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EFFECT OF VERTICALLY HETEROGENEOUS SOIL SALINITY ON MORPHOLOGICAL CHARACTERISTICS, BIOMASS ACCUMULATION, ROOT DISTRIBUTION, AND TRANSPIRATION OF SUNFLOWER (HELIANTHUS ANNUUS L.)

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ABSTRACT

Finding out the regulations of crops Morpho-Physiological Characteristics (MPC) to vertical heterogeneous salinity is significant to understand the crop salt tolerance mechanism. An outdoor pot experiment cultivated with sunflower (*Helianthus annuus* L.; *cultivar*: *LD5009*) was conducted at four initial salinity levels (S1: 4.08-9.79, S2: 6.72-11.58, S3: 8.01-13.62, and S4: 10.60-14.31 $dS \cdot m^{-1}$), three types of soil salinity distributions (A-type, greater salinity in lower soil; H-type, homogenous salinity; V-type, greater salinity in upper soil) were manually created and maintained by stratified irrigation in each salinity level. Results show the inconsistent inhibitions of salinity levels and distributions on the sunflower MPC, for S2 compared to S1, the MPC reductions were insignificant in V-type, while the maximum leaf area and flower disc diameter, shoot biomass, and transpiration were significantly decreased in A- and H-types ($P \leqslant 0.05$), while the MPC in V-type decreased over than in A-type and resembled with those in H-type for S3 and S4. Consistent with the phenomena of more root biomass distributed in lower salinity soil in salinity heterogeneous treatments, the MPC closely correlated with the minimum salinity (S_{Min}) in potting soil (R^2=0.72-0.85), S_{Min} in the lower soil improved sunflower growth more than it in the upper soil when $S_{Min} < 9$ $dS \cdot m^{-1}$ (S2), while the opposite effects were presented if $S_{Min} > 9$ $dS \cdot m^{-1}$ (S3, S4). Therefore, the status of S_{Min} and its vertical position might be important factors for crop salt tolerance determination.

Keywords: Vertical salinity heterogeneity; Sunflower; Morphology; Biomass; Root distribution; Transpiration

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Abbreviations

A	Higher salinity in the lower soil layer
H	Uniform salinity distribution
V	Higher salinity in the upper soil layer
S1, S2, S3, and S4	Four salinity levels
DAS	Days after sowing
SD	Soil depth
SL	Soil layer
MPC	Morpho-physiological characteristics, including the leaf area, crop height, stem diameter, and flower disc diameter, shoot and root biomasses, and transpiration of the sunflower in this article
MLA, MH, MSD, and MFD	Maximum leaf area, height, stem diameter, and flower disc diameter
CT	Cumulative transpiration of sunflower during the period of pot weight measurement
SB, RB	Shoot biomass and root biomass
RDW	Root dry weight
R_{Top}, R_{Mid}, and R_{Bot}	The ratios of the RDW in the top, middle and bottom SLs to the total RDW
SHI	Salinity heterogeneity index
S_{Top}, S_{Mid}, and S_{Bot}	Mean of soil salinity in the top, middle and bottom SLs during the period of sunflower growth (positional salinity heterogeneity indices)
S_{Mean}, S_{Rmean}	Arithmetic mean of soil salinity at the top, middle and bottom SLs and the mean of soil salinity of the three SLs weighted by the RWD in each SL
S_{Max}, S_{Min}	Maximum and minimum soil salinity of the top, middle, and bottom SLs

INTRODUCTION

Soil salinity is among the detrimental abiotic factors that threaten natural and agricultural ecosystems (Türkan and Demiral, 2009; Deinlein *et al*., 2014). Approximately 80 million hectares of cultivated land worldwide have suffered from soil salinization (Zhang *et al*., 2012), which has caused economic losses of over 10 billion USD annually (Qadir *et al*., 2014). Meanwhile, salinity heterogeneity is widespread in saline fields resulting from leaching of rain and irrigation, soil evaporation, crop root uptake, and groundwater fluctuation (Bazihizina *et al*., 2012a, b; Feng *et al*., 2017). In particular, for vertical soil salinity heterogeneity, studies indicated the maximum soil salinity was three to several hundred times higher than the minimum value within a vertical soil depth of 1 meter in various saline soils (Bazihizina *et al*., 2012b).

Although salinity heterogeneity exists both horizontally and vertically in soils (Bazihizina *et al*., 2012b; Quiñones Martorello *et al*., 2017), most of the studies concentrated on the plant physiological feedback to horizontal salinity heterogeneity. These studies mainly applied split-root experiments in greenhouses to divide root systems into several equal portions, each portion was treated by different salt concentrations (Shani *et al*., 1993; Flores *et al*., 2002; Bazihizina *et al*., 2012a, b; Reef *et al*., 2015; Sun *et al*., 2016; Feng *et al*., 2017). In contrast to uniform salinity treatments, alleviation phenomena were found in horizontally heterogeneous salinity treatments, such as the greater biomasses of shoots and roots in less saline soil were observed for both halophytic and glycophytic plants (Bazihizina *et al*., 2012a, Sun *et al*., 2016). These phenomena are mainly related to the crops physiological mechanism under heterogeneous salt conditions (Kong *et al*. 2012, 2016), including 1) increase the root water absorption in the low-salt root zone, 2) transport Na^+ in the high-salt root zone to the low-salt root zone through the phloem, 3) exclude Na^+ out of the root system through Na^+/H^+ reverse transportation of the plasma membrane, 4) decease the Na^+ concentration in the leaves to maintain the photosynthetic rate, etc.

However, unlike horizontal salinity treatments, for most plants, the vertical nonuniformity of root distribution and water-absorbing capacity increase the complexity of plant response to vertical salinity heterogeneity (Bazihizina *et al*., 2012b; Quiñones Martorello *et al*., 2017). Moreover, due to the geotropism of root development, it is difficult to control longitudinal water-salt migration in the root zone while ensuring natural root growth at the same time. Only a few attempts have been conducted to construct vertically heterogeneous soil salinity, but some inconsistent conclusions have been drawn for different plants and treatments (Northey *et al*., 2006; Quiñones Martorello *et al*., 2017). Shalhevet and Bernstein (1968) separated the root zone of alfalfa into two to three horizons by wax membranes and found that the plant growth reduction was related to the mean salinity of the two portions of the root system; the water uptake was increased in each portion when half of the root system was under salinity treatment. However, using similar methods, Bingham and Garber (1970) found that the top portion of the corn root system was considerably more salt-sensitive than other portions and that corn was able to withstand considerable salinization as long as at least one-third of the root zone was kept salt free. Since then only a few studies have been conducted because the similar horizontal barriers (e.g., wax membranes) were difficult to apply and maintain during the experiments, and the root resistance through the barriers differs from that in real soil matrices (Shalhevet and Bernstein, 1968; Bazihizina *et al*., 2012b). Quiñones Martorello *et al*. (2017) had used stratified irrigation method with different salinity solutions to mimic vertical salinity heterogeneity in two types of the woody root zone of *Salix matsudana x S. alba* (low drought and salinity tolerance with adventitious stem roots) and *E. camaldulensis* (high salinity tolerance with a taproot and many lateral roots), and they found greater negative effects of salinity on plants when higher salt concentrations were in deeper soil layers (SLs), and the salt tolerance thresholds depended on the distribution of salinity heterogeneity than on the average concentration of soil salinity in the root zone.

The differences in the above conclusions might be influenced by the differences in plant salt tolerance and the root distribution, stress degree and heterogeneity distribution of the salinity treatments; the universal conclusions remain to be explored by comprehensively considering these factors in experimental designs. Therefore, a moderate-salt-tolerance economic crop (Bhatt and Indirakutty, 1973; Allan *et al*., 1998; Zeng *et al*., 2016), sunflower (*Helianthus annuus* L.; cultivar: LD5009) was chosen to explore the influences of vertical salinity heterogeneity. Sunflower is a global annual oilseed crop cultivated on nearly 25 million hectares and has 8% share in the oilseed market, and it has promised to maintain stable yields across a variety of environmental condition (Zeng *et al*., 2014; Zeng *et al*., 2016; Badouin *et al*., 2017; Ma *et al*., 2017; Hussain *et al*., 2018). Three common vertical distributions of salinity heterogeneity were considered, including A (higher salinity in the lower SL), H (uniform salinity distribution) and V (higher salinity in the upper SL) types. Four salinity grades distinguished by the average salinity status of the root zone was applied and ranged from slight to heavy salinity stress for sunflower. Heterogeneous soil salinity in our study was achieved by prefilling soil with a specified salinity in different SLs, and a stratified irrigation method was used to maintain salinity heterogeneity. This method was relatively simple for experimental operation purposes, and horizontal barriers were not used for salinity

heterogeneity control in this experiment, so there was no external physical resistance to root growth.

The objectives of this study were to test two hypotheses: (1) the MPC of sunflower (including shoot morphology and biomass, root distribution, and transpiration) will be affected by vertically heterogeneous soil salinity, and (2) the alleviation degree to which the effects of vertical salinity heterogeneity on the MPC of crops will be changed in different salinity levels. Additional aims were to (1) determine the key salinity factor for crop salt tolerance by proposing three types of heterogeneity indices (including positional, average, and extreme salinity) and (2) establish quantitative relationships for the MPC of sunflower.

MATERIALS AND METHODS

Experimental site: To ensure a normal natural light and temperature for sunflower growth, the pot experiment was carried out by outdoor planting and was conducted in 2013 at the Yonglian experiment station in the Hetao irrigation district in Inner Mongolia, China (108°0'15.3"E, 41°4'2.16"N). The experimental area is in the temperate zone with a continental semi-arid and arid monsoon climate, and the meteorological data during the experiment were automatically monitored by the meteorological station within the experiment site (Table 1).

