Physio-Ecological Responses and Adaptation Strategies of Suaeda salsa under Combined Flooding and Litter Addition Conditions

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Abstract

Hydrological changes and litter accumulation are key habitat factors in the ecological restoration of coastal saline-alkali wetlands. To elucidate the physiological adaptation mechanisms of the dominant species *Suaeda salsa* to combined habitat changes, this study established three waterlogging gradients (no waterlogging, intermittent waterlogging, and continuous waterlogging) and four litter addition treatments (no litter addition, aboveground litter addition only, belowground litter addition only, and full litter addition), and systematically analyzed the response patterns of growth, photosynthetic, and physio-biochemical characteristics of *Suaeda salsa*. The results showed that: (1) Waterlogging significantly suppressed the growth of *Suaeda salsa*, with the alleviative effects of litter addition being strongly waterlogging-dependent. Full addition and belowground addition were most effective under continuous waterlogging; belowground addition performed best under non-waterlogged and intermittent waterlogging; and compensatory growth occurred under intermittent waterlogging without litter. (2) Litter addition mitigated waterlogging-induced damage to the photosynthetic apparatus, facilitating a shift from passive defense to active optimization, with belowground litter exerting a greater promoting effect on carboxylation efficiency and light use efficiency. (3) Belowground litter alone enhanced antioxidant enzyme activities and reduced lipid peroxidation, whereas full litter addition maintained cellular homeostasis via osmotic adjustment. (4) Correlation and PCA revealed waterlogging as the dominant stressor and litter components as key determinants of resource allocation, uncovering a systemic coupling from photosynthetic efficiency to biomass and antioxidant defense in *Suaeda salsa*. In summary, the waterlogging gradient determined the baseline shift in the physiological variation of *S. salsa*, and belowground litter, by synergistically regulating stomatal and non-stomatal limitations, enhancing resource use efficiency, and activating antioxidant defense, facilitated a strategic transition from defense to growth compensation. These findings can provide a scientific basis for the ecological restoration of coastal saline-alkali wetlands.

1. Introduction

Wetlands, as critical global ecosystems, not only perform irreplaceable ecological functions in biodiversity conservation and water resource regulation but also play a pivotal role in the global carbon cycle [1]. The Yellow River Delta wetland, situated at the river-sea-land interface, harbors one of the most intact and expansive coastal wetland ecosystems in the warm temperate zone, playing an essential role in nutrient cycling, energy flow, and the maintenance of ecological balance [2]. However, driven by global warming, sea-level rise, and intensifying anthropogenic activities, coastal wetlands worldwide are undergoing severe ecological degradation, manifested as vegetation decline, accelerated soil salinization, and diminished ecosystem services [3, 4]. Consequently, coastal wetland ecological restoration has emerged as a critical agenda within the context of global sustainable development, with a core objective of recovering the structure and function of dominant plant communities. Enhancing the restoration capacity and community stability of vegetation in saline wetlands has therefore become a vital topic in current ecological research and land-use management [5, 6].

As a pivotal process in wetland biogeochemical cycles, litter decomposition serves as a crucial nexus connecting vegetation and soil, establishing a continuous “vegetation-litter-soil” nutrient transfer chain. This process plays a decisive role in regulating ecosystem nutrient status, soil carbon sequestration, and the trajectory of community succession [7]. The rate of decomposition largely dictates the accumulation velocity of surface litter and the return rate of nutrients to the soil pool, subsequently influencing plant germination and growth [8, 9]. Therefore, litter accumulation and decomposition represent not only a major driver of soil nutrient dynamics but also a key factor regulating vegetation recruitment and community succession. Nevertheless, current research on litter focuses predominantly on the impacts of decomposition processes on soil carbon and nitrogen cycling, whereas its role as an independent habitat factor regulating plant growth and development remains understudied. Furthermore, prior studies have primarily focused on the single-factor effects of hydrological fluctuations or litter cover on seedlings [10]. Rare reports have documented the interactive effects of litter addition and water level fluctuations on plant growth. In coastal wetlands characterized by complex flooding regimes, the ecological effects of litter are highly likely to shift in direction or intensity depending on hydrological conditions, an interaction that warrants systematic investigation.

