

## Compensatory Growth and Salt Ion Distribution Characteristics in Sweet Sorghum After Alleviation of Soil Salt Stress: Postprint

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### Abstract

Stress compensation effects are widespread in crops and exert important influences on crop growth, development, and yield. To elucidate the compensatory growth effect of sweet sorghum following soil salinity reduction, this study employed a pot experiment, establishing three gradients of soil salt content at the jointing stage:  $5 \text{ g} \cdot \text{kg}^{-1}$  (high-salt treatment), reduction from  $5 \text{ g} \cdot \text{kg}^{-1}$  to  $2 \text{ g} \cdot \text{kg}^{-1}$  (salinity reduction treatment), and  $2 \text{ g} \cdot \text{kg}^{-1}$  (low-salt control). The dry matter growth rate and accumulation in aboveground organs (stem, leaf, and leaf sheath) of two sweet sorghum cultivars were measured, along with the contents of salt ions (Na, Cl, K) in different organs. The results demonstrated that the aboveground dry matter growth rate under high-salt treatment remained significantly lower than the control throughout the experiment; after soil salinity reduction, the dry matter growth rate of each organ increased significantly and surpassed the control, producing an overcompensation effect. At maturity, plant height and aboveground dry matter under high-salt treatment decreased substantially; following soil salinity reduction, the plant height and aboveground dry matter of 'Liaotian 1' decreased by 7.69% and 33.21% compared with the low-salt control, respectively, whereas those of 'Zhongketian 3' showed no difference from the control. After high-salt treatment, the Na and Cl contents in the dry matter of each organ increased substantially compared with the control, while the increase in K content was relatively minor. At 35 days after soil salinity reduction, although the Na and Cl contents in each organ remained higher than the control, they had already decreased substantially compared with the high-salt treatment; the K content in stem and leaf sheath increased slightly compared with the control, while the K content in leaves showed no significant difference from the control. This study indicates that following alleviation of salt stress in sweet sorghum, ion toxicity is mitigated and growth rate accelerates until exceeding the control; the compensation effect is particularly pronounced

in salt-tolerant sweet sorghum cultivars, with dry matter yield at maturity comparable to the control. The results of this study can provide a theoretical basis for sweet sorghum cultivation in saline-alkali soils.

## Full Text

### Compensation Growth and Salt Ion Distribution in Sweet Sorghum (*Sorghum bicolor* L. Moench) Following Alleviation of Soil Salinity Stress

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#### Abstract

Adversity compensation effects are ubiquitous in crops and significantly influence plant growth, development, and yield. To elucidate the compensatory growth response of sweet sorghum following reduction of soil salt stress, a pot experiment was conducted with three salinity gradients applied at the elongation stage:  $5 \text{ g} \cdot \text{kg}^{-1}$  (high salt treatment), reduction from  $5 \text{ g} \cdot \text{kg}^{-1}$  to  $2 \text{ g} \cdot \text{kg}^{-1}$  (salt stress reduction treatment), and  $2 \text{ g} \cdot \text{kg}^{-1}$  (low-salt control). Two sweet sorghum varieties were assessed for dry matter growth rates and accumulation in aboveground organs (stem, leaf, and leaf sheath), along with salt ion (Na, Cl, K) distribution patterns.

Results showed that the aboveground dry matter growth rate under high salt stress remained significantly lower than the control throughout the experiment. Following soil salinity reduction, growth rates of all organs increased markedly and eventually exceeded control levels, demonstrating an overcompensation effect. At maturity, high salt treatment caused substantial reductions in plant height and aboveground dry matter. In contrast, after salt reduction, 'Liaotian 1' showed decreases of 7.69% in plant height and 33.21% in aboveground dry matter compared to the low-salt control, while 'Zhongketian 3' exhibited no significant differences from the control. High salt treatment dramatically increased Na and Cl contents in all organs, with smaller increases in K content. Thirty-five days after salinity reduction, Na and Cl contents remained higher than the control but had decreased significantly compared to the high salt treatment. K content in stems and leaf sheaths showed slight increases over the control, while leaf K content was not significantly different from the control.