Table 1. Meteorology observations during the experimental period in 2013.

Month	Maximum temperature (°C)	Minimum temperature (°C)	Mean temperature (°C)	Relative humidity (%)	Wind speed ($m \cdot s^{-1}$)	Solar radiation ($W \cdot m^{-2}$)	Precipitation (mm)	Evaporation (mm)
4	29.7	-10.3	9	44.1	2.7	153.7	0	104.1
5	31.7	4.5	7.7	47.7	2.3	222.6	16.6	157.2
6	35.6	8.4	7.1	58.2	1.8	220	25.4	121.6
7	35.2	11.7	7.1	69	1.2	222.5	8.8	121.3
8	35.2	5	7.7	69.6	1.3	215.9	27.6	119.8
9	30.2	-1.9	8.7	63.8	1.5	182	24.4	97.9
10	28.8	-8.5	8.5	59.1	1.4	152.6	2.6	72.7

Experimental system design

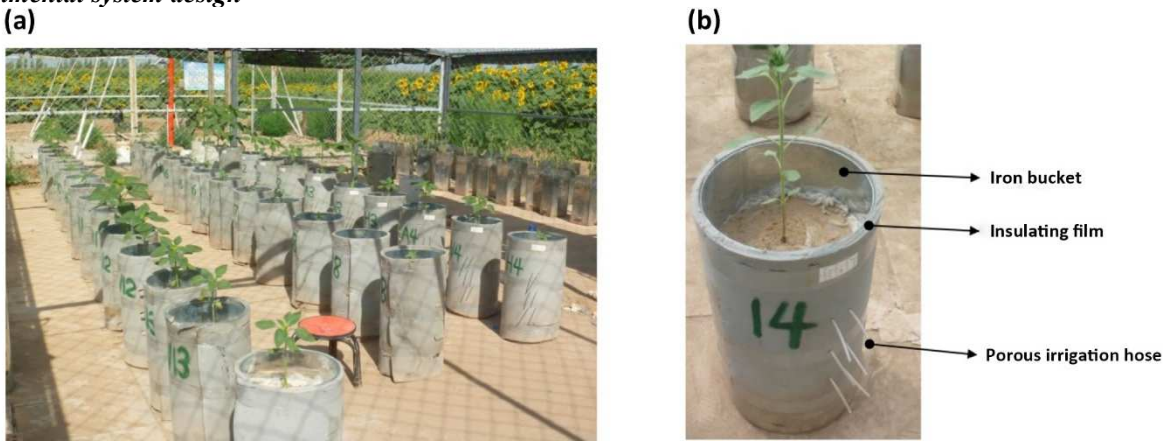

Figure 1. View of the experimental scene (a) and pot device (b).

The experimental soil was taken from the tillage soil in nearby farmland and was silty clay loam soil, consisting of 11.64% sand, 49.81% silt, and 38.56% clay. The soil was divided into different parts by its EC_e ($dS \cdot m^{-1}$), which was calculated from $EC_{1:5}$ ($EC_e = 7.4 \times EC_{1:5}$) (Zeng *et al*., 2016); $EC_{1:5}$ ($dS \cdot m^{-1}$) was the electrical conductivity of the soil supernatant solution (the mixed volume rate of soil with deionized water was 1:5). The air-dried fresh soils were sieved with a 2 mm screen, and then these different-salinity soils were evenly mixed with deionized water according to the designed salinity (shown in Table 2). Meanwhile, the fertilizers urea (597 $kg \cdot ha^{-1}$) and calcium superphosphate (936 $kg \cdot ha^{-1}$) were mixed into the soils, and the soil water content was adjusted to the field capacity (~ 25.6% dry weight of soil). The new mixed soils were filled layer by layer according to the experimental design (see Table 2) into a cylindrical iron bucket (30 cm in diameter, 40 cm in height, shown in Figure 1b.). The filling depth was 30 cm, and the soil density was controlled at 1.3 $g \cdot cm^{-3}$. The soil surface was covered with a transparent film to slow down the soil evaporation, and each pot was wrapped with a 2 cm thick

insulating film to reduce heat exchange between the potting soil and surrounding air (shown in Figure 1b). Additionally, to effectively control the soil salt and water status of the pots, a simple rain roof was installed on the top of pots and was expanded only on rainy days.

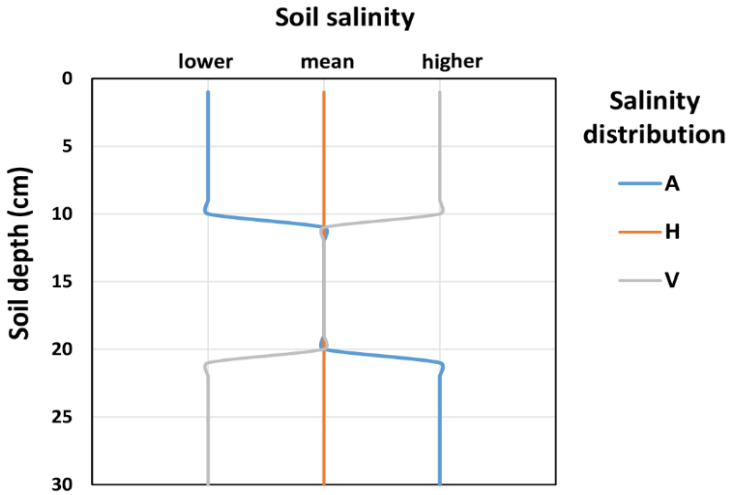

Figure 2. Schematic diagram of soil salinity vertical heterogeneity.

Constant salinity was controlled within each 10 cm soil starting at the soil surface, designated 0-10 cm, 10-20 cm, and 20-30 cm as the top, middle, and bottom soils. The vertical salinity gradients of the three SLs were set into three categories: A-, H-, and V-type (as shown in Figure 2.). Four salinity levels were used for each type of salinity gradient; therefore, there were 12 salinity treatments, and three replicates were conducted in each treatment. The initial salinity status of each SL (shown in Table 2) was measured during the soil filling process.

Table 2. Initial salinity (EC_e, saturated electrical conductivity) of each treatment in the pot experiment.

Salinity level	Soil depth (cm)	Initial salt distribution/ Mean ± SD (EC_e, $dS \cdot m^{-1}$)		
		A	H	V
S1	2.5	4.28 ± 1.84	6.3 ± 1.51	9.69 ± 2.46
	7.5	4.33 ± 1.82	6.52 ± 1.24	9.72 ± 2.45
	15	7.08 ± 1.02	6.57 ± 1.26	7.04 ± 1.07
	25	9.79 ± 2.44	6.76 ± 1.05	4.44 ± 1.57
S2	2.5	6.72 ± 0.64	8.87 ± 0.93	11.54 ± 0.73
	7.5	6.75 ± 0.67	8.91 ± 0.93	11.58 ± 0.71
	15	9.22 ± 0.70	8.96 ± 0.97	9.14 ± 0.78
	25	11.50 ± 0.85	9.04 ± 1.02	6.81 ± 0.44
S3	2.5	8.05 ± 1.53	10.52 ± 0.40	13.51 ± 1.84
	7.5	11.18 ± 1.69	10.58 ± 0.38	13.59 ± 1.96
	15	12.35 ± 3.11	10.76 ± 0.34	10.74 ± 0.38
	25	13.62 ± 2.06	10.89 ± 0.39	8.01 ± 1.49
S4	2.5	10.73 ± 1.01	12.51 ± 1.11	14.16 ± 1.01
	7.5	10.79 ± 0.95	12.55 ± 1.10	14.18 ± 0.97
	15	12.75 ± 1.14	12.59 ± 1.11	12.71 ± 1.23
	25	14.31 ± 0.88	12.68 ± 1.08	10.60 ± 1.04

Sunflower (Helianthus annuus L.; cultivar: LD5009) seeds, a commercial variety, were sown on June 18, 2013, and harvested on Sept. 29, 2013. The hole sowing method was used in this experiment. Three seeds were initially sown in each hole, and the sowing depth was 2-3 cm. The seedling representing average growth status was retained, and the other two seedlings were cut off by scissors when the first pair of cotyledons appeared. Foliar fertilizer was added during the budding and flowering stages of sunflower.

To reduce the vertical migration of soil salt and water in the pots, the root zone of the sunflower was

layer-irrigated through 5 mm diameter porous irrigation hoses at depths of 5, 15, and 25 cm below the surface (shown in Figure 1b.). The water was slowly injected by using a syringe, and the hoses were opened only during irrigation. The potted soil water content was maintained by 70-90% of the field capacity, the irrigation amounts used in the experiment were based on the daily (or two-day) transpiration measurements of the sunflower, and the irrigation amount of each SL was determined by the water consumption ratio of the corresponding depth, which was calculated from two consecutive soil water measurements.

Soil salt and water measurements: The dynamic monitoring of soil water and salt was performed by soil stratification sampling, and the sampling holes were located at 2.5, 7.5, 15, and 25 cm below the soil surface. The soil (~15 g) was carefully collected by a soil-specific drill (nearly 1 cm in diameter) on days after sowing (DAS) 1, 14, 41, 60, 80, and 96. The soil salt content was represented by EC_e ($dS \cdot m^{-1}$), and the measurement method is described in the last section. The soil volumetric water content (θ_v) was determined by fresh soil oven drying 8 h at 105 °C.