Litter influences plants through dual attributes: physical barriers and biochemical modifications, with distinct functional differentiation observed between aboveground and belowground components [11]. Aboveground litter affects seed germination, seedling emergence, and subsequent plant growth mainly through the interception effects of physical microhabitats, such as shading, temperature buffering, moisture retention, and mechanical barriers, and its regulation of early species establishment is strongly environment-dependent [12]. For halophytes like *Suaeda salsa*, their litter is rich in saline ions, and the release of salt during decomposition may alter rhizosphere soil salinity dynamics, thereby influencing plant water absorption and ionic balance. In contrast, belowground litter primarily optimizes the rhizosphere microenvironment through the input of nutrients and organic matter released during decomposition, which regulates soil structure, enhances nutrient availability, and alters microbial community composition [13]. Under flooding stress, shifts in soil redox conditions directly affect the decomposition rate and nutrient release patterns of belowground litter [14], thereby modulating its mitigation effects on plant photosynthesis and growth. Based on this, decoupling the differentiated ecological effects of aboveground and belowground litter is essential for fully elucidating plant adaptation mechanisms under fluctuating hydrological conditions [15].

Suaeda salsa is a typical halophyte, as well as a dominant and pioneer species in the coastal wetlands of the Yellow River Delta. Its distribution spans 27.9% of the total wetland area, playing an important role in maintaining regional ecosystem stability and ameliorating saline soils [16, 17]. Although existing studies have explored the salt-tolerance mechanisms of *Suaeda salsa* in depth, research regarding the impacts of the dual compound conditions of litter input and flooding on its growth and physiological-ecological characteristics remains a blank [18]. In coastal wetland ecosystems, *Suaeda salsa* simultaneously faces dual habitat modifications from periodic flooding and litter accumulation. This compound condition may generate interactive effects distinct from those of single factors, exerting complex impacts on plant survival, growth, and physiological functions.

In view of this, this study simulated typical hydrological habitats of the Yellow River Delta wetlands by setting up three flooding treatments and four litter addition modes to systematically analyze the growth development and physiological response patterns of *Suaeda salsa* under compound stress. The specific objectives of this study were:

(1) To clarify the interactive effects of flooding gradients and litter components on the morphological traits and biomass allocation of *Suaeda salsa*, thereby revealing the hydrological dependence of litter mitigation effects;

(2) To explore the predominant role of non-stomatal limitations under continuous flooding and the protective pathways of litter on the photosynthetic apparatus by analyzing the coupling relationships among stomatal conductance, intercellular CO_2 concentration, and carboxylation efficiency;

(3) To elucidate the physiological trade-off strategies of *Suaeda salsa* achieved through antioxidant enzyme activation and osmotic adjustment under compound stress;

(4) To integrate aboveground-belowground ecological processes with physiological plasticity mechanisms, thereby constructing a multidimensional theoretical framework for vegetation restoration and adaptive management in degraded coastal wetlands. The findings of this study will provide theoretical support for formulating vegetation restoration strategies for *Suaeda salsa* and enhancing ecological functions in the degraded saline wetlands of the Yellow River Delta, particularly offering a scientific basis for zoned litter management based on hydrological conditions.

2. Materials and methods

2.1 Experimental materials

The seeds and litter materials of *Suaeda salsa* used in this study were collected from the Yellow River Delta Wetland Nature Reserve, Hekou District, Dongying City, Shandong Province, China (38.044829°N, 118.916204°E). The seeds were collected on October 18, 2024, and the litter materials (dead branches and dead roots) were collected on April 28, 2025. The species was formally identified by Professor Jingkuan Sun based on morphological characteristics. Voucher specimens (No. 250102) were deposited at the Herbarium of the Yellow River Delta Ecological Environment Research Center, Shandong University of Aeronautics. After collection, the seeds were air-dried in the shade, and seeds of uniform size and plump shape were selected for subsequent use. The collected litter was divided into aboveground and belowground parts using pruning shears, and each part was cut into 1–2 cm segments. The cultivation substrate was saline-alkali soil, which was sun-dried and then sieved through a 10-mesh screen. The cultivation containers were plastic pots with an upper outer diameter of 24 cm, a lower bottom outer diameter of 19.5 cm, and a height of 26 cm. Seven plants were grown per pot. The seeds were germinated on June 3, 2025, and the seedlings were cultivated in a greenhouse at the Yellow River Delta Ecological Environment Research Center under controlled conditions for the experiment.

