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RESEARCH ARTICLE

Abscisic acid-mediated yield gain through reduced oxidative damage caused by salt and water stress in *Cyperus esculentus*

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KEYWORDS

Cyperus esculentus, salt stress, water stress, yield, abscisic acid

HIGHLIGHTS

- Negative Synergy of homogeneous limitation caused by combined water and salt stress.
- A pivotal role of abscisic acid in the response to combined salt and water stress.
- *Cyperus esculentus* sustain organic matter production by reallocating resources.
- Morphological changes are more sensitive to water limitation.

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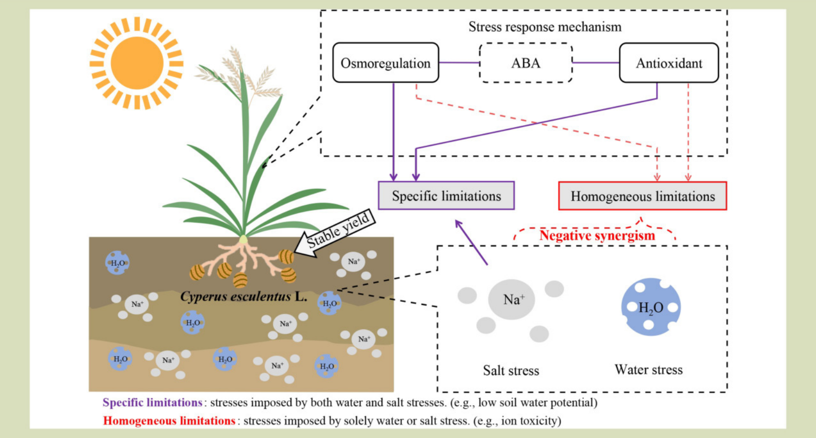
GRAPHICAL ABSTRACT



Specific limitations: stresses imposed by both water and salt stresses. (e.g., low soil water potential)
Homogeneous limitations: stresses imposed by solely water or salt stress. (e.g., ion toxicity)

ABSTRACT

The investigation of the response mechanisms of *Cyperus esculentus* to water and salt stresses is crucial for the enhancement of the productivity of saline soils. Previous studies have indicated that plant hormones, antioxidant systems, and osmoregulation may contribute to the stabilization of yield. However, the contributions and interactions of these mechanisms remain poorly understood under combined water and salt stress in natural environments. A dual-factor (salt and water) orthogonal test was used to investigate the growth and biochemical responses of *C. esculentus*, under combined salt and water stress in a field experiment conducted on a typical saline area in northern China. The findings reveal that *C. esculentus* adjusted its biomass allocation strategies and activated hormone responses, antioxidant system, and osmoregulation mechanisms to maintain stable yield. Due to the negative synergism when salt and water stress coexist, the homogeneous limitations of both are weakened. Thus, the key to maintaining yields under combined water and salt stress may depend on indirectly enhancing tolerance to oxidative damage through abscisic acid, rather than focusing on accumulating low molecular weight osmoregulants and antioxidant enzymes to directly alleviate homogeneous limitations. Also, under combined salt and water stress, insufficient irrigation may have a greater impact on morphological characteristics than high salinity. The above results contribute to a deeper understanding of the process of adapting *C. esculentus* to combined salt and water stress.

1 Introduction

Soil salinization is a major abiotic stress that affects global agriculture, with nearly 1 billion hectare of land affected by this problem worldwide to date[1]. It poses a significant threat to global agricultural productivity by reducing arable land, degrading arable soils, and decreasing crop yields[2]. Determining how to best use low productivity saline areas has become a significant challenge to global food supply as the global population continues to grow[3]. Exploring effective ways to increase the productivity of Solonchak soils is crucial for ensuring global food security. In general, the primary method for improving soil productivity in saline areas are irrigation and planting salt-tolerant crops in salinized areas[4]. However, irrigation may not be sufficient to achieve the desired results in large salinized areas[5,6], especially with the exacerbation of soil salinization due to global climate change[7,8]. In this context, the cultivation of salt-tolerant crops is important for improving soil productivity and effective use of saline soil[9].

Cyperus esculentus is a perennial herbaceous plant, native to Africa and the Mediterranean region. After its introduction to China, it was discovered that both the above- and belowground parts possess high economic value: the stem and leaves are nutritious, can provide high-quality fodder, with a yield of up to 10–15 $t \cdot ha^{-1}$[10]; the tuber has a high oil content, and the oil yield per unit area can be up to four times that of soybean[11]. Additionally, the oil quality is excellent[12], making it a high-quality oil crop with considerable yield[13]. Also, the press cake produced from the tubers is nutritious, including flavonoids, vitamin E, vitamin C, zinc, and other nutrients, and it contains about 60% starch, 20% sugar, and 8% crude protein, and can serve as a substitute for corn as a high-quality feed[14]. Recent studies have found that *C. esculentus* can thrive in saline soil[15,16], implying that it has the potential to be an excellent economic crop in saline areas.

To elucidate the system of growth habitat alignment mapping of *C. esculentus* and to capitalize on the economic advantages of cultivating it in saline areas, researchers have conducted studies to ascertain response mechanism *C. esculentus* and adaptive capacity under high salinity or insufficient irrigation under controlled laboratory conditions, which are the two primary factors limiting crop growth in saline area[17–20]. Studies on the salt tolerance of *C. esculentus* have found that as the intensity of salt stress increases, it can mitigate salt damage in the low to medium intensity range by increasing the level of antioxidant enzymes, accumulating low molecular weight osmoregulants and secreting hormones[16,21]. Although these mechanisms can contribute to the ability of this crop to tolerate salt, this enhancement alone is often insufficient to handle increasingly high levels of salt stress. This can result in significant oxidative damage under more severe salt stress conditions, as well as a marked decline in root biomass and yield[15,22]. However, studies had also shown that salt stress may result in beneficial effects, such as an increase in tiller number, leaf number, and fresh weight of aboveground parts[15]. These findings indicate that predicting the growth of *C. esculentus* based solely on changes in environmental salinity may not be accurate, and other factors may need to be considered to better predict its growth.