Dynamic observations of morphological characteristics (MPC): The MPC of leaf area, crop height, and stem and flower disc diameter of sunflowers were measured dynamically. The length (L) and width (W) of leaves were measured at DAS 42, 50, 59, 67, 70, 82, 90, 96 and 99, and the leaf area was equivalent to the area of a circle with a diameter of D = (L + 2W) / 3 (Zhao, 2015). The height of each sunflower was measured once every alternate day from emergence until the observations were stable. The height before flowering was equal to the vertical distance between the soil surface and the sunflower top, while after flowering, the crop height was the vertical distance between the soil surface and the flower disc bottom. The diameter of the stem was measured once every alternate day from DAS 20; the values were determined 1 cm above the soil surface. The diameter of the flower disc was measured once every alternate day from DAS 44, and the measured values were determined as the mean of the minimum and maximum diameters obtained in different directions. Additionally, the times of the emergence, budding, flowering, and maturity stages of sunflowers under different treatments were recorded.

Transpiration measurements: The weight of each pot was measured at 8:00-9:00 am once every alternate day from DAS 12 to DAS 77. Then, the transpiration of the sunflower during this period was calculated by mass conservation: the evaporation was ignored because the soil surface in pots was covered by transparent films, therefore, the transpiration was the difference between two consecutive pot weights minus the irrigation amount during this period.

Shoot and root biomass measurements: The shoots of sunflower were retrieved and divided after harvest according to the different organs of leaves, stem, flower disc, and seeds. The fresh organs were placed in an oven for deactivation of enzymes 30 min at 105 °C and then oven-dried to constant weight at a constant 80 °C. The dry weight of organs was measured when it had cooled to room temperature. The soil in the pots was excavated in 5 cm layers starting at the soil surface, and the roots were manually selected, washed with deionized water and sieved with a 0.2 mm screen. The clean roots were then placed in an oven and dried at a constant 70 °C to constant weight. The dry weight of the roots in each SL was measured.

Salinity heterogeneity characterization: To characterize the heterogeneity of soil salinity, three types evaluation indices of soil salinity heterogeneity were considered: firstly, the positional heterogeneity indices, which is the mean of soil salinity at the top (0-10 cm), middle (10-20 cm), and bottom (20-30 cm) soils throughout the sunflower growth stage (S_{Top}, $S_{Middle,}$ and S_{Bottom}, respectively), calculated via Eqs. 1-3; the second was the average heterogeneity index, which includes the arithmetic mean value of the three positional heterogeneity indices (S_{Mean}), as well as the weighted mean value of the three positional heterogeneity indices based on the root dry weight (RDW) density in each SL (S_{RMean}), calculated via Eq. 4-5; and the third was the extreme index, which includes the maximum and minimum EC_e values of the positional heterogeneity index (S_{Max} and S_{Min}, respectively), calculated via Eqs. 6-7.

$$S_{Top} = (Mean(EC_{e,2.5,j}) + Mean(EC_{e,7.5,j}))/2 \quad (1)$$

$$S_{Mid} = Mean(EC_{e,15,j}) \quad (2)$$

$$S_{Bot} = Mean(EC_{e,25,j}) \quad (3)$$

$$S_{Mean} = Mean(S_{Top}, S_{Middle}, S_{Bottom}) \quad (4)$$

$$S_{RMean} = Mean(S_{Top} \times R_{Top}, S_{Mid} \times R_{Mid}, S_{Bot} \times R_{Bot}) \quad (5)$$

$$S_{Max} = Maximum(S_{Top}, S_{Mid}, S_{Bot}) \quad (6)$$

$$S_{Min} = Minimum(S_{Top}, S_{Mid}, S_{Bot}) \quad (7)$$

In Eqs. 1-3, $EC_{e,i,j}$ is the soil EC_e at a soil depth of i cm in the j-th measurement; R_{Top}, $R_{Mid,}$ and R_{Bot} are the ratios of the RDW in the top, middle and bottom soils, respectively, to the total RDW.

Statistical analysis: Statistical analyses were achieved by using R version 3.5.1 (Copyright (C) 2018 the R Foundation for Statistical Computing ISBN 3–900,051–07-0). The least significant difference (LSD) at a 0.05 level of probability was applied to detect differences among the measured variables in the 12 salinity treatments with four salinity levels and three types of salinity distributions. Additionally, the coefficient of

determination (R^2) was applied to characterize the correlations between the morpho-physiological responses of sunflower and the soil heterogeneity indices (SHIs).

RESULTS

Soil salinity distributions: The overall EC_e values in different SLs based on six measurements during the growth period of sunflower are shown in Figure 3, the dynamic fluctuations were existing in each potted SL, especially in top and bottom SLs. Compared with the initial salinity status (at Das 1), the highest median EC_e values of the top soil (SD = 2.5 and 7.5 cm) in all measurements increased by nearly 1-5 $dS \cdot m^{-1}$ for the H and V soil types, while the value increased 4-6 $dS \cdot m^{-1}$ for the A-type. In contrast to the upper soil, the highest median EC_e values of the bottom soil (SD = 25 cm) increased by 6-7.5 $dS \cdot m^{-1}$ for the V-type, which was slightly higher than the increases observed for the A (5-7 $dS \cdot m^{-1}$) and H (5-6.5 $dS \cdot m^{-1}$) types. The average EC_e values of all measurements (the median and main distribution (between Q1 and Q3 of the boxplots) of EC_e boxplots) show that in each SL in the higher-salinity treatments were generally higher than those in in the lower-salinity treatments. The lower limit (Q1) of the EC_e main distribution for the three salinity distributions gradually improved with increasing salinity levels: EC_e was nearly 4 and 10 $dS \cdot m^{-1}$ for levels S1 and S2, respectively, while EC_e was greater than 9 and 11.5 $dS \cdot m^{-1}$ for levels S3 and S4, respectively. Additionally, the median values and main distributions of EC_e values throughout the whole sunflower growth period essentially maintained the initial trends (except in several treatments for the soils at SD = 2.5 and 25 cm), the median values of the EC_e boxplots for different salinity distributions at top soil (SD = 2.5 cm and SD = 7.5 cm) followed the order V > H > A; at bottom soil (SD =25 cm), the order A > V > H was obtained, and similar results were found at middle soil (SD = 15 cm), as shown in Figure 3.

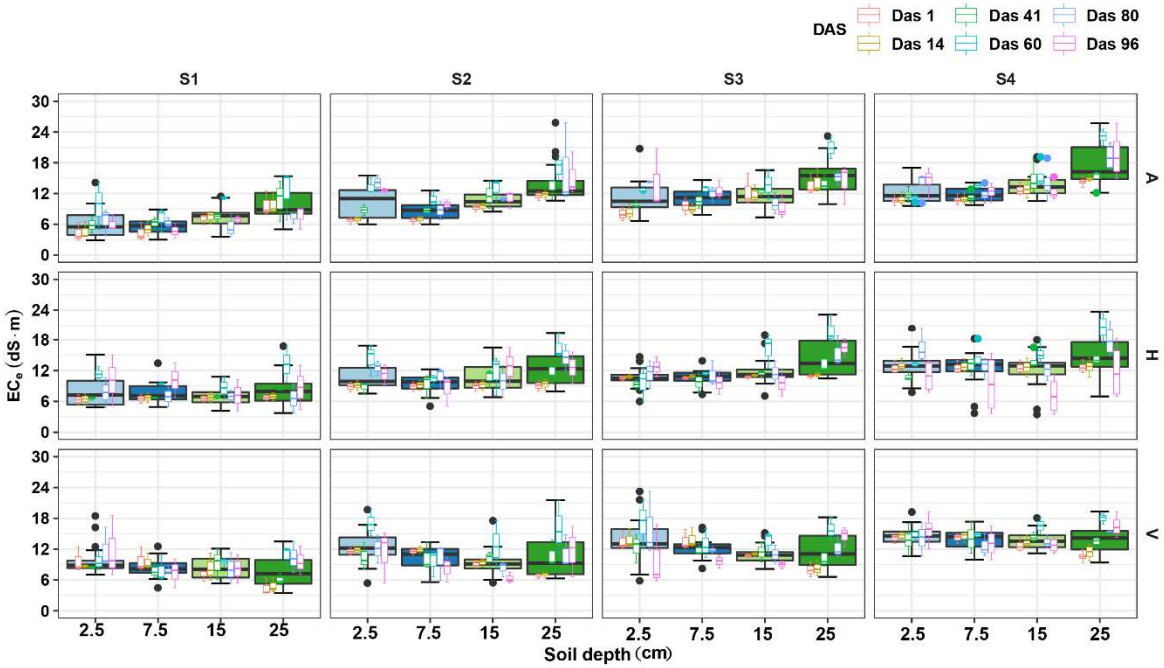

Figure 3. Statistical results of soil salinity (EC_e) measurements on DAS 1, 14, 41, 60, 80 96 (small boxplots) and average status of all measurements (big boxplots) at different soil depths (SD =2.5, 7.5, 15, and 25 cm) with different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. The 25th percentile (Q1), medians, and 75th percentile (Q3) of the estimation objects were represented by the upper, middle bold lines, and lower edges of the boxes, respectively; the vertical lines of the boxes indicated the estimation objects extend to 1.5 × (Q3 - Q1).

Shoot morphology and biomass response: Clear differences in the times for the seed germination and seedling stages of sunflower were observed for different salinity treatments (in Figure 4). The time of seed germination slowly increased with increasing soil salinity level when the salinity level was lower than S4, while the time abruptly increased to DAS 12-13 in the S4 treatments with H and V soil salinity distributions, and the germination times for A-type were shorter than those for H- and V-types at the same salinity level. Moreover, the time to reach the seedling stage of sunflower was also increased with an increase in salinity level. The longest

increase time was obtained in the H-type when the salinity level was lower than S4 (39, 47, and 45 days for levels S1, S2, and S3), respectively; however, for the S4 salinity level, the longest increase (46 days) was observed in the V-type. No significant differences (in Figure 4) of sunflower stage times among the different treatments after seedling, but sunflower could not enter the flowering stage in V-type when the salinity level reached S4.