2.2 Two-factor experimental design of waterlogging stress and litter addition for *Suaeda salsa*

To investigate the effects of litter addition and soil moisture variation on plant growth and physiological status in a *Suaeda salsa* wetland ecosystem, three waterlogging treatments were established: no waterlogging (NF), intermittent waterlogging (IF), and continuous water-logging (CF); and four litter treatments: only aboveground litter addition (A), only belowground litter addition (B), both aboveground and belowground litter addition (T), and no litter addition (N). The addition ratio of aboveground to belowground litter was 3:1. Each treatment had three replicates, giving a total of 36 experimental pots, which were used to examine the effects of different litter additions and waterlogging conditions on the growth of *Suaeda salsa* (Fig. 1).

2.3 Measurement methods

2.3.1 Measurement of growth indicators of *Suaeda salsa*

Five plants were randomly selected from each treatment. The number of branches and leaves were recorded. Plant height, crown width, and branch length were measured using a measuring tape (precision 0.01 cm), and stem diameter was measured with a vernier caliper (precision 0.02 mm). The *Suaeda salsa* plants were carefully removed from the pots, and the taproot length was measured. In addition, the plants were completely separated into roots, stems, and leaves, oven-dried at 60 ℃ to constant weight, and the biomass of roots, stems, and leaves was determined separately.

2.3.2 Photosynthetic characteristics and chlorophyll content

On windless, clear days between 9:00 AM and 11:00 AM, fully expanded leaves were selected to measure gas exchange parameters using a LI-6400XT portable photosynthesis system. The photosynthetically active radiation (PAR) inside the leaf chamber was set to 1000 μmol·m^{-2}·s^{-1}. The net photosynthetic rate (P_n, μmol·m^{-2}·s^{-1}), transpiration rate (T_r, mmol·m^{-2}·s^{-1}), stomatal conductance (G_s, mol·m^{-2}·s^{-1}), and intercellular CO_2 concentration (C_i, μmol·mol^{-1}) were recorded[19]. Chlorophyll content was determined by immersing leaf tissue in 95% ethanol for 24 hours, followed by absorbance measurements using a microplate reader and a spectrophotometer to quantify chlorophyll a, chlorophyll b, and carotenoid contents, respectively. Additionally, the following eco-physiological indices were calculated:

Stomatal limitation value (L) = 1 − C_i / C [20] (where C is the ambient CO_2 concentration)

Instantaneous water use efficiency (*WUE*, μmol·$mmol^{-1}$) = P / T_r [21]

Apparent light use efficiency (*LUE*, mmol·mol^{-1}) = P / *PAR* [22]

Carboxylation efficiency (*CE*, μmol·m^{-2}·s^{-1}) =*P*□ /C_i [23]

2.3.3 Measurement of physiological indicators of *S. salsa*

The contents of photosynthetic pigments (chlorophyll a, chlorophyll b, and carotenoids) were determined by ethanol extraction colorimetry. Catalase (CAT) activity was measured by potassium permanganate titration. Peroxidase (POD) activity was assayed using the guaiacol method. Superoxide dismutase (SOD) activity and malondialdehyde (MDA) content were determined by the xanthine oxidase method and the thiobarbituric acid method, respectively. Soluble sugar (SS) content was measured by the anthrone colorimetric method, and soluble protein (SP) content was determined by the Coomassie Brilliant Blue G-250 dye-binding method[24].

2.4 Data analysis

SPSS (v.27.0) was used for intergroup difference tests, Z-score standardization, and Spearman correlation analysis of the various indicators. Data compilation and figure preparation were performed using Microsoft Office Excel 2011 and Origin 2026. All experimental data are presented as mean ± standard deviation.

