction of soil salt content by subsoiling tillage may be much higher than we have observed. The next step was to investigate the soil water and salt migration patterns and their effects on the root system of summer maize under the conditions of coastal saline-alkali farmland before and after irrigation.

Regulation mechanism of photosynthetic performance in upper, middle, and bottom leaf groups of summer maize under salt stress

Except for W_k and Φ_{P0} in the bottom leaf group of R5, there was a significant or extremely significant correlation between the fluorescence parameters of each leaf group and the soil salt content of 0–40 cm at all other stages. With the increase of soil salinity, W_k and V_J showed an upward trend, while PI_{ABS}, Ψ_0, Φ_{P0}, and Φ_{E0} showed a downward trend. There was a significant or extremely significant

Table 3. Summer maize yield and its component factors under different tillage methods. S – subsoiling tillage; R – rotary tillage; FP – no-tillage. Values are means, $n = 5$. *Letters* (a, b, c) indicate statistical differences by LSD test ($P<0.05$) between different treatments in S, R, FP.

Tillage method	Ears number [× 10^4 ears ha^{-1}]	Kernels per ear	1,000-grain mass [g]	Yield [kg ha^{-1}]
S	6.36 ± 0.15[a]	551.92 ± 4.04[a]	250.74 ± 1.13[a]	8,240.94 ± 61.91[a]
R	6.21 ± 0.06[a]	532.82 ± 6.19[b]	245.34 ± 0.96[a]	7,705.10 ± 82.62[b]
FP	6.41 ± 0.17[a]	547.18 ± 11.04[ab]	229.05 ± 0.45[b]	7,469.10 ± 64.64[c]

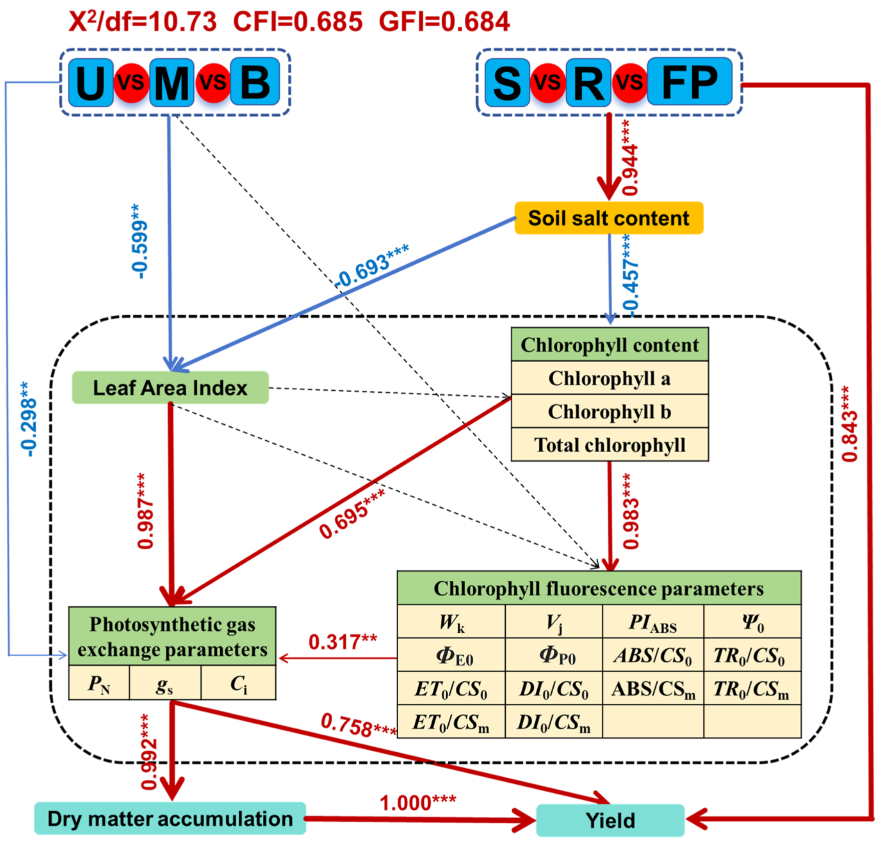

Fig. 5. Pathway analysis of photosynthetic performance parameters in upper, middle and bottom leaf groups of coastal saline-alkali farmland summer maize under different tillage methods. The analysis uses the structural equation model (SEM), with the single arrow indicating the causality. *The red* and *blue arrows* indicate the positive and negative relationship, and *the black arrow* indicates the relationship is insignificant. Numbers adjacent to the arrow are standardized path coefficients. The path width is scaled proportional to the path coefficient. U – upper leaf group (leaf position 14–16); M – middle leaf group (leaf position 11–13); B – bottom leaf group (leaf position 8–10); S – subsoiling tillage; R – rotary tillage; FP – no-tillage.