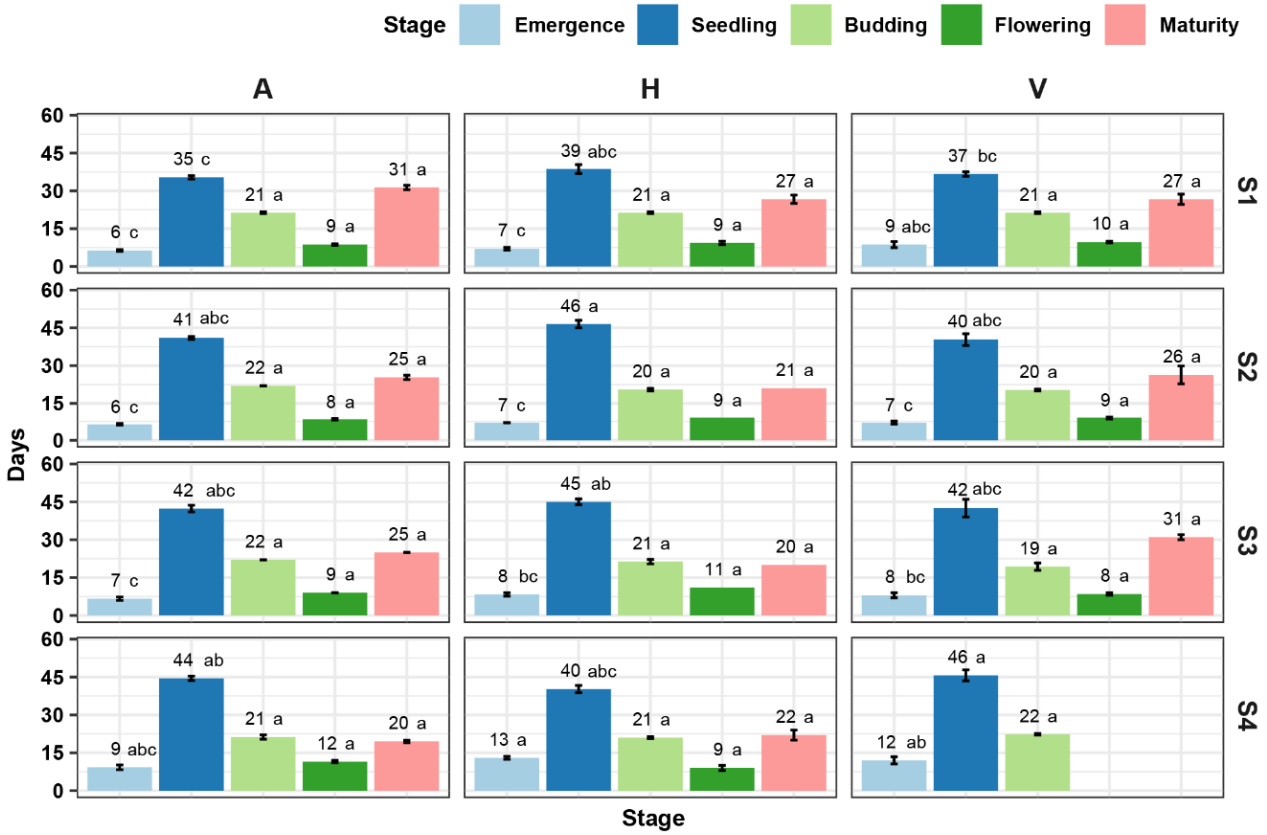

Figure 4. Time periods for the seed germination and growth stages of sunflower in different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE (in levels S3 and S4, the times for sunflower flowering and maturity in H-type were measured from one sample, where n=1). The letters above the bars represent significant differences among the 12 salinity treatments for each growth stage of sunflower (LSD test; P ⩽ 0.05). The different numbers at the ends of the bars represent the days of sunflower each growth stage.

The dynamic characteristics of sunflower morphology in different treatments are presented in Figure 5. Leaf area increased first and then decreased slowly, reaching a maximum near DAS 75. The height and stem diameter of sunflower grew rapidly at first and then gradually stabilized after DAS 75 and 60, respectively, while the flower disc grew linearly throughout the measuring period. The growth of sunflower morphological features was gradually inhibited with increasing soil salinity level; for example, the maximum leaf area, height, stem diameter and flower disc diameter of sunflower in salinity level S4 decreased by 75%, 40%, 50%, and 55% respectively compared to those in salinity level S1. Moreover, at the S2 salinity level, the MPC in the V type were larger than those in the A-type, and the smallest MPC were obtained in the H-type, particularly, the maximum of leaf area and flower disc diameter of sunflower in the V-type was significantly greater than those in the H-type (P ⩽ 0.05). In contrast to the S2 salinity level, the maximum MPC of sunflower at the S3 salinity level were observed in the A-type, and the growth of morphological features in the H- and V-types were similar. Additionally, at the S4 salinity level, minor differences in MPC were observed between the A- and H-types, while minimum morphological feature growth was obtained in the V-type.

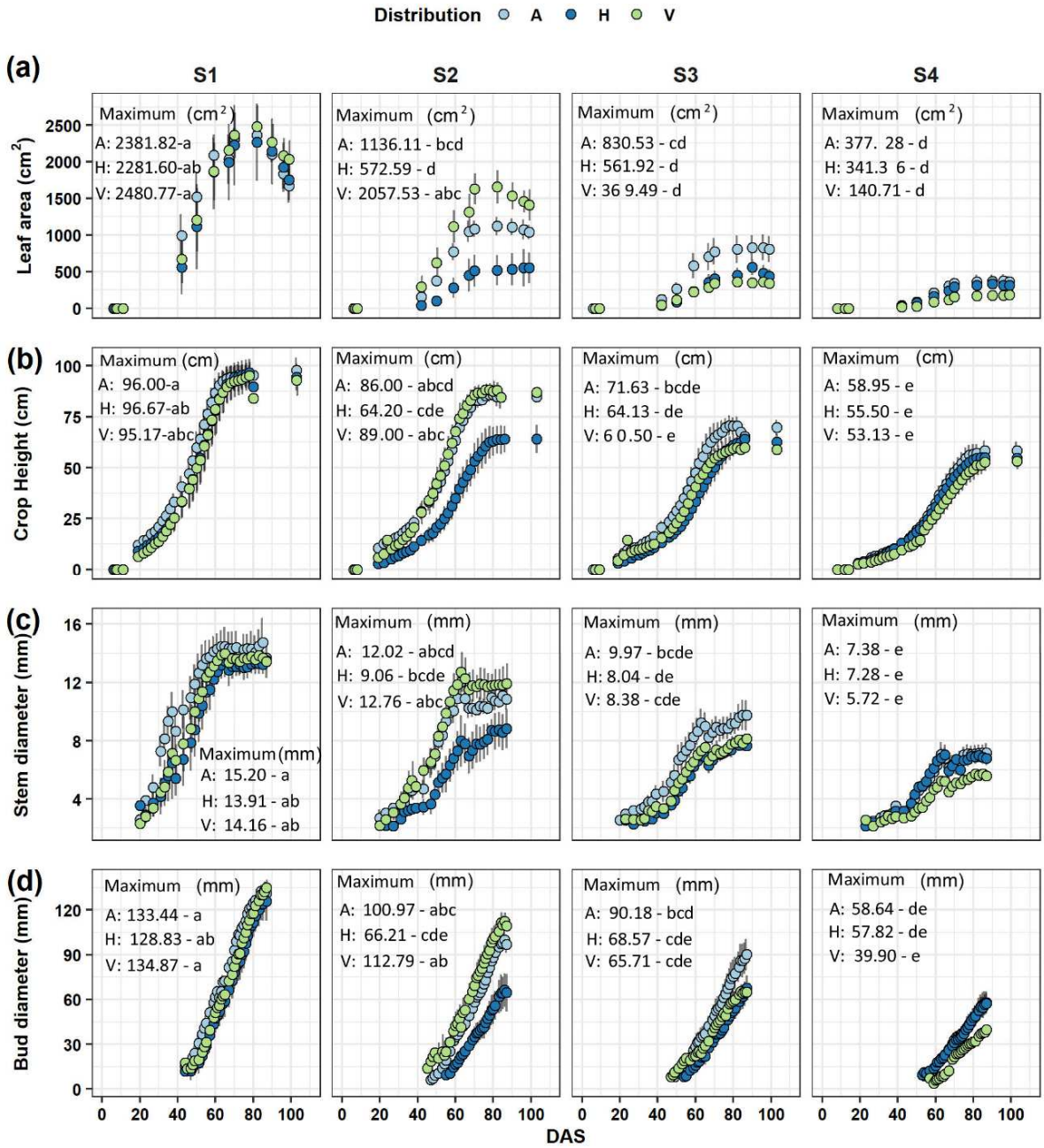

Figure 5. Dynamic growth of leaf area, height, stem diameter, and flower disc diameter of sunflower under different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE. The maximum MPC values (mean values of three replicates) in different salinity distributions are listed in the top left of each figure. Significant differences in these values among the 12 salinity treatments are indicated by letters after the maximum MPC values (LSD test; P ⩽ 0.05).