These findings indicate that alleviation of salt stress in sweet sorghum reduces ion toxicity and accelerates growth rates to surpass control levels, with salt-tolerant varieties showing particularly pronounced compensation effects and

achieving dry matter yields comparable to the control at maturity. This study provides a theoretical basis for sweet sorghum cultivation in saline-alkali soils.

**Keywords:** Salt stress; Soil salinity reduction; Sweet sorghum; Compensation effect; Dry matter; Ion content

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## Introduction

China possesses approximately 37 million hectares of saline-alkali soils. As arable land resources become increasingly scarce, the improvement and utilization of these soils has emerged as a critical task for agricultural development[1]. Influenced by monsoon climate patterns, salinity in Chinese soils exhibits seasonal variation: concentrated summer rainfall causes seasonal desalination, while reduced precipitation in spring and autumn leads to salt accumulation. The degree of desalination and salt accumulation varies regionally depending on climate conditions. In areas with abundant rainfall, particularly coastal saline soils and tidal flats in eastern China, soil salinity decreases significantly after the rainy season, providing important opportunities for high-yield and efficient crop production[2].

Sweet sorghum (*Sorghum bicolor* L.) offers high biomass yield and broad adaptability, with particular advantages in salt-alkali tolerance, drought resistance, and waterlogging tolerance. It has become a novel sugar crop, energy crop, and excellent forage crop both domestically and internationally[3,4], suitable for cultivation in Northeast, North, Northwest, and Huang-Huai regions of China, as well as in marginal lands such as arid, semi-arid, low-lying, saline-alkali, and sandy areas[5]. Previous research on sweet sorghum salt tolerance has primarily focused on the effects of specific or varying salt levels on growth and development, material screening, and underlying mechanisms[6–10]. However, systematic studies are lacking on how reduced soil salinity following rainfall or irrigation affects sweet sorghum growth, development, and yield formation—a factor that may play a crucial role in crop performance in saline-alkali soils.

Studies have shown that under adverse conditions, plant growth is inhibited, but within non-lethal stress levels, growth gradually recovers after stress alleviation to compensate for negative impacts[2,11]. Compensation effects are widespread in the plant kingdom, with most research focusing on post-drought rewatering in crops such as wheat (*Triticum aestivum*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), peanut (*Arachis hypogaea*), pea (*Pisum sativum*), broom-corn millet (*Panicum miliaceum*), and cork oak (*Quercus variabilis*). These studies demonstrate that drought stress followed by rewatering promotes compensatory growth effects, including accelerated plant height and leaf growth and increased dry matter accumulation rates[12,13]. Guo et al.[2] reported that after soil salinity reduction at the cotton bud stage, compensation growth first manifested in the formation of fruit branches and fruit nodes, subsequently achieving yield compensation. Wen et al.[14] investigated salt tolerance compen-

satory growth characteristics in four forage species, finding that all exhibited compensatory growth under salt stress within a concentration range of 0.2%–0.8%. However, systematic research on how salt damage compensation effects influence growth, development, and yield formation in other crops, as well as the underlying mechanisms, remains limited.

This study examined compensatory growth and salt ion distribution patterns in sweet sorghum organs following soil salinity reduction at the elongation stage, aiming to clarify the compensatory growth effects and provide a theoretical foundation for sweet sorghum cultivation in saline-alkali soils.