3. Results and analysis

3.1 Changes in growth indicators of *Suaeda salsa* under different treatments

Two-way analysis of variance (ANOVA) indicated that plant height, root length, stem diameter, and total biomass were all significantly influenced by litter addition, flooding regimes, and their interactive effects (Table 1). With the intensification of flooding stress, both plant height and root length exhibited an overall declining trend; however, distinct variations were observed among the different litter treatments (Fig. 2A, B). Under IF conditions, plant height and root length in the N treatment were significantly higher than those under NF conditions, exhibiting substantial increases of 28.21% and 8.04%, respectively ($p < 0.05$). Under CF conditions, the T treatment significantly out-performed the N treatment, with plant height and root length increasing by 32.9% and 36.6%, respectively.

Table 1
ANOVA on the effects of litter addition, water variation, and their interaction on growth indicators of *Suaeda salsa*.

Factors	Indicators							
	Plant height		Root length		Stem diameter		Total biomass	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Litter treatment	21.631	< 0.001	4.27	0.015	13.741	< 0.001	13.132	< 0.001
Flooding treatment	69.384	< 0.001	5.609	0.01	206.4	< 0.001	83.88	< 0.001
Litter× Flooding treatment	43.176	< 0.001	7.415	< 0.001	14.597	< 0.001	10.468	< 0.001

Stem diameter contracted significantly with increasing flooding intensity, reaching its lowest values across all treatments under CF conditions (Fig. 2C). Notably, the B treatment maintained a relatively stable stem diameter across all hydrological contexts; particularly under CF conditions, the stem diameter in Treatment B was significantly higher than that in Treatments N and A, by 21.19% and 36.79%, respectively. Regarding total biomass, Treatment B exhibited highly significant promotional effects under both NF and IF conditions, outperforming all other treatments (Fig. 2D). Although biomass accumulation was generally suppressed under CF conditions, Treatment T remained at the highest level, significantly surpassing Treatments N and A.

3.2 Photosynthetic physiological character-istics of *Suaeda salsa* under different treatments

3.2.1 Changes in gas exchange parameters

Two-way analysis of variance indicated that P_n, G_s, C_i and T_r were all significantly influenced by litter addition, flooding regimes, and their interactive effects (Table 2). In our experiment, P_n (Fig. 3A) exhibited a significant gradient-dependent declining trend with the intensification of flooding stress ($p < 0.05$). Under CF conditions, the P_n value of Treatment N decreased by 47.86% compared to that under NF conditions, whereas the Treatments T and B exhibited significantly higher P_n values than the Treatment N.

Table 2
ANOVA on the effects of litter addition, water variation, and their interaction on photosynthetic indices of *Suaeda salsa*.

Factors	Indicators							
	P_n		G_s		C_i		T_r	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Litter treatment	6.247	0.003	40.352	< 0.001	4.883	0.017	86.422	< 0.001
Flooding treatment	19.641	< 0.001	95.519	< 0.001	27.397	< 0.001	510.649	< 0.001
Litter× Flooding treatment	5.868	0.001	3.994	0.007	16.148	< 0.001	116.216	< 0.001

Although G_s generally decreased with increasing flooding intensity, the regulatory effects of litter additions on G_s exhibited a distinct dependency on hydrological conditions (Fig. 3B). Under NF conditions, no significant differences in G_s were observed among the litter treatments, with all treatments maintaining relatively high levels. Under IF conditions, G_s values in Treatments B and N were 0.239 and 0.224 $mol \cdot m^{-2} \cdot s^{-1}$, respectively, which were significantly higher than those in Treatments A and T ($p < 0.05$). Under the CF regime, G_s dropped to its minimum across all treatments; however, Treatments B and T maintained significantly higher G_s values than Treatments N and A, with Treatment B exhibiting the maximum value of 0.189 $mol \cdot m^{-2} \cdot s^{-1}$.

Under NF and IF conditions, no significant differences in C_i were detected among the various litter treatments. However, the treatments diverged significantly under CF conditions; C_i values in Treatments N and A decreased to 178 and 165 $\mu mol \cdot mol^{-1}$, respectively, representing a reduction of approximately 25%-30% compared to the NF conditions. Conversely, Treatments B and T maintained relatively high C_i levels of 245 and 232 $\mu mol \cdot mol^{-1}$, respectively, which showed no significant variance from those under NF and IF conditions.