Earlier studies on the growth of *C. esculentus* under insufficient irrigation have shown that it can also improve its tolerance to water stress by accumulating low molecular weight osmoregulants, increasing antioxidant enzymes concentrations, and secreting more abscisic acid (ABA) under low irrigation water availability[23]. Although these processes may mitigate the effects of water stress, they might not be able to eliminate the adverse effects of water stress given that it was found that the number of tillers, leaf area, and above- and belowground biomass of it decreased significantly with increasing water stress[24]. However, the pattern is not consistently reported. Some studies have found that for a given level of water stress (ranging from 100% to 70% irrigation), *C. esculentus* yields actually increased with increasing water stress[25,26]. These differences mean the impact of water stress could not be precisely evaluated by solely modifying the irrigation level. In combination, the results from these single-stress studies demonstrate that a single stress may not fully explain the effects on growth of *C. esculentus* in natural environments. In the field, the growth of *C. esculentus* is often affected by a combination of salt and water stress[27–29], which is difficult to assess from the results of a water or salt stress are study independently. This may be due to hormone responses, osmoregulation, antioxidant systems, and other mechanisms triggered by plants, which may have different contributions and complex interactions (e.g., negative synergism with the combined effects worse than the sum of individual effects) when facing the combined limitations imposed by the coexistence of water and salt stresses (e.g., low soil water potential) and specific limitations induced by salt stress (e.g., ion toxicity)[30,31]. However, there has been no studies on the response of *C. esculentus* to combined salt and water stress, which severely limits knowledge of its response mechanism and adaptive capacity when subjected to combined salt and water stress.

In summary, despite many studies investigating the effects of salt or water stress on *C. esculentus*, the inconsistent results indicate that knowledge of its response to salt and water stress is not well established. Therefore, we selected a typical saline area in northern China to conduct a field experiment and set up an dual-factor (salt and water) orthogonal experiment to observe the growth and biochemical responses of *C. esculentus* to the combined salt and water stress.

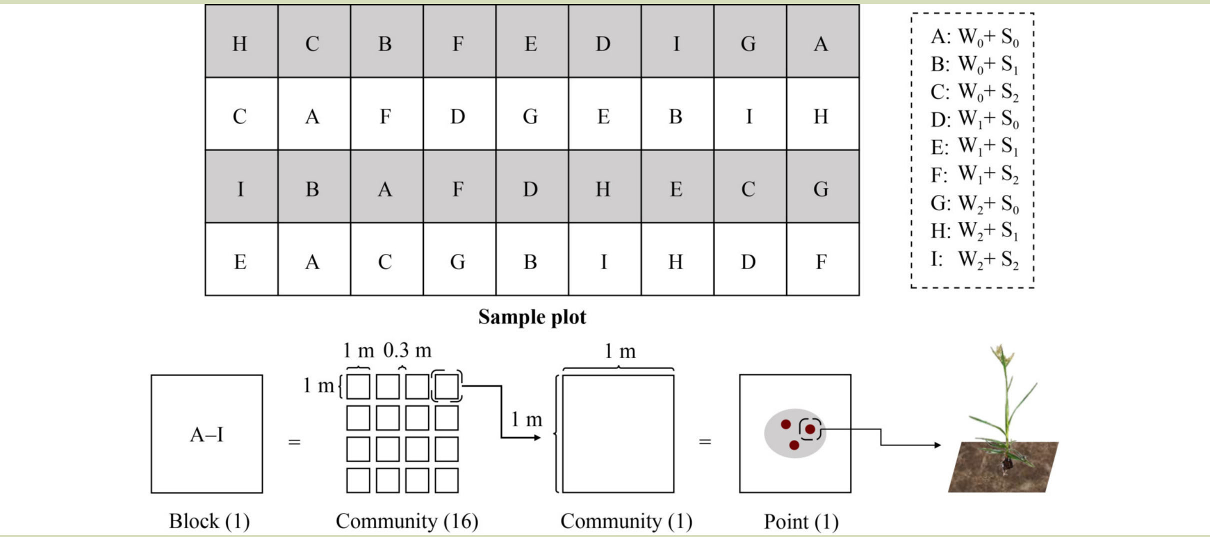
2 Materials and methods

2.1 Site description

This experiment was conducted at the Nong'an Farm in Jilin. The farm is located in Nong'an County, Jilin Province (124°31′–125°45′ E, 43°55′–44°55′ N, 145–300 m above sea level) with a local irrigation quota of about 1050 $m^3 \cdot ha^{-1}$, but most farmland is unirrigated. The typical local crop is maize, which yields 4–5 $t \cdot ha^{-1}$ when grown on Solonchak (lower than the average yield of 6.4 $t \cdot ha^{-1}$ in China). The study area has a temperate continental monsoon climate with an average annual temperature of 4.7 °C, a frost-free period of 145 days, and an annual rainfall of 508 mm. The distribution of rainfall within the year is non-uniform, with the rainy season mainly concentrated from June to August, accounting for 59.9% of the annual rainfall. The average annual evapotranspiration is 1501 mm, and the effective cumulative temperature is 2800 °C. The study area consists mainly of saline soils, with a field capacity ranging from 20% to 50% and a soil pH between 7.3 and 7.8.

2.2 Experimental design and sample collection

The experimental field was arranged in randomized block design with nine treatments. These treatments consisted of three irrigation levels and three salt addition levels, organized in a dual-factor design that considered both salt and water stress (Fig. 1). The experimental area was divided into four



H	C	B	F	E	D	I	G	A
C	A	F	D	G	E	B	I	H
I	B	A	F	D	H	E	C	G
E	A	C	G	B	I	H	D	F

A: $W_0 + S_0$
B: $W_0 + S_1$
C: $W_0 + S_2$
D: $W_1 + S_0$
E: $W_1 + S_1$
F: $W_1 + S_2$
G: $W_2 + S_0$
H: $W_2 + S_1$
I: $W_2 + S_2$

Fig. 1 Experimental plot treatments and design. W_0, control irrigation group; W_1, moderate irrigation group; W_2, low irrigation group; S_0, control salinity group; S_1, moderate salinity group; S_2, heavy salinity group.

planting lines, each of which included nine blocks corresponding to the nine different treatment levels, resulting in a total of 36 blocks, with the order of blocks within each planting line randomly assigned. Every block was divided into 16 communities, each in 1 m × 1 m plots. A 0.3-m spacing was maintained between communities to facilitate investigation and avoid interference with experimental treatments on neighboring communities. For each community, one sowing point was selected for sowing *C. esculentus* seeds. Additionally, a soil moisture monitor (RS-EC5W5S-N01-TR-5, Shandong Renke Control Technology Co.,Ltd., Jinan, Shandong, China) was buried in each community group of the sample blocks to determine the relative soil moisture before sowing.