## Materials and Methods

### 1.1 Experimental Design

The experiment was conducted in 2014 under a rain shelter at the Institute of Industrial Crops, Jiangsu Academy of Agricultural Sciences, using pot culture methods. The test soil was yellow-brown loam with the following properties in 2014: organic matter  $14.34 \text{ g} \cdot \text{kg}^{-1}$ , total nitrogen  $0.85 \text{ g} \cdot \text{kg}^{-1}$ , available phosphorus  $32.78 \text{ mg} \cdot \text{kg}^{-1}$ , available potassium  $177.94 \text{ mg} \cdot \text{kg}^{-1}$ , and salt content  $0.35 \text{ g} \cdot \text{kg}^{-1}$ . Pots measured 40 cm in diameter and 40 cm in height, each containing 20 kg of soil that was air-dried, sieved, and cleaned of debris before filling. Based on the initial salt content, mixed salts (77.7% NaCl, 7.27% MgCl, 9.6% MgSO, 3.3% CaCl, 2.1% KCl) were incorporated to achieve approximately 0.2% salt content.

Two sweet sorghum varieties were tested: the moderately salt-tolerant ‘Liaotian 1’ and the highly salt-tolerant ‘Zhongketian 3’ [15]. Seeds were sown on May 8 using direct seeding. At the elongation stage, one uniformly vigorous seedling was retained per pot. Basal fertilizer consisted of 6 g of compound NPK fertilizer per pot, with additional applications of 1.5 g urea per pot on July 10 and August 2.

Three treatments were established: (1) Low-salt control (CK) with soil salt content maintained at approximately  $2 \text{ g} \cdot \text{kg}^{-1}$ ; (2) Soil salinity reduction treatment (SD) with initial soil salt content of  $2 \text{ g} \cdot \text{kg}^{-1}$ , where mixed salts were added every 7 days after the two-leaf stage to increase salinity by  $1 \text{ g} \cdot \text{kg}^{-1}$  each time, reaching approximately  $5 \text{ g} \cdot \text{kg}^{-1}$  after three applications, maintained for 25 days until the elongation stage when salinity was reduced to approximately  $2 \text{ g} \cdot \text{kg}^{-1}$  within one day through leaching with water; (3) High salt treatment (S) with initial soil salt content of  $2 \text{ g} \cdot \text{kg}^{-1}$ , where mixed salts were added every 7 days to increase salinity by  $1 \text{ g} \cdot \text{kg}^{-1}$ , reaching a final concentration of  $5 \text{ g} \cdot \text{kg}^{-1}$  that was maintained throughout.

Each treatment comprised 120 replicates (360 pots total). Soil water content was regulated gravimetrically throughout the growth period, with relative soil water content maintained at 70%–80% for both the low-salt control and high salt treatment. For the salinity reduction treatment, soil water content increased

only during the leaching process, while remaining at 70%-80% at other times.

## 1.2 Experimental Methods

Soil salt content was measured using a salt meter before the experiment and every 2-3 days during the treatment period, with water controlled to maintain target salinity levels. After salt reduction, three uniformly growing sweet sorghum plants were selected from each treatment every 7-10 days (five sampling events) and at maturity[16], with three replicates. Aboveground parts were harvested and separated into stem, leaf, and leaf sheath components. Samples were killed at 105°C for 30 minutes, then oven-dried at 75°C to constant weight for dry matter determination. Salt ion contents (K , Na , Cl , etc.) were subsequently measured[17].

## 1.3 Data Analysis

Data were analyzed using SPSS 15.0 statistical software, with multiple comparisons performed using the SSR method. Following Zhao et al.[18], compensation after soil salinity reduction was classified into three categories: overcompensation ( $Q/Q > 1$ ), equal compensation ( $Q/Q = 1$ ), and partial compensation ( $Q/Q < 1$ ), where  $Q$  represents the measured value after stress reduction and  $Q$  represents the control value. This classification was applied to evaluate compensation effects on dry matter growth rates and accumulation.

## Results

### 2.1 Effects of Soil Salinity Reduction on Aboveground Dry Matter Growth Rates

All treatments entered a rapid growth phase after the elongation stage. Under high salt treatment, the aboveground dry matter growth rates of both ‘Liaotian 1’ and ‘Zhongketian 3’ remained significantly lower than the control throughout the experiment. Following soil salinity reduction, growth rates of all organs increased substantially, successively reaching or exceeding control levels and producing compensatory or overcompensatory effects.