correlation between the gas-exchange parameters and fluorescence parameters in each leaf group at different stages (Figs. 3S, 4S; *supplement*). The improvement of performance index on absorption basis (PI_{ABS}) significantly increased the net photosynthetic rate of maize leaves (Figs. 2, 3). We concluded that there was a negative correlation between net photosynthetic rate and soil salt content in the upper, middle, and bottom leaf groups of maize. The soil salinity increase led to increasing thermal dissipation (Fig. 4), which could be interpreted as salinity leading to the activation of the protective mechanism at the level of PSII function. The decrease in soil salt content improves the photosynthetic performance of maize leaves, which is consistent with the results of previous studies on crops such as cotton and soybean (Feng *et al*. 2021, Ju *et al*. 2021). There was a significant correlation between the upper, middle, and bottom leaf groups of summer maize, which was consistent with the results of previous studies on spring maize and other crops (Wang *et al*. 2021). Among them, the decrease of salt content in the 20–40 cm soil layer was significantly positively correlated with the increase of PSII performance in the bottom leaf group of maize (Fig. 3S), and physical and chemical properties of soil in this layer were significantly positively correlated with the strength of maize root performance (Zhang *et al*. 2022). The change in salt content in the 20–40 cm soil layer directly affected the photosynthetic performance of the bottom leaf group. At the same time, we found that the decrease of salt content in the 20–40 cm soil layer improved the photosynthetic performance of the bottom leaf group by enhancing the PI_{ABS} of the photosystem and reducing the thermal dissipation, rather than increasing the photosynthetic area.

For most crops, the root system and the shoots were interdependent, and the improvement of photosynthetic performance in the bottom leaf group was significantly beneficial to the root performance in terms of leaf functionality, which could increase the water and fertilizer uptake of roots and delay senescence (Burton *et al*. 2013, Bian *et al*. 2016). There was a negative correlation between the net photosynthetic rate of summer maize leaves and soil salinity, which may be due to the combined action of soil salt content and the photosynthetic performance of the bottom leaf group, which affected the root activity, which in turn caused the change of photosynthetic performance in the middle and upper leaf groups, thus showing a synergistic effect and strong correlation between the upper, middle and bottom leaf groups. It is worth noting that there was no significant difference in LAI between the bottom leaf groups at flowering stage and milk maturity stage, but there was a substantial difference in net photosynthetic rate between the bottom leaf groups ($P<0.05$) (Figs. 1, 2). Therefore, we believe that the high net photosynthetic rate of the bottom leaf group provides sufficient sources for the root system and promotes the growth and development of the root system (Borrell *et al*. 2001, Kitonyo *et al*. 2018).

Synergistic relationship of photosynthetic performance in upper, middle, and bottom leaf groups of summer maize and its contribution to yield improvement

The strength of crop photosynthetic performance plays a key role in the yield (Sun *et al*. 2009, Wang *et al*. 2021, Suárez *et al*. 2022). The OJIP has a good ability to analyze the performance of the photosystem and the performance of multiple key sites in the electron transport chain of the photosystem under crop stress conditions (Zushi *et al*. 2017). There was a correlation between different leaf groups of maize (Pierik and de Wit 2014). The analysis of the OJIP showed that the Chl fluorescence parameters of the bottom leaf group and the middle leaf group in the middle and early stages of grain filling (R1 to R3) showed a significant positive correlation (Fig. 3S). The W_k and V_J of the bottom leaf group at the flowering stage of subsoiling tillage were significantly lower than those of rotary tillage and no-tillage, improving the efficiency of the electron transport chain, optimizing the energy capture (Φ_{P0}) and transfer (Φ_{E0}) per unit of leaf cross-section, and improving the photosynthetic performance index (PI_{ABS}) (Figs. 3, 4). This provides a basis for improving the photosynthetic electron transfer efficiency of the middle leaf group during the milk maturity stage. The correlation between Chl fluorescence parameters between the upper leaf group and the middle leaf group in the middle and late stages of grain filling (R3 to R5) was significant (Figs. 3S, 4S), and the W_k and V_J of the middle leaf group in the subsoiling tillage were significantly lower than those in the rotary tillage and no-tillage, which optimized the electron transfer chain efficiency and improved the photosynthetic performance index, thereby improving the photosynthetic electron transfer efficiency of the upper leaf group at the maturity stage (Figs. 3, 4). Therefore, subsoiling tillage improved the energy transfer efficiency of electron transfer chains which is the main reason for improving the photosynthetic performance of leaf groups.