NaCl was chosen for soil salt addition as it is the main salt that affects plant growth in the field environment. The experiment involved three groups with different levels of salinity: a control salinity group (initial total soil salinity with chloride ion concentration of about 0.02%; S_0), a moderate salinity group (salt added to increase chloride ion concentration to the range of 0.02%–0.04%; S_1), and a heavy salinity group (salt added to increase chloride ion concentration to the range of 0.04%–0.1%; S_2). The process involved dissolving the required amount NaCl in deionized water and spraying it evenly onto the soil surface of the relevant group. All sprayed salts were then fixed in the 50 cm deep soil layer. The water gradients were controlled at three levels: a control irrigation group (100% standard irrigation rate, 1050 $m^3 \cdot ha^{-1}$; W_0), a moderate irrigation group (70% standard irrigation rate, 735 $m^3 \cdot ha^{-1}$; W_1), and a low irrigation group (50% standard irrigation rate, 525 $m^3 \cdot ha^{-1}$; W_2). Irrigation was applied by drippers in a drip tape pattern with 1 tube and 2 rows.

Seeds were sown in May 2021 with seeds of similar size selected after germination experiments. All seeds were shade-dried and stored at room temperature, they were sterilized using 70% ethanol and 1 $g \cdot L^{-1}$ mercuric chloride, germination was considered successful for seeds with roots larger than 1 cm with these experiments repeated three times. Before sowing, the sample plot was tilled, and a salt gradient control was applied to the soil. After tilling and setting the salt gradient, three seeds of *C. esculentus* were sown at each point. To ensure the emergence of all seedlings, sufficient water was dripped before sowing. Irrigation treatments were applied during the four main periods of the whole growing season: three times during the sowing stage, two times during the leaf development stage, two times during the flowering stage, and two times during the fruiting stage.

The tissue samples were collected and the morphological characteristics were measured during the flowering period. For each salinity treatment, three *C. esculentus* plants were randomly selected within the same block, and total of 108 treated plants were measured across nine treatment levels. We measured the plant height (PH; defined as the plant height of the *C. esculentus* seedling from the tip to the sand surface), tillers number (TLN), tuber number (TBN), root dry weight (RDW), leaf dry weight (LDW), tuber dry weight (TDW), and leaf area (LA). After measuring, we collected tissue samples and taken to the laboratory for measurements of active intracellular substances in leaves, and nitrogen and phosphorus in roots, stems and leaves. PH, LA, TLN, TBN, RDW, TDW, and LDW were measured by measuring tape, visual inspection, and weighing by electronic balance at the time of plant tissue collection; root-shoot ratio (R/S) is the ratio of root dry weight to leaf dry weight.

2.3 Measurements of plant physiological and ecological properties

The nitrogen concentration of the plant organs was determined using a carbon and nitrogen analyzer, and the phosphorus concentration was determined using a molybdenum-antimony colorimetric assay[32]. To assess the antioxidant system of plants[33], we measured the levels of leaf superoxide dismutase (an enzyme that can remove harmful free radicals from plant cells), peroxisome (an enzyme that can remove harmful free radicals from plant cells), and malondialdehyde (a product of plant membrane lipid peroxidation) using enzyme kit assays (Berlin-Chemie, Berlin, Germany). Of the three main substances of the plant osmoregulatory system[34], soluble sugars (low molecular weight osmoregulants) were determined by kit assay (Berlin-Chemie, Berlin, Germany), dimethylthetin (low molecular weight permeant) by high-performance liquid chromatography (HPLC) and proline (low molecular weight permeant) by a water bath extraction method[35]. Phosphoenolpyruvate (an enzyme related to the initial carbon fixation processes in C_4 plants) level was determined by enzyme kit assay (Berlin-Chemie, Berlin, Germany). Abscisic acid (plant hormone; ABA) content was determined by HPLC[36].

2.4 Data analysis

To reflect the trend of each index under different salt and water treatment levels, we used thin plate splines to interpolate the data points and construct a 2D smooth surface.

To obtain correlations between the above phenotypic characteristics of *C. esculentus* and salt and water stresses, principal component analysis (PCA) was performed on the phenotypic characteristics including morphological characteristics, biomass, and active intracellular substances in leaves. Using structural equation modeling (SEM), we tested the direct and indirect relationships among hormone responses, osmoregulation, antioxidant system, morphological characteristics, and biomass in *C. esculentus* under combined salt and water stress, based on the results of PCA. The model results were evaluated by comparing the fit function (CFI > 0.80) with the root-mean-square error of approximation (RMSEA < 0.12). *P* of < 0.05 was deem to be a significant difference between treatment means.

PCA was performed in Origin 2019b (OriginLab Corporation, Northampton, MA, USA). Structural equation modeling was performed using packages “lavaan”[37] and “Hmisc”[38] in R (3.6.1) for model construction and goodness-of-fit testing. Significant differences between the data were compared using one-way analysis of variance. The chi-square of the data was determined using the least significant difference method and analyzed using IBM SPSS Statistics for Windows, Version 25.0 (IBM, Armonk, NY, USA).

3 Results

3.1 Effect of different salt and water treatments on biomass and morphological characteristics

Figure 2 shows that, when facing combined salt and water stress, the variation in biomass and morphological characteristics of *C. esculentus* is mostly affected by the water treatment than the of salt treatment. Of the biomass indicators, under the three water treatments, as the salt treatment level increases (S_0–S_2), LDW did not change. LDW under the three salt treatments, decreased as the watering level increased (W_0–W_2) (Fig. 2(a)). TDW did not change ($P < 0.05$) with increasing salt level under the water treatments. Under S_2, TDW decreased under increasing watering level (Fig. 2(b)). RDW did not change under increasing salt level under the water treatments, and under S_2 and S_0, RDW decreased with increasing watering level (Fig. 2(c)). For morphological characteristics, R/S only decreased with the increase of watering level under S_0 (Fig. 2(d)). Under the water treatments, there is no change in LA as the salt level increased. Under the salt treatments, LA first increased and then decreased as the watering level increased (Fig. 2(e)). PH did not change with the increase of salt level under the water treatments. Also, under the salt treatments, PH increased with the watering level (Fig. 2(f)). TLN decreased with increasing salt level under W_1. Under S_1 and S_2, TLN decreased with increased watering level, while under S_0, it first increased and then decreased with increased watering level (Fig. 2(g)). TBN did not change with increasing salt level under the water treatments. Under S_2, TBN decreased with increasing watering level, whereas under S_0, it first increased and then decreased (Fig. 2(h)).