‘Liaotian 1’ exhibited overcompensation in leaf, leaf sheath, stem, and total aboveground dry matter growth rates at 45, 35, 45, and 45 days after treatment, respectively. At 45 days after treatment, the total aboveground dry matter growth rate reached  $3.40 \text{ g} \cdot \text{plant}^{-1} \cdot \text{d}^{-1}$  compared to  $2.98 \text{ g} \cdot \text{plant}^{-1} \cdot \text{d}^{-1}$  in the control. ‘Zhongketian 3’ showed overcompensation in leaf, leaf sheath, stem, and total dry matter growth rates at 28, 45, 28, and 28 days after treatment, respectively, with a total aboveground dry matter growth rate of  $1.84 \text{ g} \cdot \text{plant}^{-1} \cdot \text{d}^{-1}$  at 28 days after treatment versus the control value [Figure 1: see original paper].

## 2.2 Effects of Soil Salinity Reduction on Plant Height and Above-ground Dry Matter Accumulation

At maturity, high salt treatment reduced plant height by 36.54% and 35.42% and aboveground dry matter by 57.32% and 49.77% for ‘Liaotian 1’ and ‘Zhongketian 3’, respectively, compared to the control. Under salinity reduction treatment, ‘Liaotian 1’ showed decreases of 7.69% in plant height and 13.21% in aboveground dry matter relative to the control, while ‘Zhongketian 3’ exhibited only 1.74% and 2.98% reductions, respectively, with no significant differences from the control, demonstrating equal compensation effects.

## 2.3 Effects of Soil Salinity Reduction on Ion Content in Sweet Sorghum Organs

Thirty-five days after salinity reduction, analysis revealed that high salt treatment dramatically increased Na content in all organs, with the greatest increase in stems, followed by leaf sheaths, and the smallest in leaves. In ‘Liaotian 1’ and ‘Zhongketian 3’, stem, leaf sheath, and leaf Na contents were 3.85, 2.82, and 1.94 times, and 2.13, 2.14, and 1.26 times the control values, respectively. After salt reduction, Na content decreased substantially compared to the high salt treatment, though stem Na contents remained 2.36 and 1.16 times the control in ‘Liaotian 1’ and ‘Zhongketian 3’, respectively; leaf sheath contents were 1.55 and 1.16 times the control; and leaf contents were 1.06 and 0.89 times the control, respectively.

High salt treatment also increased K content in all organs. In ‘Liaotian 1’ and ‘Zhongketian 3’, average K contents in stems, leaf sheaths, and leaves were 1.27, 1.27, and 1.07 times, and 1.08, 1.08, and 1.03 times the control values, respectively. After salinity reduction, K content in stems and leaf sheaths remained slightly elevated (1.23 and 1.15 times the control in ‘Liaotian 1’; 1.07 and 1.10 times in ‘Zhongketian 3’), while leaf K content showed no significant difference from the control.

High salt treatment increased Cl content in all organs as well. In ‘Liaotian 1’ and ‘Zhongketian 3’, stem, leaf sheath, and leaf Cl contents were 1.79, 1.41, and 1.30 times, and 1.06, 1.17, and 1.20 times the control values, respectively. After salinity reduction, Cl content decreased significantly in all organs, with stem contents at 1.36 and 1.03 times the control, leaf sheath contents at 1.32 and 1.02 times the control, and leaf contents at 1.04 and 0.82 times the control for ‘Liaotian 1’ and ‘Zhongketian 3’, respectively.