T_r exhibited a general upward trend as flooding stress intensified (Fig. 3D). Under NF conditions, T_r values were similar across all treatments with no significant differences. Under IF conditions, T_r in Treatment B increased to 6.49 $mmol \cdot m^{-2} \cdot s^{-1}$, whereas it decreased to 3.53 $mmol \cdot m^{-2} \cdot s^{-1}$ in Treatment A. Under CF conditions, Treatment T reached the maximum value among all combinations, peaking at 7.37 $mmol \cdot m^{-2} \cdot s^{-1}$.

3.2.2 Changes in photosynthetic efficiency indicators

Two-way analysis of variance indicated that the L_s, *CE* and *LUE* were all significantly influenced by litter addition, flooding regimes, and their interactive effects, whereas the *WUE* was significantly affected

solely by litter addition (Table 3).

Table 3
ANOVA of the effects of litter addition, water variation, and their interaction on photosynthetic efficiency indicators of *Suaeda salsa*.

Factors	**Indicators**							
	L_s		***WUE***		***CE***		***LUE***	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Litter treatment	25.848	< 0.001	56.974	< 0.001	5.921	0.004	6.247	0.003
Flooding treatment	30.075	< 0.001	2.391	0.094	24.427	< 0.001	19.641	< 0.001
Litter× Flooding treatment	12.456	< 0.001	1.068	0.409	9.441	< 0.001	5.868	0.001

L_s generally decreased with increasing flooding intensity (Fig. 4A). Under NF and IF conditions, no significant differences in L_s were observed among the various litter treatments. However, under CF conditions, L_s values in Treatments N and A decreased to 0.318 and 0.279, respectively, whereas Treatment B maintained a significantly higher L_s value of 0.36 compared to Treatment A ($p < 0.05$).

Increasing flooding intensity exerted a significant inhibitory effect on *WUE* (Fig. 4B). Under NF conditions, Treatment N exhibited the maximum *WUE* (4.419 $mmol \cdot mol^{-1}$), while Treatment T exhibited the minimum (2.125 $mmol \cdot mol^{-1}$), representing a reduction of approximately 51.9% compared to Treatment N. Under IF and CF conditions, the *WUE* of all treatments decreased further compared to that under NF conditions; notably, Treatment N consistently maintained the highest *WUE*, whereas Treatment T remained at the lowest level throughout.

Flooding stress significantly suppressed the carboxylation activity of leaves (Fig. 4C). With the intensification of flooding, a distinct gradient-dependent declining trend was observed across all litter treatments ($p < 0.05$). Under CF conditions, the *CE* value in Treatment B was 0.056$\mu mol \cdot m^{-2} \cdot s^{-1}$, which was significantly higher than that in Treatment A (0.035 $\mu mol \cdot m^{-2} \cdot s^{-1}$).

The *LUE* of all treatments was significantly impaired by the aggravation of flooding stress (Fig. 4D). Compared to NF conditions, the *LUE* value of Treatment N under CF conditions dropped from 0.022 $mmol \cdot mol^{-1}$ to 0.015 $mmol \cdot mol^{-1}$, representing a decline of 31.82%. Litter addition led to a distinct divergence under CF conditions; specifically, the *LUE* in Treatment B recovered to 0.017 $mmol \cdot mol^{-1}$, which was approximately 54.5% and 21.4% higher than those in Treatments A and T, respectively ($p < 0.05$). No significant variance was detected between Treatments T and N.

3.2.3 Changes in photosynthetic pigment indicators

Two-way analysis of variance indicated that the contents of chlorophyll a, chlorophyll b, and carotenoids were all significantly influenced by litter addition, flooding regimes, and their interactive effects, whereas the chlorophyll a/b ratio was significantly affected solely by the individual factors, with their interaction effect failing to reach statistical significance (Table 4).

Table 4
ANOVA of the effects of litter addition, water variation, and their interaction on photosynthetic pigment indicators of Suaeda salsa.