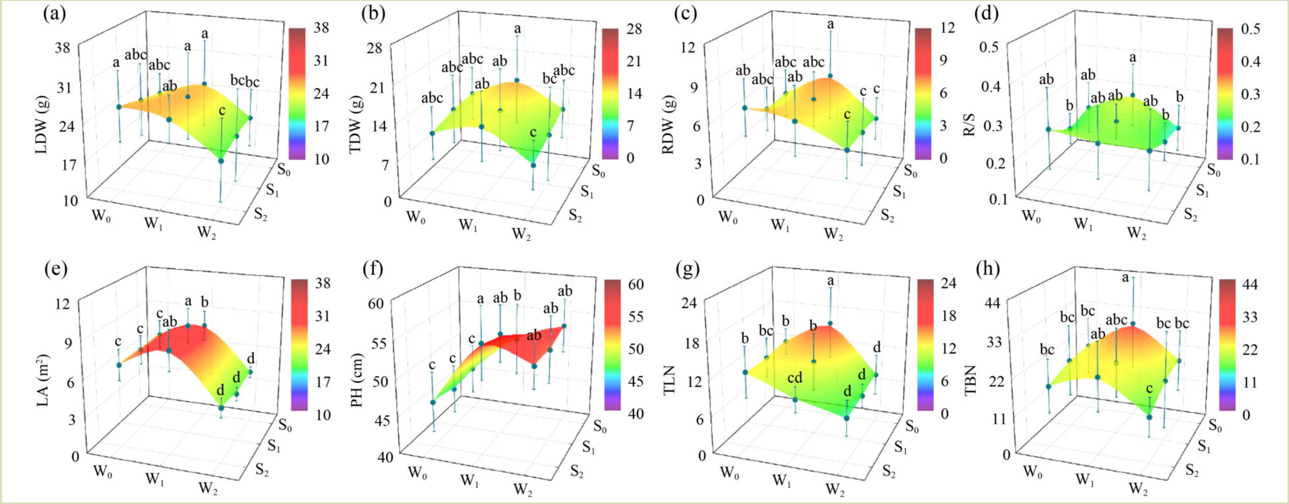


Fig. 2 Response of measured variates in response to three levels each of salt and water treatment in field-grown in *Cyperus esculentus*. (a) LDW, leaf dry weight; (b) TDW, tuber dry weight; (c) RDW, root dry weight; (e) LA, leaf area; (d) R/S, ratio of root dry weight to leaf dry weight; (f) PH, plant height; (g) TLN, tiller number; and (h) TBN, tuber number. W_0, control irrigation group; W_1, moderate irrigation group; W_2, low irrigation group; S_0, control salinity group; S_1, moderate salinity group; S_2, heavy salinity group.

3.2 Nitrogen and phosphorus concentration under different salt and water treatments

The patterns of nitrogen and phosphorus variation in the leaves, roots and tubers of *C. esculentus* had differential responses at different water and salt treatment levels (Fig. 3). Leaf N decreased with increasing salt level under the water treatments and a decreased with increasing watering level under S_0 (Fig. 3(a)). Root N decreased with increasing salt level under W_2 and increased with increasing watering level under S_1 and S_0 (Fig. 3(b)). Tuber N was not affected by the level of salt under the water treatments, but it increased with increasing watering level under S_0 and S_1 (Fig. 3(c)). Leaf P decreased with increasing salt level in the water treatment, and decreased with increasing of watering level under S_0 (Fig. 3(d)). Root P decreased with increasing salt treatment under W_1 and W_2, and increased with increasing watering level under S_1 (Fig. 3(e)). Under W_1, tuber P decrease with increasing salt level, whereas under S_0 and S_1, it decreased with increasing watering level (Fig. 3(f)).

3.3 Active intracellular substances in leaves under different salt and water treatments

The results indicated that the concentration of active intracellular substances in the leaves of *C. esculentus* were generally more affected by changes in watering level than in salt level (Fig. 4). Figure 4 shows that dimethylthetin increased with the increased salt levels in W_0 and W_1 and under S_1 and S_2 (Fig. 4(a)). Soluble sugars only increased significantly (P < 0.05) with the increase of the salt treatment level at W_0; at S_0 and S_1, it decreased with the increased watering level, while at S_2, it first increases and then decreases (Fig. 4(b)). Proline decreased with increasing salt level under W_0 and first decreased and then increased under W_1, under S_2, there was an increase with increasing watering level (Fig. 4(c)). Malondialdehyde only increased with increasing salt level under W_2, and across the three salt levels, there was a decrease with increasing watering level (Fig. 4(d)). Peroxisome decreased with increasing salt level under W_0 and W_1 but increased under W_1, and it first increased and then decreased with increasing watering level under S_2 whereas under S_0 the reverse response was observed (Fig. 4(e)). Superoxide dismutase decreased with increasing salt level across the three watering levels but only responded to watering level under S_1 (Fig. 4(f)). Phosphoenolpyruvate decreased with increasing salt level across the three watering levels as well as decreased with increasing watering level across the three salt levels (Fig. 4(g)). ABA only responded to changes in salt level under W_1 and increased with decreasing watering level under S_1 and S_2 (Fig. 4(h)).