## Discussion and Conclusion

High soil salinity forces crops to absorb and accumulate salt ions, causing ion toxicity and osmotic stress that inhibit growth and development[19]. This study demonstrated that maintaining soil salt content at  $5 \text{ g} \cdot \text{kg}^{-1}$  severely inhibited sweet sorghum growth and resulted in low yield. After reducing soil salinity to

$2 \text{ g} \cdot \text{kg}^{-1}$  at the elongation stage, sweet sorghum exhibited rapid growth with dry matter growth rates exceeding the control, producing an overcompensation effect consistent with previous research[2,14]. At maturity, ‘Liaotian 1’ showed partial compensation in plant height and aboveground dry matter accumulation, while the salt-tolerant variety ‘Zhongketian 3’ demonstrated equal compensation, indicating substantial variation in compensatory growth effects among sweet sorghum varieties. Guo et al.[20] found that 21 days after soil salinity reduction in cotton, root vigor approached or exceeded control levels, malondialdehyde content (a key indicator of cellular oxidative damage) decreased, and catalase activity increased. Similar results have been observed in sweet sorghum after salt stress alleviation (unpublished data), where substantial recovery and enhancement of physiological characteristics provide the material basis for compensatory growth.

An important mechanism of salt tolerance in higher plants involves regulating the types, quantities, and ratios of inorganic ions to maintain stable intra- and extracellular microenvironments[17].  $\text{Na}^+$  in salt can readily cause single-salt toxicity[21]. Following salt stress,  $\text{Na}^+$  content increased in sweet sorghum stems, leaf sheaths, and leaves—a pattern consistent with most plants under salt stress, such as oat (*Avena sativa*), rice (*Oryza sativa*), and pumpkin (*Cucurbita moschata*)[19,22]. In this study,  $\text{Na}^+$  content in sweet sorghum stems was substantially higher than in leaf sheaths and leaves. As stems serve as transport, support, and storage organs while leaves are the primary source of dry matter production with strong metabolic activity[23], limited  $\text{Na}^+$  accumulation in leaves reduces damage to photosynthetic organs. The compartmentalization and regulation of ions among organs represents an adaptive response to salt stress[24]. This salt tolerance strategy in sweet sorghum differs markedly from crops such as *Leymus chinensis*, wheatgrass (*Triticum aestivum*-*Agropyron intermedium*), and cotton (*Gossypium hirsutum*), which maintain equivalent  $\text{Na}^+$  contents in stems and leaves under high salinity, suggesting diverse mechanisms of salt stress action and plant adaptation[25,26]. After salinity reduction,  $\text{Na}^+$  content decreased substantially in all organs, but responses varied among organs, with leaves showing more pronounced recovery—leaf  $\text{Na}^+$  content was equivalent to or lower than the control 35 days after treatment. Reduced  $\text{Na}^+$  toxicity promotes increased net photosynthetic rate and stomatal conductance, enhanced activities of antioxidant enzymes SOD and POD, and increased utilization of organic substances such as amino acids and carbohydrates[11], creating favorable conditions for accelerated growth.

Salt stress increased  $\text{K}^+$  content in sweet sorghum stems and leaves, contrasting with observations in *Leymus chinensis*[25], oat[19], and *Suaeda australis*[22]. While glycophytes exhibit reduced  $\text{K}^+$  uptake under low salt concentrations, halophytes maintain  $\text{K}^+$  uptake under moderate salinity[27]. This suggests that sweet sorghum’s salt adaptation mechanism resembles that of halophytes, where moderate salinity promotes  $\text{K}^+$  uptake to maintain a low  $\text{Na}^+/\text{K}^+$  ratio and preserve normal cellular function. High salt treatment also increased  $\text{Cl}^-$  content in all organs.  $\text{Cl}^-$  may help balance  $\text{Na}^+$  charges[28], mitigating their toxic effects

and representing an important adaptation mechanism to salt stress.

In conclusion, sweet sorghum exhibits significant compensatory effects following salt stress alleviation, particularly in salt-tolerant varieties. These effects include reduced ion toxicity, accelerated growth rates exceeding control levels, and final aboveground dry matter weights approaching those of low-salt controls. Therefore, sweet sorghum cultivation in saline-alkali soils should select varieties with strong compensatory responses under salt stress and implement appropriate management measures during the critical period of rapid growth and yield formation after the rainy season to promote balanced growth and enhance yield.

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