The total shoot biomass of sunflower (in Figure 6) gradually decreased with increasing salinity levels beyond S1. All organ biomasses of sunflower shoots at the S2 level were considerably decreased in the A- and H-types, except stem biomass in the A-type, but there was no significant reduction in biomass for all organs in the V-type. However, all sunflower shoot organ biomasses significantly decreased in all salinity distributions when the salinity level was greater than S2, while the organ biomass reduction in the A-type was smaller than that in the H- and V-types. Moreover, the organ biomass distributions of sunflower shoots were different at different salinity levels and distributions, especially the biomass distributions of reproductive organs. At level S1, the distribution coefficients of the vegetative organs and reproductive organs of sunflower

were similar in the three salinity distributions. However, at level S2, the partition coefficients of flower discs increased but the partition coefficients of seeds decreased in the A- and H-types, while the partition coefficients of flower discs changed little and the partition coefficient of seeds increased in the V-type. At level S3, the partition coefficients of discs and seeds in A-type did not change significantly compared with S2, but the partition coefficient of flower discs increased, and the partition coefficient of seeds decreased in the H- and V-types. The seed partition coefficients at level S4 were reduced in the three types of salinity distributions: the order was A > H > V.

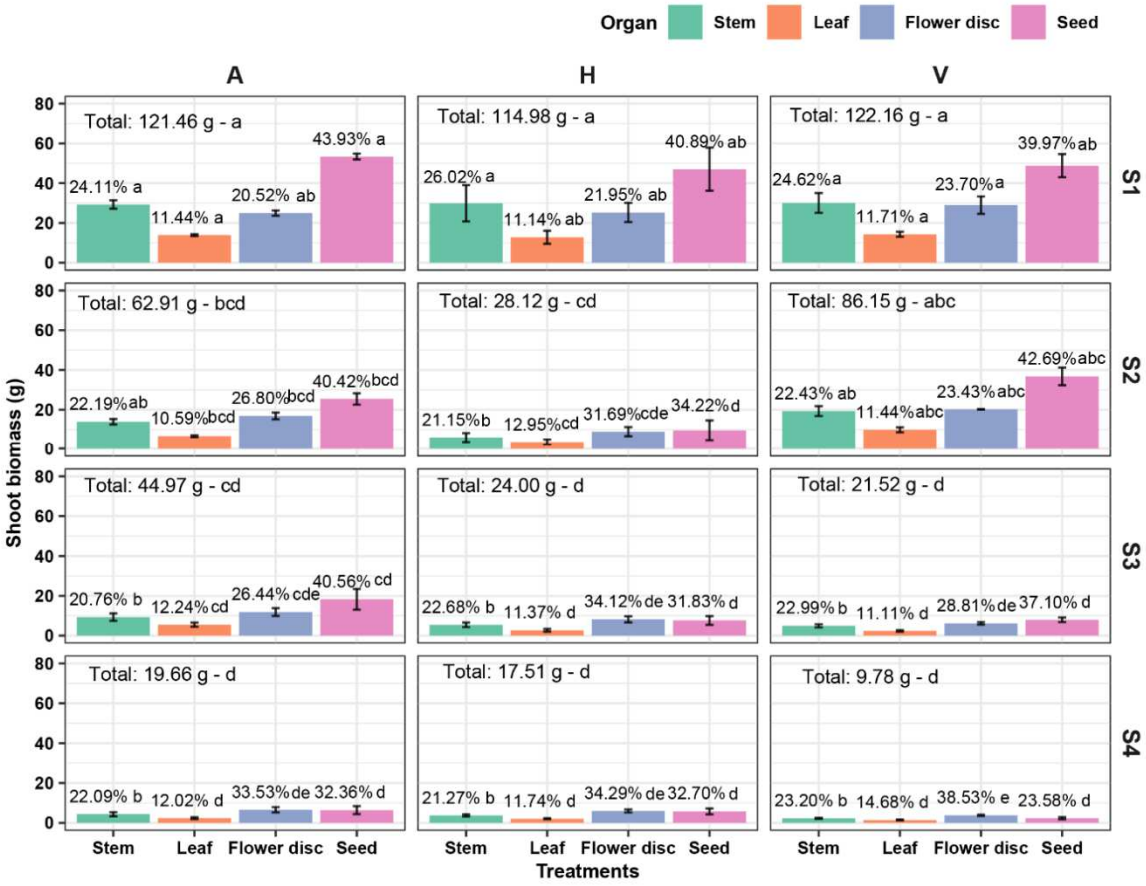

Figure 6. Biomass of stem, leaf, flower disc, and the seed of sunflower at harvest in different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE. The total shoot biomass of sunflower (mean value of three replicates) in each salinity treatment is listed in the top left of each figure. The letters represent significant differences of 12 salinity treatments for organ and total biomass of sunflower shoot (LSD test; P ⩽ 0.05). The different percentages at the ends of the bars represent the relative proportion of each shoot organ.

Root distribution and transpiration: The total RDW (in Figure 7) gradually decreased with increasing soil salinity; in particular, when the salinity level was over S3, the total RDW decreased significantly. Although there were no obvious differences in total RDW among different salinity distributions at the same salinity level, the maximum significant reduction (71.85%) in total RDW for the whole soil profile was found in the H-type when the salinity level was S2 compared with the that for S1, and at the S4 salinity level, the root biomass in the V-type salinity distribution was less than that in the other salinity distributions. Meanwhile, in the A-type, the RDW at the soil depth of 0-10 cm accounted for 84.19%, 89.14%, 96.21%, and 92.45% of the total root system at levels S1, S2, S3, and S4, respectively; these values were higher than those in other salinity distributions except in V-type at the S2 level. In the V-type, the decreases in RDW at a soil depth of 0-5 cm were 67.84% and 91.25% at levels S3 and S4 respectively relative to that for S1; these values were greater than those in the other two salinity distributions, but the relative distributions of RDW at a soil depth of 20-30 cm (2.61% in S3) and 10-20 cm (10.51% in S4) were higher than those in other salinity distributions.

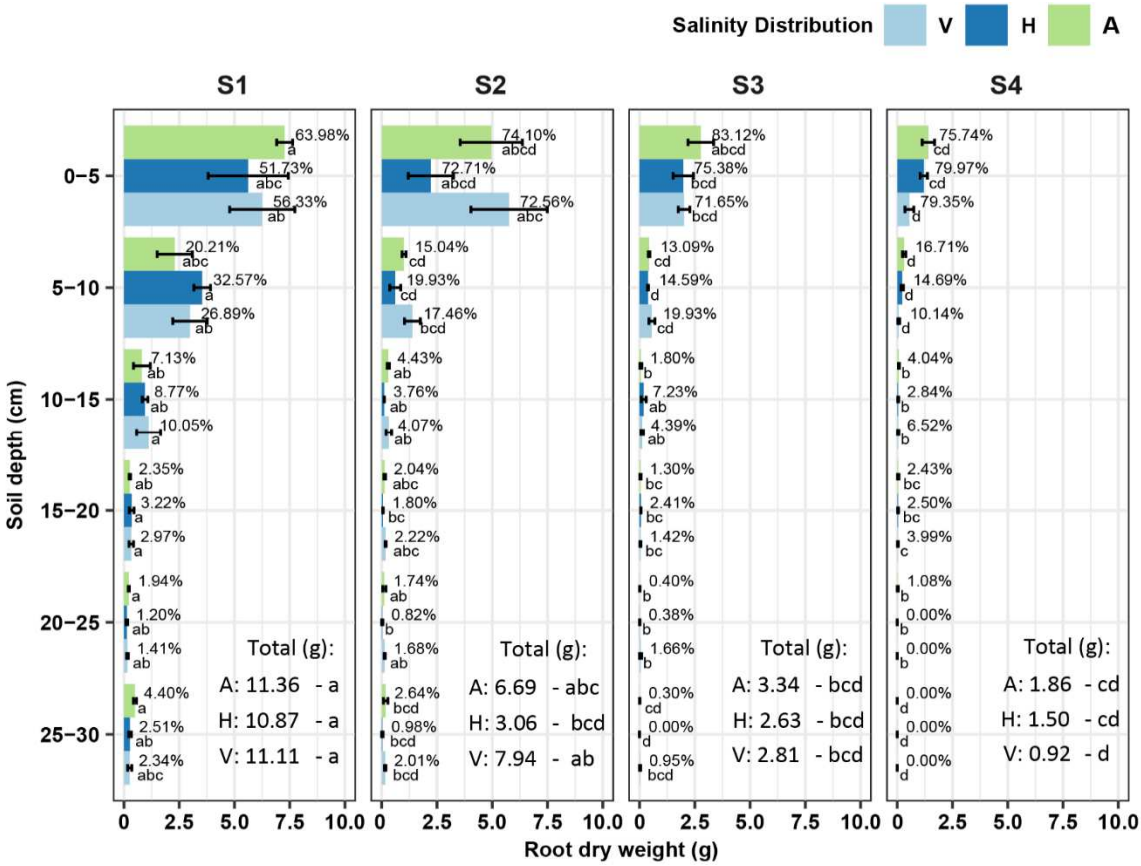

Figure 7. Distributions of root dry weight (RDW) of sunflower under different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE. The total root biomass (mean value of three replicates) in each salinity treatment is listed in the bottom right of each figure. The letters at the ends of the bars and after the total root biomass values indicate significant differences among the 12 salinity treatments (LSD test; P ⩽ 0.05). The different percentages at the ends of the bars represent the relative proportion of RDW distributed in each SL.