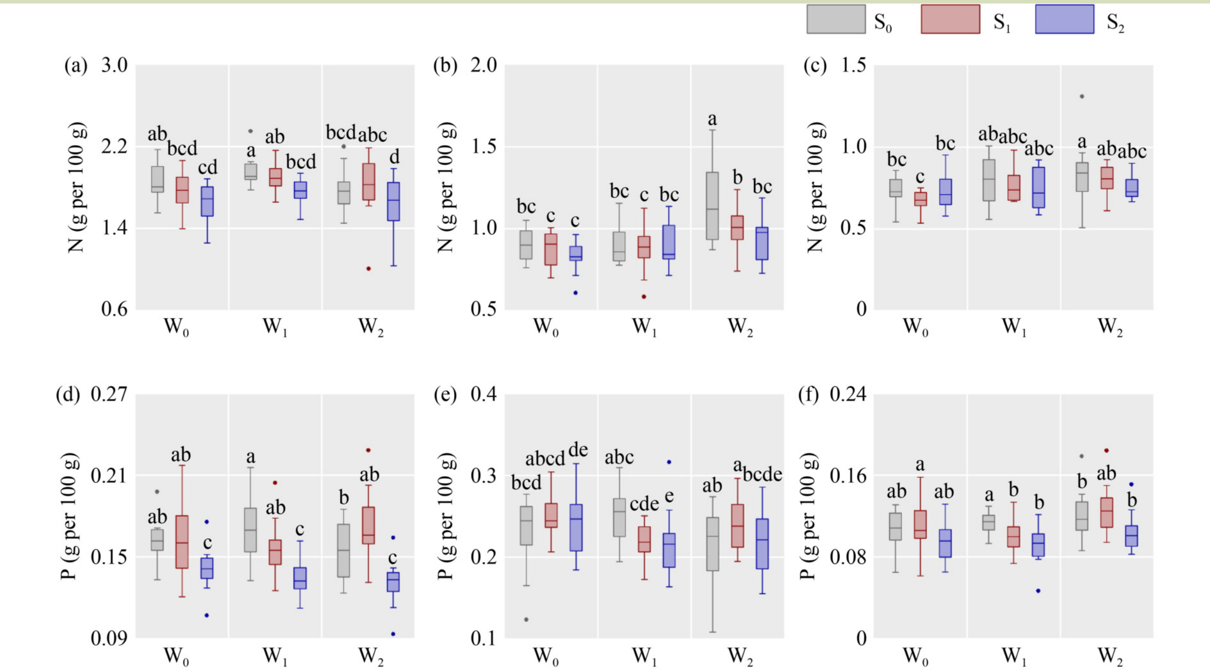


Fig. 3 Concentration of nitrogen (a–c) and phosphorus (d–f) in the leaves, roots, and tubers under three levels each of salt and watering levels in field-grown in *Cyperus esculentus*. The significance (P < 0.05) between different treatment combinations is indicated above each column. W_0, control irrigation group; W_1, moderate irrigation group; W_2, low irrigation group.

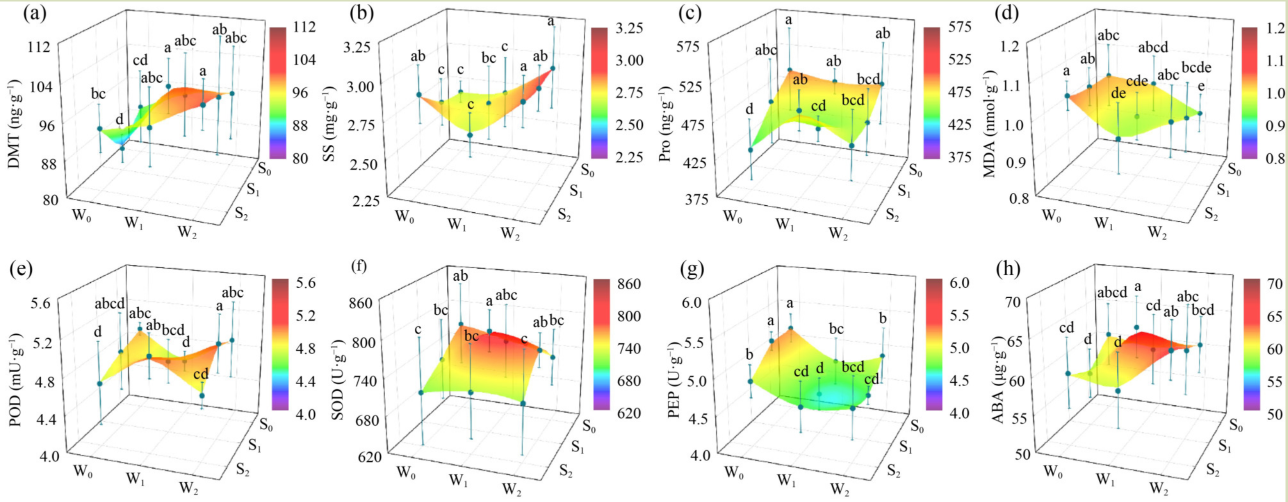


Fig. 4 Active intracellular active substances in leaves of field-grown *Cyperus esculentus* under three levels each of salt and water treatment. DMT, dimethylthetin; SS, soluble sugars; Pro, proline; MDA, malonic dialdehyde; POD, peroxisome; SOD, superoxide dismutase; PEP, phosphoenolpyruvate; and ABA, abscisic acid. W_0, control irrigation group; W_1, moderate irrigation group; W_2, low irrigation group; S_0, control salinity group; S_1, moderate salinity group; S_2, heavy salinity group.

3.4 Interactions among different phenotypic traits

For the combined salt and water stress (Fig. 5(a)), single water stress (Fig. 5(b)) and single salt stress (Fig. 5(c)) models, SEM explained 64.6%, 85.0%, and 71.2% of the biomass changes, respectively. In the combined salt and water stress model, there was only a negative correlation between environmental pressure and hormone response, with a path coefficient of −0.415. The hormone response was correlated with the morphological characteristics and biomass, with path coefficients of −0.291 and 0.168, respectively. There was a positive correlation between morphological characteristics and biomass, with a path coefficient of 0.798. The single water stress model revealed negative correlations between environmental pressure and hormone response, as well as osmoregulation, with path coefficients of −0.225 and −0.897, respectively (Fig. 5(b)). Additionally, there was a negative correlation between hormone response and morphological characteristics, with a path coefficient of −0.313. Finally, a positive correlation was observed between morphology characteristics and biomass, with a path coefficient of 0.859. In the single salt stress model (Fig. 5(c)), there were correlations between environmental pressure, and the antioxidant system and osmoregulation, with path coefficients of 0.542 and −0.915, respectively. The hormone response was correlated with the antioxidant system and morphology characteristics, with path coefficients of −0.369 and −0.261. A positive correlation was found between morphological characteristics and biomass, with a path coefficient of 0.802. Also, for the three stress models there was no evident direct relationship between environmental stress and biomass.