This study showed that soil salinity content significantly affected the photosynthetic performance of maize leaves (Fig. 4; Fig. 5S, *supplement*). The P_N of the upper, middle, and bottom leaf groups of post-anthesis subsoiling tillage was significantly higher than that of rotary tillage and no-tillage (Fig. 2). In the middle and early stages of grain filling, there was a significant positive correlation between the gas-exchange parameters of the bottom leaf group and the middle leaf group, indicating that the salinity reduction effect of subsoiling tillage on the tillage layer significantly enhanced the photosynthetic performance of the bottom leaf group, and then improved the photosynthetic performance of the middle leaf group. In the middle and late stages of grain filling, there was a significant correlation between the gas-exchange parameters between the upper leaf group and the middle leaf group (Table 1S, *supplement*), indicating that the green retention of the upper leaf group in the middle and late stage of grain filling was increased during the critical period of maize yield formation, which potentially provided necessary or additional photosynthetic chemicals for the middle ear, which was beneficial to maize grain filling in saline-alkali farmland (Borrell *et al*. 2001, Abeledo *et al*. 2020). Delaying leaf senescence after flowering can increase dry matter accumulation (Zhang *et al*. 2019). Slowing down the senescence of the bottom leaf group can effectively improve the grain yield and grain number per spike (Kitonyo *et al*. 2018). The main reasons for the higher yield of subsoiling tillage than other treatments were the high photosynthetic rate (Fig. 2) and the leaf area (Fig. 1) significantly better than other treatments. Compared with other treatments, the bottom leaf group in the middle and early stage of growth of subsoiling can effectively delay the senescence rate of leaves and improve the photosynthetic performance, to ensure the normal function of the root system and supply nutrients to the middle and upper leaf groups in time (Pommel *et al*. 2006). The photosynthetic performance of the middle and upper leaf groups was improved, and finally the whole leaf senescence was delayed (Table 2), the mass of the spike increased (Fig. 2S), and the number of grains per spike and 1,000-grain mass significantly increased (Table 3), and the yield increased (Fig. 5; Fig. 5S).

Conclusion: Under the experimental conditions, subsoiling tillage has a good salt suppression effect on coastal saline-alkali farmland. The reduction of soil salt content improves the photosynthetic performance of the bottom leaf group by enhancing the PSII donor–acceptor side performance rather than increasing leaf area. Meanwhile, there is a strong positive correlation between photosynthetic parameters between the bottom and middle leaf groups, as well as between the middle and upper leaf groups. Therefore, the decrease in soil salt content significantly alleviated the salt stress in the bottom leaf group of summer maize and laid the foundation for a strong 'source' of the middle and upper leaf group after flowering. The photosystem performance of the bottom, middle, and upper leaf groups was synergistically improved to maintain their strong photosynthetic performance and long functional duration. Therefore, the subsoiling tillage in coastal saline-alkali farmland can synergistically enhance the photosynthetic performance of different leaf groups of summer maize and increase the yield.

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Appendix 1. Formulae and terms used in the analysis of the O-J-I-P fluorescence induction dynamics curve.

Formulae	Definitions
F_0	Minimal recorded fluorescence intensity
F_m	Maximal recorded fluorescence intensity
t_{Fm}	Time to reach maximal fluorescence intensity F_m
$V_J = (F_J - F_0)/(F_m - F_0)$	Relative variable fluorescence intensity at the J-step
$W_k = (F_k - F_0)/(F_J - F_0)$	definition?
$PI_{ABS} = (RC/ABS)\ [\Phi_{P0}/(1 - \Phi_{P0})]\ [\psi_0/(1 - \psi_0)]$	Performance index on absorption basis
$\Phi_{P0} = TR_0/ABS = [1 - (F_0/F_m)]$	Maximum quantum yield for primary photochemistry (at t = 0)
$\Psi_0 = ET_0/TR_0 = (1 - V_J)$	Probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^- (at t = 0)
$\Phi_{E0} = ET_0/ABS = [1 - (F_0/F_m)]\ \psi_0$	Quantum yield for electron transport (at t = 0)
$ABS/CS_0 \approx \Phi_{P0}$	Absorption flux per CS (at t = 0)
$TR_0/CS_0 = \Phi_{P0}\ (ABS/CS_0)$	Trapped energy flux per CS (at t = 0)
$ET_0/CS_0 = \Phi_{E0}\ (ABS/CS_0)$	Electron transport flux per CS (at t = 0)
$DI_0/CS_0 = (ABS/CS_0) - (TR_0/CS_0)$	Dissipated energy flux per CS (at t = 0)
$ABS/CS_m \approx F_m$	Absorption flux per CS (at t = t_{Fm})
$TR_0/CS_m = \Phi_{P0}\ (ABS/CS_m)$	Trapped energy flux per CS (at t = t_{Fm})
$ET_0/CS_m = \Phi_{E0}\ (ABS/CS_m)$	Electron transport flux per CS (at t = t_{Fm})
$DI_0/CS_m = (ABS/CS_m) - (TR_0/CS_m)$	Dissipated energy flux per CS (at t = t_{Fm})