The irrigation amount (in Figure 8) increased during the sunflower growth period but decreased with increasing soil depth. There were no obvious differences in total irrigation amounts among different salinity distributions at the same salinity level. However, the irrigation amount for each SL decreased with increasing salinity level; in particular, for salinity levels S3 and S4, the total irrigation amounts at a soil depth of 20-30 cm were less than 400 cm^3. The irrigation amount for each SL was similar among different salinity distributions at the S1 salinity level. However, at the S2 salinity level, the irrigation amounts required for all SLs in the V-type were higher than those in the A-type, and the minimum irrigation amounts were required in the H-type. In contrast to S2, the irrigation amounts for each SL in the A-type at S3 level were higher than those in the V-type, and the minimum amounts were also required in the H-type. Small irrigation amounts were required for sunflower in all salinity distributions at the S4 salinity level, especially for sunflower in the V-type.

The transpiration process of sunflower (Figure 9) increased rapidly after DAS 40, and cumulative transpiration (CT) reached 20 ($\times 10^{-3}$ m^3) at the S1 salinity level. There was no obvious difference in the CT of sunflower among salinity distributions at the same salinity level, while CT gradually decreased with increasing salinity level; for instance, CT was less than 0.5 ($\times 10^{-3}$ m^3) in the treatment with an S4 salinity level and a V-type distribution. The CTs of sunflower were relatively similar among the three types of salinity distribution at the S1 salinity level. However, at the S2 level, the CT of sunflower in the V-type was higher than that of sunflower in the A-type, and the minimum CT was found in the H-type. At the S3 level, the CT of sunflower in the A-type was higher than that of sunflower in the V- and H-types. In addition, at the S4 salinity level, the CTs of sunflower in the three types of salinity distributions were similar, while the CT of sunflower in the V-type was lower than those in the A- and H-types after DAS 65.

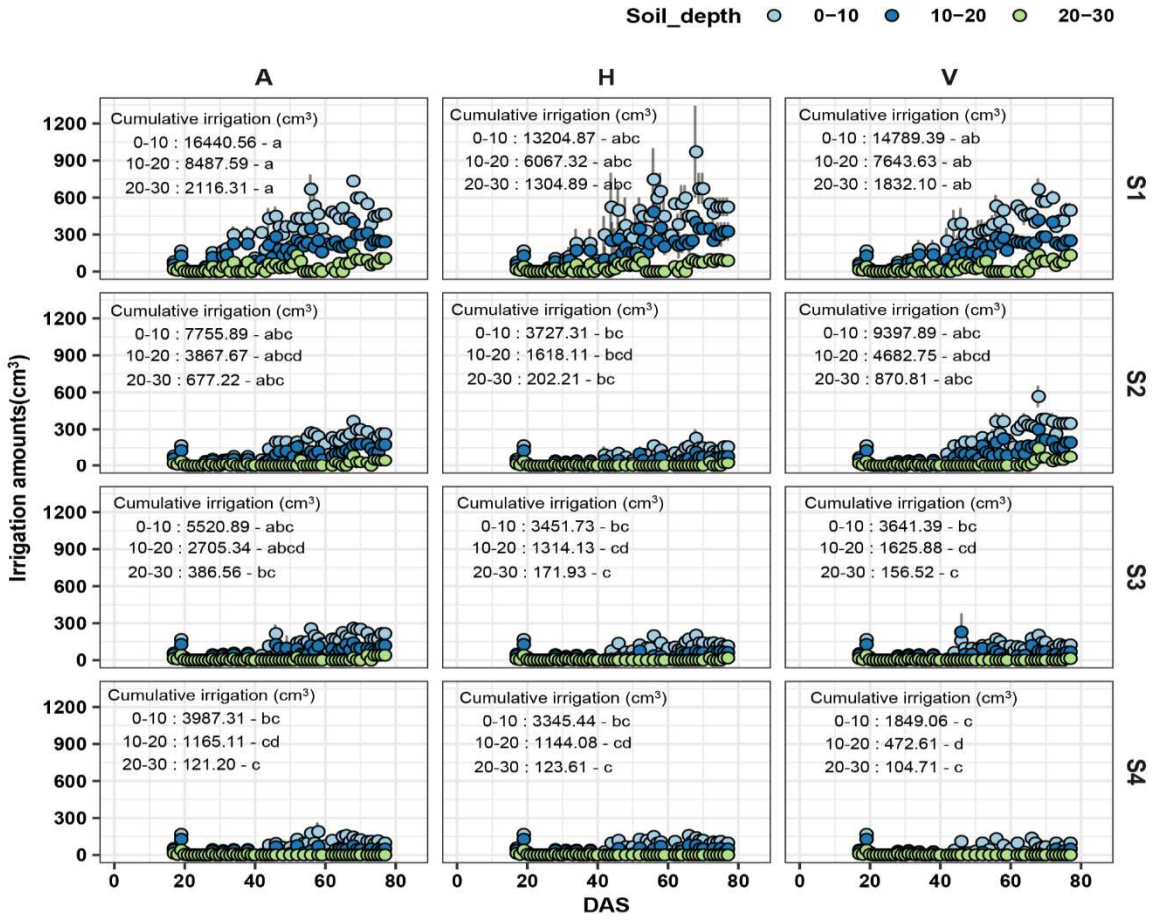

Figure 8. Irrigation amounts for each SL under different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE. The cumulative irrigation (mean value of three replicates) for each salinity treatment is listed in the top left of each figure. The letters after the cumulative irrigation values indicate significant differences among the 12 salinity treatments (LSD test; P ⩽ 0.05).

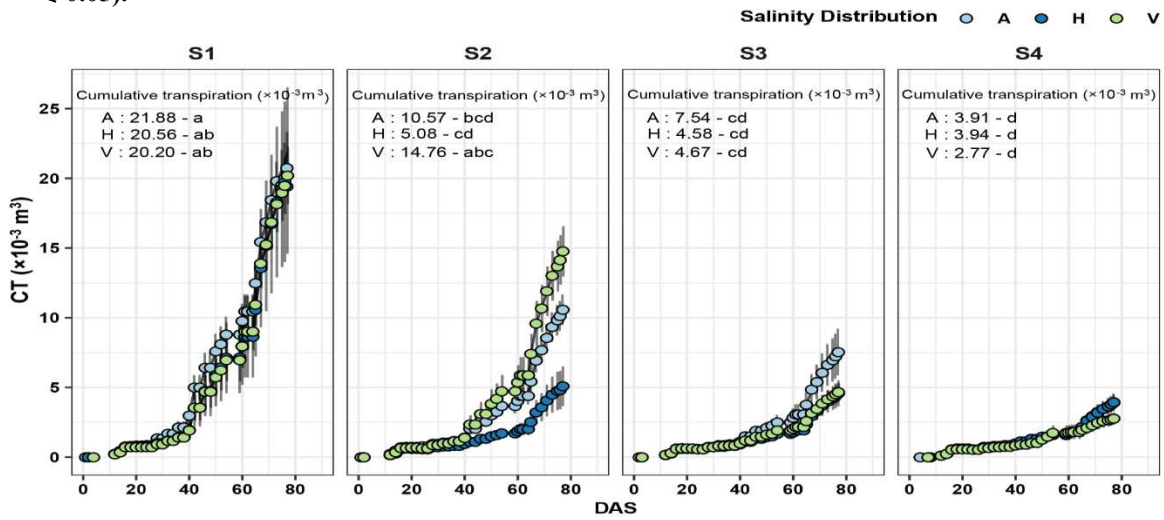

Figure 9. Cumulative transpiration (CT) of sunflower under different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments. Values are means (n = 3) ± SE. The CT (mean value of three replicates) in each salinity treatment is listed in the top left of each figure. The letters after the CT values indicate significant differences among the 12 salinity treatments (LSD test; P ⩽ 0.05).

Correlations between sunflower MPC and soil heterogeneity index (SHI): The determination coefficients (in Figure 10) between sunflower MPC and positional heterogeneity indices indicated that MPC was more strongly correlated with S_{Mid} (R^2 of 0.59-0.73) than with S_{Top} (R^2 of 0.59-0.67), while the weakest correlations were obtained between MPC and S_{Bot} (R^2 of 0.38-0.65). In terms of the correlations of MPC with average heterogeneity indices, MH, MSD, and MFD were similarly correlated with S_{Mean} (R^2 of 0.63-0.7) and S_{Rmean} (R^2 of 0.66-0.7), while MLA, CT, SB, and RB were more strongly correlated with S_{Mean} (R^2 of 0.74-0.84) than S_{Rmean} (R^2 of 0.64-0.73). Moreover, the determination coefficients between MPC and extreme heterogeneity indices showed that MPC was more closely related to S_{Min} (R^2 of 0.73-0.86) than S_{Max} (R^2 of 0.46-0.73). Overall, among the positional, average and extreme heterogeneous indices, MLA, CT, SB, and RB were similarly closely correlated with S_{Mean} and S_{Min} (R^2 of 0.74-0.85), while MH, MSD, and MFD were better correlated with S_{Min} (R^2 of 0.72-0.78) than S_{Mean} (R^2 of 0.65-0. 70).