The morphological characteristics, biomass (Fig. 6(a,b)), and active intracellular substances in leaves (Fig. 6(c,d)) were clustered with 95% confidence intervals under salt and water treatments, respectively. The first and second PCA components after downscaling explained 46.5% and 15.1% of the cumulative variance for morphological characteristics and biomass, respectively (Fig. 6(a,b)). There were no significant differences in the distribution of morphological characteristics between three salt treatments. The confidence ellipses for the distribution of the three salt treatment levels roughly overlapped (Fig. 6(b)). In contrast, variations in water treatment levels led to more noticeable differences in the distribution of loads for morphological characteristics. The confidence ellipses for W_0 and W_1 had more distinct clustering differences (Fig. 6(a)). For the active intracellular substances in leave, the first and second PCA components after downscaling explained 18.1% and 17.0% of the cumulative variance, respectively, but there is no significant difference in clustering between their confidence ellipses (Fig. 6(c,d)).

4 Discussion

The combined effect of salt and water stress had a significant impact on the biomass and morphological characteristics of *C. esculentus*. LDW, TDW, RDW, LA, TLN and TBN had significant decreases with the increase of combined salt and water stress (Fig. 2), with the greatest decreases observed for LDW, LA, and TLN (Fig. 2(a,e,g)). These results showed that

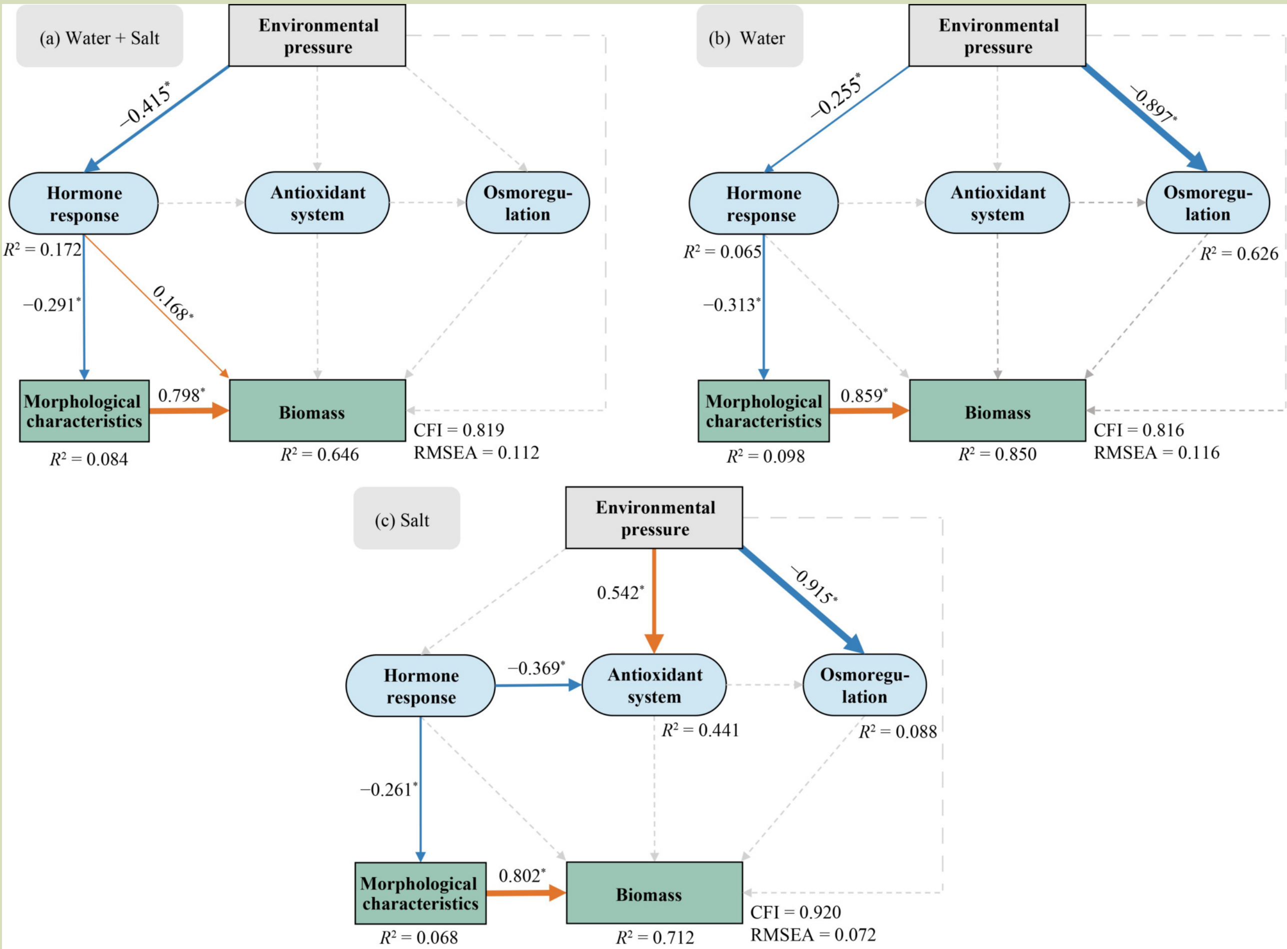


Fig. 5 Structural equation modeling of associations between hormone response (abscisic acid), antioxidant regulation, osmoregulation, morphological characteristics and biomass in field-grown in *Cyperus esculentus*. The arrows in the diagram represent correlations between variables, with red arrows indicating positive correlations and blue arrows indicating negative correlations. Standardized path coefficients are shown in the middle of the arrows. The solid and dashed lines indicate the significance (P < 0.05) the correlations between variables. R^2 represents the degree of explanation of potential variables in the model.