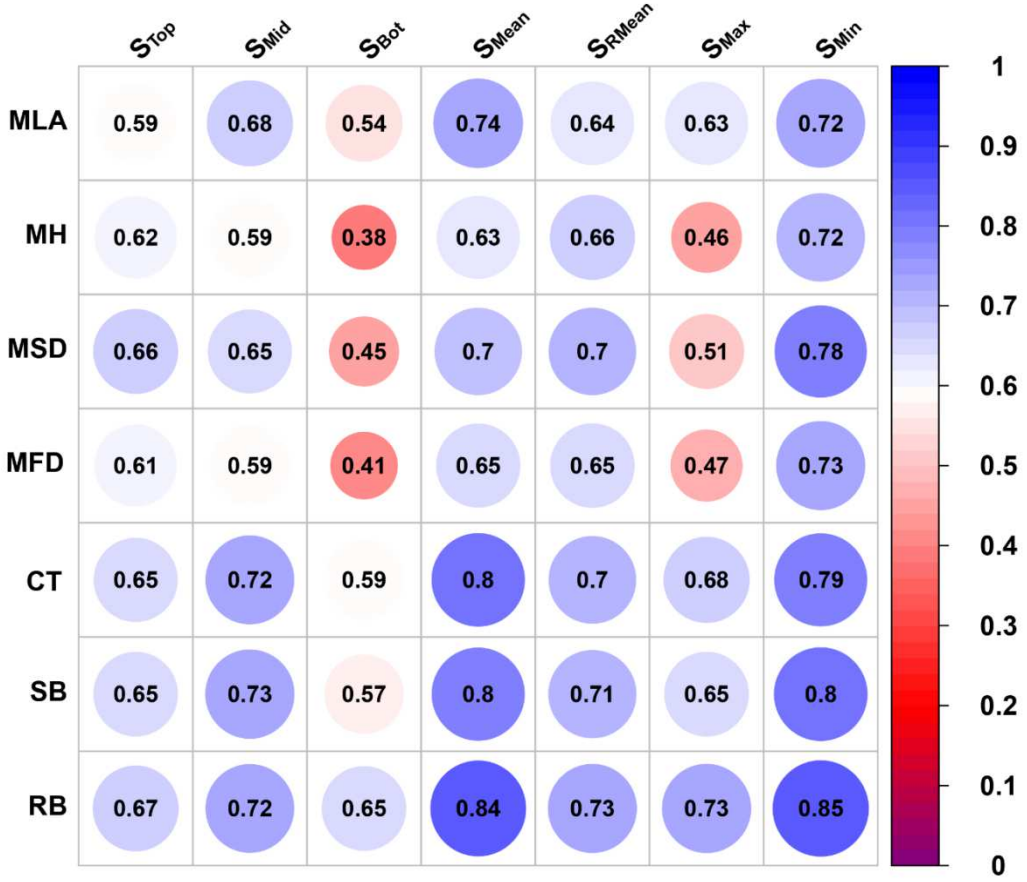

Figure 10. Determination coefficients (R^2) between the morpho-physiological characteristics (MPC) of sunflower (MLA, MH, MSD, and MBD are the maximum leaf area, height, stem, and bud diameter during the growth period, respectively; CT indicates the cumulative transpiration of sunflower; and SB and RB are the shoot and root biomass of sunflower at harvest, respectively) and heterogeneous indices of soil salinity. The significances of the above correlations were smaller than 0.01 ($P < 0.01$). The MPC data were obtained from 36 individual sunflowers under different salinity levels (S1, S2, S3, and S4) and heterogeneity (A, H, and V) treatments.

The correlations of MPC with S_{Min} showed that all MPC of sunflower were negatively linearly correlated with S_{Min}, and Figure 11 shows that when S_{Min} changed from 3 to 15 $dS \cdot m^{-1}$, MH, MSD, and MFD decreased by nearly 57%, 69%, and 76%, respectively, from their respective maximum values, while the values of MLA, CRWU, SB, and RB decreased by nearly 92-95%. Moreover, the quantitative relationships between MPC and S_{Min} were established by the linear regression method (in Figure 11). Relatively good fitting effects were acquired, especially for the fitting curves of SB and RB with S_{Min} (R^2 reached 0.8).

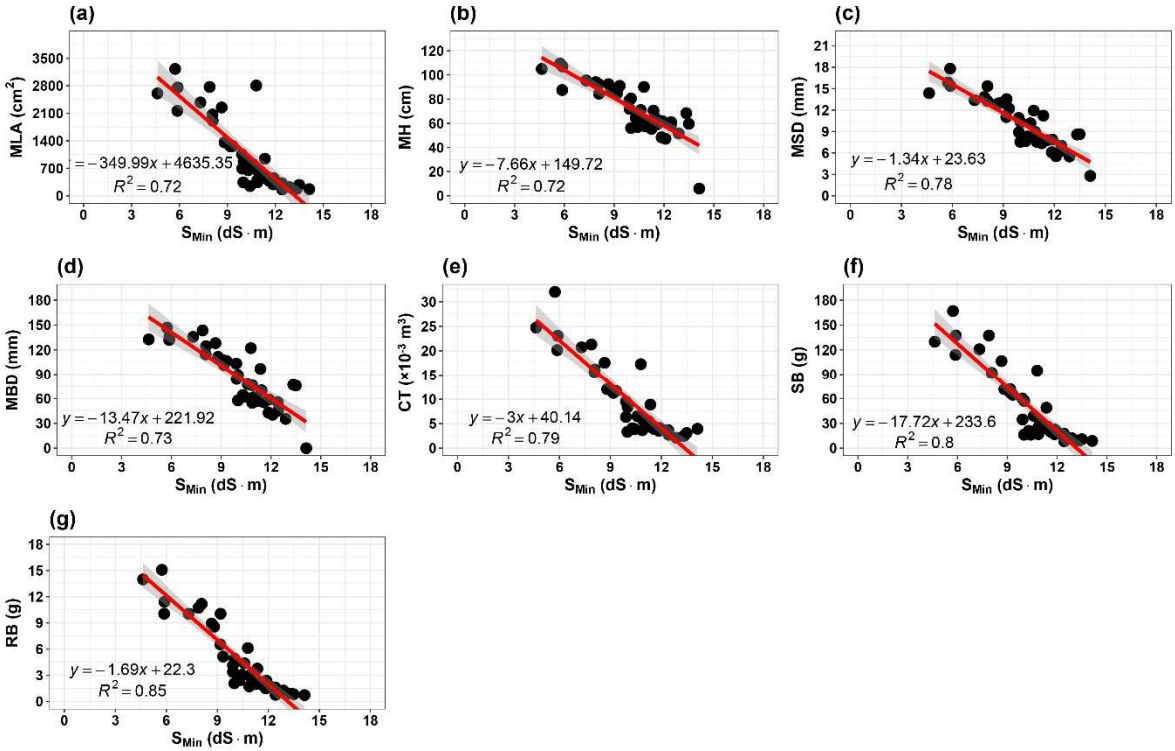

Figure 11. Quantitative relationships (P < 0.01) between the morpho-physiological characteristics (MPC) of sunflower (MLA, MH, MSD, and MFD are the maximum leaf area, height, stem, and bud diameter during the growth period, respectively; RWU indicates the cumulative root water uptake; and SB and RB are the sunflower shoot and root biomasses at harvest, respectively) and the positional heterogeneity index of minimum EC_e in potting soil (S_{Min}). The red lines are fitting linear curves for these quantitative relationships, and the grey shaded areas represent the 95% confidence intervals. Each point was obtained from one individual sunflower.

DISCUSSION

Vertical distribution of soil salinity: The median and main distribution of EC_e values in different SLs (in Figure 3) indicated that vertically heterogeneous soil salinity was essentially achieved according to the A, H, and V-types during the period of sunflower growth, and the initial trend in salinity with respect to depth was maintained at the same salinity level among different salinity distributions (in Table 2). Therefore, the experimental method used in this research was feasible for soil salinity heterogeneity controlling as experiments demand. While the soil salinity of each SL was dynamic changed during the experiments (in Figure 3), which might result from several reasons: First, although the stratified irrigation was applied in our experiments, while the water consumptions were different among different SLs, the greater water was usually irrigated in the upper SL because of the greater water consumption in these layers (shown in Figure 8), which might leach soil salt to the bottom SL with a certain extent; meanwhile, the greater water consumption of top SL also might drive soil salt accumulation on the top SL from lower SLs.

Additionally, unique phenomena were observed in the top soil: the increases in the median EC_e values for all A-type measurements were greater than those for the H and V salinity types. However, in the bottom soil (SD = 25 cm), the maximum increase in median EC_e was obtained in V-type conditions. These phenomena might result from roots compensatory water uptake in lower salinity layers (Bazihizina *et al*., 2012a; Sun *et al*., 2016), the water potential gradient could drive more salt to the low-salinity soil from the high-salinity layer, and soil salt might be transported by phloem and then extruded by the roots in lower-salinity soil (Kong *et al*., 2012, 2016).

MPC and biomass of sunflower shoot under different salinity levels and vertical distributions: Salinity affects the germination and emergence processes of plants by lowering the osmotic potential and causing toxicity, which inhibits seed water uptake and changes the nucleic acid metabolism enzymes activities (Katembe *et al*., 1998; Parihar *et al*., 2015). Our study found that the emergence of sunflower was significantly delayed in high-salinity treatments. Because sunflower seeds were directly sown in the top layer of soils with different salinities, differences in sunflower emergence were

caused by differences in the initial salinity of the top soil among the different treatments. The emergence of sunflower was abruptly prolonged to 12-13 days from 8 days in the H- and V-types when the salinity level was greater than S3, which indicated that the soil EC_e threshold for sunflower emergence is about 11.4 - 13.6 $dS \cdot m^{-1}$ (from Figure 3). Delgado and Sánchez‐Raya (2007), Liu *et al*. (2010) also reported similar postponement phenomena of sunflower germination and emergence in their studies.