the growth of *C. esculentus* was inhibited by combined salt and water stress, the aboveground parts, especially the leaves, were most severely affected. The severe effects on leaf development indicate that combined salt and water stress can limit photosynthetic capacity by reducing leaf surface area. In contrast, the belowground effects, particularly RDW, were less pronounced, indicating that *C. esculentus* may maintain relatively stable yields despite the impairment of its photosynthetic capacity. It is possible that the changes in resource allocation strategies of *C. esculentus* under stress conditions are responsible for this. When subjected to abiotic stress such as water, salt and high temperature, the plant can increase water use efficiency to maintain plant organic matter production activities by inhibiting canopy development and increasing nitrogen and phosphorus nutrient concentration of the belowground parts[39–42], and some studies have found this mechanism of *C. esculentus* under single water or salt stress conditions[15,25]. Consistent with previous studies, our results show that LA decreased (P < 0.05) with increasing combined salt and water stress (Fig. 2(e)). Additionally, the belowground nitrogen and phosphorus concentration increased (Fig. 3), while the yield remained relatively stable (Fig. 2(b)). These results indicate that *C. esculentus* may have adapted to combined salt and water stress by reducing the allocation of water and nutrient resources to the leaves. The combined salt and water stress had an inhibitory effect on the growth of both the above- and belowground parts. However, the belowground parts, particularly the yield, were less affected than the aboveground parts, indicating it may maintain relatively stable yields by sacrificing the level of aboveground part development

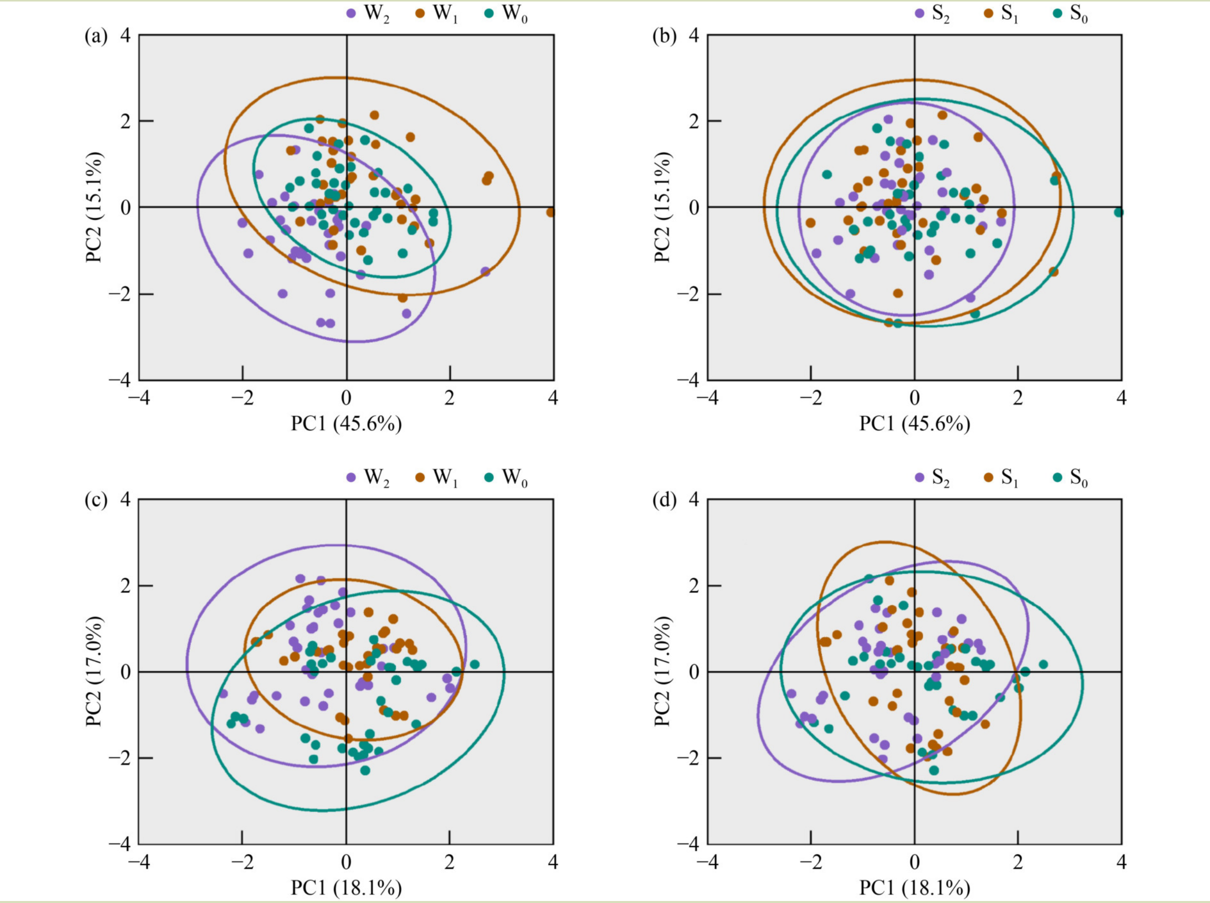


Fig. 6 Principal component analysis clustering of morphological characteristics and biomass (a and b), and active intracellular substance (c and d) in field-grown in *Cyperus esculentus* under water (a and c) and salt (b and c) treatments. The treatments are represented by different colors for the individual points and 95% confidence ellipses. PC1, The first PCA components after downscaling; PC2, The second PCA components after downscaling. W_0, control irrigation group; W_1, moderate irrigation group; W_2, low irrigation group; S_0, control salinity group; S_1, moderate salinity group; S_2, heavy salinity group.

under the combined salt and water stress.

Maintaining reactive oxygen species (ROS) homeostasis under combined salt and water stress may be another crucial factor in maintaining the yield stability. When salt and water stresses are present, osmotic and ionic stresses are triggered, resulting in the production of large amounts of ROS. If these ROS are not scavenged promptly, cell membranes may suffer oxidative damage, which in turn adversely affects photosynthesis and plant growth[43–46]. However, our results indicate that *C. esculentus* accumulated low molecular weight osmoregulants and its ABA levels as well as antioxidant enzyme levels were increased under combined salt and water stress (Fig. 4(a–c,e,f)), which helped to maintain the balance of intracellular ROS production and scavenging[47,48]. Meanwhile, the intracellular malondialdehyde concentration in *C. esculentus* leaves remained relatively stable in all combinations of salt and water stress (Fig. 4(d)), which further means that *C. esculentus* can remove excess ROS produced in the cell timely, even under severe salt and water combined stress. Therefore, the ability of *C. esculentus* to maintain the balance between intracellular ROS production and scavenging may be a key factor in maintaining stable yields under combined salt and water stress.

In our study, the changes in yield and active intracellular substances of *C. esculentus* under combined salt and water stress were smaller than the changes observed under single salt or water stress[15,49]. By comparison, previous studies have generally found that although *C. esculentus* also can initiate response mechanisms including hormone responses, osmoregulation and antioxidant system to resist when exposed to a single water or salt stress, these mechanisms are insufficient to remove the excess ROS produced under high water or salt stress, resulting in a drastic reduction in yield. Thus, these differences imply a negative synergism on the yield and active intracellular substances of *C. esculentus* under combined salt and water stress. This may be related to the similarities between salt and water stresses, as both salt and water stresses can cause reduced water potential, production of toxic molecules and a series of identical metabolic changes in plants[50–52], and these effects were also observed in recent studies[53]. Based on this similarity, the negative synergism in the coexistence of salt and water stresses may be attributed to the response initiated by *C. esculentus* simultaneously mitigates the homogeneity constraints imposed by salt and water stresses.

Although the negative synergism contributed to alleviating environmental stress when *C. esculentus* is exposed to combined salt and water stress, this is unable to alleviate specific stressors (e.g., ion toxicity) generated by salt stress[50,54]. Our results indicate that hormone response might make a significant contribution to in reducing salt-specific stress. SEM (single salt stress) had a negative correlation between hormone response and the antioxidant system (Fig. 5(c)), it means that hormone response effectively reduced the salt stress pressure on the *C. esculentus* antioxidant system. This may be attributed to the multiple functions of hormones in mediating plant adaptation to salt stress, including processes such as transduction of salt stress signals, control of stomatal closure, and mediation of ion transport[55,56]. In addition, hormones are crucial for plant adapting to specific stress factors, particularly in multiple stress combinations. When plants encounter multiple abiotic stress combinations, hormones that transduce different stress signals or promote the synthesis of different metabolites may promote or inhibit other pathways, ultimately increasing the ability of plants to tolerate different stress combinations[57–60]. This is consistent with our finding that when for single water or salt stress model, hormone response plus osmoregulation and antioxidant system plus osmoregulation had significant responses to their respective environmental stresses (Fig. 5(b,c)). These results reveals their prominent role in adapting to the water (or salt) stress in combined salt and water stresses[61,62]. In contrast, hormone response replaced both as the only mechanism that significantly responded to environmental stress in the combined salt and water stress model (Fig. 5(a)), indicating that hormone response is more critical than the antioxidant system or osmoregulation in the adaptation to combined salt and water stress. This may be attributed to the contribution of ABA to enhance the ability of plants to tolerate compound multiple stresses. However, hormones such as ABA can regulate plant growth as well as plant responses to stress[63,64]. Some stress hormones (especially ABA) in plant response to a particular stress often simultaneously increase tolerance to other stresses as well, including the accumulation of transcripts and metabolites specific for different stresses[59,60]. Thus, hormones may help plants adapt to multiple abiotic stress conditions in a more rapidly and efficiently by initiating and linking different response mechanisms. This process may explain why the ABA was more important than the antioxidant system and osmoregulation in response to combined salt and water stress in this study. Also, similar conclusions made from studies conducted on other salt- or drought-tolerant crops[65–67].

Additionally, of the three response mechanisms, only hormone response had a significant positive relationship with biomass. This may be related to the function of ABA in helping synthesize more organic matter accumulation under stress conditions by mediating the opening and closing of leaf stomata, inhibition of canopy development and photosynthate partitioning to increase crop water use efficiency under water deficit[68–70]. Our results validate this function with SEM in the three stress models revealing that only ABA had positive correlations with biomass by affecting the morphological characteristics (Fig. 5). Thus, the allocation strategies of *C. esculentus* under combined salt and water stress conditions, as discussed previously, may be regulated by hormone responses as well. Overall, these results indicate that ABA is crucial for the adaptation of *C. esculentus* to combined salt and water stress.

Also, our study made another noteworthy finding. Although previous studies have generally concluded that the specific role of salt in ion toxicity exceeds the effect of water[50], which means its effect on productivity may be stronger in combined salt and water stress than in water stress[51]. Our results showed that the morphological characteristics and biomass of *C. esculentus* were more sensitive to water than salt (Fig. 2; Fig. 6(a)). Considering the degree of cellular oxidative damage in *C. esculentus* under combined salt and water stress remained stable (Fig. 4(d)), this phenomenon may be due to the salt stress-induced ion toxicity was kept within tolerable limits and was not sufficient to cause specific effects on normal growth. In this case, reducing morphological changes, such as leaf area and leaf dry weight, may be more effective in improving the ability of plants to adapt to soil water resource limitations caused by combined salt and water stress[35,71]. These processes partly explain why the morphological characteristics and biomass of *C. esculentus* were more sensitive to water stress in this study, and why the pattern that root, leaf and tuber biomass of *C. esculentus* can increase under mild single salt or water stress[25,26], still exist under combined salt and water stress (Fig. 2(a–c)).

5 Conclusions

Our results indicate that while combined salt and water stress affect the growth of *C. esculentus*, it may reduce the allocation of water and nutrient resources to the aboveground part, and relied on ABA, low molecular weight osmoregulants and antioxidant system to maintain the balance between intracellular ROS production and scavenging, ultimately resulting in the relative stability of yield. ABA is crucial for enhancing the tolerance of *C. esculentus* to combined salt and water stress. It mediated the regulation of the allocation of limited water and nutrient resources and initiated the responses to homogeneous and especially the specific limitation under the combined salt and water stress. It is important to note that, while it is often assumed that increased salinity-induced ion toxicity would result in a stronger impact of salt stress on plant growth and development compared to water stress, our findings indicate that changes in morphological characteristics of *C. esculentus* were more sensitive to water stress. This may be due to the negative synergism of coexisting salt and water stresses, which reduced the degree of oxidative damage to cells. Overall, *C. esculentus* suffered less yield decline than most other crops in environments where salt and water stress coexisted. Therefore, the excellent tolerance of *C. esculentus* to combined salt and water stress indicates its economic value and agricultural potential for cultivation in salinized lands with inadequate irrigation.

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Compliance with ethics guidelines

Jing Xu, Lang Liu, Fang Kang, Boyuan Liu, Minghan Yu, and Keyu Fa declare that they have no conflict of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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