The seedling time of sunflower gradually increased with increasing soil salinity in our study, the results indicated plants were sensitive to salinity during early vegetative growth stage (Parihar *et al*., 2015), similar results were observed by Uniyal and Nautiyal (1998); Wu *et al*. (2016) and Alam *et al*. (2011) for *Ougeinia dalbergioides Benth.* and *Oryza sativa L. Pokkali*. Noticeably, the seedling times of sunflower in the A- and V-types were shorter than that in the H-type when the salinity level was lower than the S4 level (S_{Min} smaller than 11.5 $dS \cdot m^{-1}$), which provided evidence that sunflower growth in heterogeneous soil salinity distributions can relieve salinity stress at the seedling stage compared with that in homogeneous-salinity soil. After the seedling stage, the growth stage of sunflower in this experiment was not significant among the different salinity treatments, which implied sunflower decrease the sensitivity to salinity than vegetative growth, Maas and Poss (1989) also found the similar phenomena for the reproductive development of cowpea, wheat, and sorghum. Meanwhile, at the S4 salinity level, the compensation effects of plant growth and root water uptake were restricted by the heavy salinity stress existed in the whole roots zone (S_{Min} greater than 11.5 $dS \cdot m^{-1}$). In this situation, sunflower could not supply sufficient photosynthate to the reproductive organs and seeds, particularly in the V-type, sunflower did not enter the flowering and maturity stages (Jenks *et al*., 2007).

Cells will dehydrate and shrink to reduce cell elongation and division when plants suffer salinization for a few moments to hours, while over several days or weeks, cell division and elongation reductions will result in the slower appearance of certain organs and reductions in size (Jenks *et al*., 2007; Munns and Tester, 2008; Volkov and Beilby, 2017). The present results showed that the growth of sunflower morphological features among different salinity distributions were similar at the S1 level, while the growth of sunflower morphological features and biomass accumulation were inhibited with increasing salinity levels, and the degree of MPC reduction varied at different salinity distributions and salinity levels. At the S2 level, the MPC decreases in the V-type were slightly less than the decreases in the A-type, and the greatest reductions were observed in the H-type. Similar to the MPC of sunflower, comparing shoot biomass at the S1 level, obvious reductions were observed in the A (except stem biomass) and H-types, particularly in H-types; however, the biomass reductions and organ distribution changes in the V-type were slight. These results indicated that compared with salinity homogeneity, salinity heterogeneity alleviated the salinity stress on morphological feature growth and biomass accumulation in sunflower when the salinity of the whole soil was not too high (S_{Min} smaller than 11.5 $dS \cdot m^{-1}$); Bazihizina *et al*. (2009), Sun *et al*. (2016), Feng *et al*. (2017), and Xiong *et al*. (2018) observed similar responses for *Atriplex nummularia*, *alfalfa*, and *Lycium chinense* in horizontally heterogeneous salinity soil, and Shalhevet and Bernstein (1968), Bingham and Garber (1970), and Quiñones Martorello *et al*. (2017) found similar results for alfalfa, corn, *Salix matsudana x S. alba* and *Eucalyptus camaldulensis Dehnh* in vertically heterogeneous salinity soil. Interestingly, the experiment results showed that lower salinity in lower soil will diminish the damage to morphological feature growth of sunflower under the mild salinity ($S_{Min} < 9$ $dS \cdot m^{-1}$, as shown in Figure 3), which might be because plant roots rapidly expand into deeper, less saline soil when the salinity is higher in upper soil (Kent and Lauchli, 1985; Verma *et al*., 2014), Quiñones Martorello *et al*. (2017) also found the reductions of *Salix sp.* and *E. camaldulensis* shoot biomass were decreased when deeper soil had lower salinity than upper soil. However, when the salinity level exceeded S2, the characteristics and biomass of sunflower in the A-type were higher than those in the other salinity distributions, and worse growth and less biomass of sunflower were observed in the V-type when the salinity level was S4. These results indicated that when salinity stress was high overall ($S_{Min} >$ 9 $dS \cdot m^{-1}$, as shown in Figure 3), because most of the roots are distributed in the upper soil (Figure 9), lower salinity in the upper soil would create more opportunities to alleviate damage to RWU and retain fewer absorbed toxic ions in the plant, therefore benefit sunflower morphological feature growth.

Root distribution and transpiration under different salinity levels and vertical distributions: Roots are essential to plant survival, and studies indicated that plants can adjust root proliferation and water absorption efficiency to adapt to soil environmental stresses (Steudle, 2000; Bazihizina *et al*., 2012b; Dara *et al*., 2015; Ma *et al*., 2017). In this study, the root total biomass, irrigation amount, and transpiration of sunflower (Figure 7-9) presented the same trends with different salinity treatments. These indices gradually decreased with increasing soil salinity levels, especially at S3 and S4 salinity levels. Reductions in root biomass and water uptake under salinity stress were also observed by Munns (1993), Dolatabadian *et al*. (2011), Sun *et al*. (2016), Soda *et al*. (2017), etc.

Contrast to homogeneous salinity stress,

heterogeneous salinity stress can trigger root compensatory growth and extraction in low-salinity soil, which will alleviate the salt stress for plant growth (Kong *et al*., 2012; Sun *et al*., 2016; Feng *et al*., 2017). Bingham and Garber (1970) also found that the root biomass and water uptake of Zea mays in soils with a uniform salinity distribution were smaller than those in vertically heterogeneous salinity soil (with two-thirds of the root system irrigated with saline solution). This phenomenon was also observed in our study, such as relative to the status of total root biomass, irrigation amount and transpiration in S1, the reductions of these values in higher salinity level were varied in different salinity distributions. The greatest decrease in total root biomass and transpiration were observed in the homogeneous salinity distribution (H) when the salinity levels were S2 and S3.

The root biomass and transpiration in the V-type were greater than those in the A- and H-types when the salinity level was S2 (S_{Min} < 9 dS·m^{-1}, as shown in Figure 3), which provided evidence for the hypothesis by Bazihizina *et al*. (2012b), which suggested that the roots of phreatophyte genotypes can explore into deep soils when growing in higher superficial salinity soil. Moreover, Quiñones Martorello *et al*. (2017) also found the total root biomass of *E. camaldulensis* was greater when lower salinity was present in deep soil than under uniform salinity and lower salinity in upper soil, because many roots of *E. camaldulensis* (nearly 50%) and the high water extraction of roots in the lower soil enable the plant to uptake highly saline water (~ 40 dS·m^{-1}) from groundwater (Feikema and Bandara, 2012). However, in our experiment, at the S4 salinity level (S_{Min} > 11.5 dS·m^{-1}), the greatest root biomass reduction was found in V-type even when the salinity in deeper soil was smaller, which indicated that if the salinity of the lower soil was greater than the specific threshold (11.5 dS·m^{-1}), the serious inhabitation of sunflower root growth would happen.

Correlations between soil salinity heterogeneity and sunflower MPC: The above analysis showed that the level and heterogeneous distribution of soil salinity affected the MPC of sunflower. The correlations between MPC and positional stress indices showed that the MPC of sunflower were more correlated with S_{Mid} than with S_{Top} and S_{Bot}. Two aspect reasons might for this result, first, the salinity in the top and bottom soils difficult to reflect the salinity status of pot soils due to the stronger fluctuations; second, the analysis from this research showed that the relationships between MPC and positional salinity were affected by salinity level, while S_{Mid} could better represent the information of soil salinity level. Moreover, the correlations between MPC and S_{Mean} were better than those between MPC and S_{RMean}, which indicated that the MPC of sunflower depended more on the arithmetic mean soil salinity than the root distribution. Whereas this phenomenon differed from some studies at the field scale that reported the significant effects of the root distribution on salt tolerance of crops (Ma *et al*., 2017; Lei *et al*., 2019). This difference might result from denser roots in the potting soil; additionally, root compensatory water and nutrition uptake existed in the heterogeneous-salinity soil, which could weaken the effects of realistic root distribution, Sun *et al*. (2016) also suggested that compensatory water uptake was not controlled by the compensatory root growth.

However, the strongest correlation between MPC and SHI was found between MPC and S_{Min}. Because S_{Min} indicates the least saline part of the soil, this correlation implied that compensatory root growth and water uptake in low saline soils might effectively alleviate the salinity stress for the MPC of sunflower. The results of root distribution might support this hypothesis in our study, the relative more root biomasses were found in upper soil in A salinity type and lower soil in V salinity type (in Figure 7). This finding was consistent with the conclusions for alfalfa obtained by Bazihizina *et al*. (2012a) and Sun *et al*. (2016) as for horizontal salinity heterogeneity. Based on correlation analysis between MPC and SHI, linear quantitative relationships were established. These relationships indicated that MLA, CRWU, SB, and RB of sunflower were more sensitive to S_{Min} than MH, MSD, and MFD, especially for CRWU, SB, and RB.

Conclusion: Soil salinity heterogeneity affects the MPC of sunflower, but the impact varies with the salinity level. At lower salinity levels (S_{Min} < 9 dS·m^{-1}), soil heterogeneity can better alleviate the salinity stress on sunflower growth than salinity homogeneity: the MPC reductions of sunflower in heterogeneous soil are less than those in homogenous soil, and a minimum salinity in the lower soil can improve sunflower growth more than a minimum salinity in the upper soil. However, at higher salinity levels, once the minimum salinity of the soil is substantially greater than 9 dS·m^{-1}, the mitigation of salinity stress on sunflower growth by salinity heterogeneity will be weakened, while minimum salinity in the upper soil will be more beneficial to the MPC of sunflower. Moreover, correlation analysis between MPC and SHI indicated that the minimum salinity of potting soil is the key factor for the MPC of sunflower, and good linear relationships were found between S_{Min} and MPC in sunflower. However, although salinity heterogeneity was maintained in this experiment, the soil salinity in the top and bottom soils might be influenced by irrigation methods, the process of compensatory water uptake in less saline soil was not directly observed; meanwhile, the effects of heterogeneous distribution and levels of soil salinity on plant MPC were only analyzed at pot scale. Therefore, more detailed and greater scale experiments of

crop response mechanisms to vertically heterogeneous soil salinity are still needed for further exploration.

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