Factors	**Indicators**							
	Chlorophyll a		**Chlorophyll b**		**Carotenoids**		**Chlorophyll a/b**	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Litter treatment	17.835	< 0.001	9.376	< 0.001	3.595	0.028	21.685	< 0.001
Flooding treatment	40.14	< 0.001	26.004	< 0.001	41.202	< 0.001	22.577	< 0.001
Litter× Flooding treatment	12.367	< 0.001	4.098	0.006	8.461	< 0.001	2.342	0.064

Chlorophyll a content (Fig. 5A) significantly decreased with the intensification of flooding stress ($p < 0.05$). Under CF conditions, Treatment N exhibited the most drastic reduction, dropping by approximately 55.4% compared to NF conditions to a value of 0.058 mg/g. Conversely, the B treatment maintained a higher content of 0.092 mg/g, which was approximately 58.6% higher than that in the N treatment. No significant difference was detected between the T and B treatment, though both were significantly higher than the N treatment. Under NF and IF conditions, the variances among the different litter treatments did not reach statistical significance.

Chlorophyll b content displayed an overall declining trend as flooding intensified, but the mitigation effects varying distinctly across different litter additions (Fig. 5B). Under NF conditions, Treatment B exhibited the maximum value (0.201 mg/g), while Treatment T exhibited the minimum (0.123 mg/g). Under IF conditions, substantial reductions were observed in Treatments N and A, dropping to 0.133 mg/g and 0.117 mg/g, respectively, whereas Treatment B maintained a relatively high level. Under CF conditions, Treatment N dropped to its minimum (0.104 mg/g), whereas Treatment B remained the highest (0.139 mg/g). Notably, Treatment T rebounded to 0.130 mg/g under this extreme condition.

Carotenoid content significantly decreased with increasing flooding intensity (Fig. 5C). Compared to NF conditions, the carotenoid content in Treatment N under CF conditions dropped from 0.0189 mg/g to 0.0041 mg/g, representing a reduction of 78.3%. Concurrently, under CF conditions, Treatment T rebounded to 0.0113 mg/g, which constituted an approximate 130% recovery compared to its value under IF conditions, significantly outperforming Treatments N and A ($p < 0.05$). Under NF and IF conditions, variances among the litter treatments remained minimal.

The chlorophyll a/b ratio generally decreased under IF conditions, with Treatment N dropping from 0.757 to 0.620 (Fig. 5D). However, under CF conditions, the chlorophyll a/b ratio in Treatment N recovered to 0.744, approaching its baseline level under NF conditions. Treatments A and B also experienced recoveries, rising to 0.641 and 0.612, respectively. Treatment T reached 0.656, as all treatments exhibited a universal recovery in their ratios compared to those under IF conditions.

3.3 Effects of different treatments on the physiological and biochemical characteristics of *Suaeda salsa*

3.3.1 Effects of different treatments on antioxidant enzyme activities of *Suaeda salsa*

Two-way analysis of variance indicated that the activities of CAT, POD and SOD were all significantly influenced by litter addition, flooding regimes, and their interactive effects (Table 5).

Table 5
ANOVA of the effects of litter addition, water variation, and their interaction on on antioxidant enzyme indicators of Suaeda salsa.

Factors	**Indicators**					
	CAT activity		**POD activity**		**SOD activity**	
	F	*p*	*F*	*p*	*F*	*p*
Litter treatment	17.835	< 0.001	12.219	< 0.001	13.18	< 0.001
Flooding treatment	94.445	< 0.001	44.842	< 0.001	45.449	< 0.001
Litter× Flooding treatment	10.353	< 0.001	11.856	< 0.001	5.725	0.001

Table 6
ANOVA of the effects of litter addition, water variation, and their interaction on on osmotic adjustment enzyme indicators of *Suaeda salsa*.

Factors	**Indicators**					
	MDA activity		**SP**		**SS**	
	F	*p*	*F*	*p*	*F*	*p*
Litter treatment	4.201	0.016	1.848	0.166	15.539	< 0.001
Flooding treatment	4.389	0.024	5.028	0.015	6.198	0.007
Litter× Flooding treatment	8.472	< 0.001	11.773	< 0.001	9.626	< 0.001

The response of CAT activity to the combined treatments of flooding and litter additions exhibited significant variations (Fig. 6A). Under NF conditions, Treatment A reached the maximum activity of 49.17 $U \cdot g^{-1}$. With the intensification of flooding stress to IF condition, CAT activity across all treatments

decreased drastically, with Treatment A exhibiting a substantial reduction of 82.9%. Under CF conditions, CAT activities in Treatments A and B rebounded to 20.58 and 22.45 $U \cdot g^{-1}$, respectively, whereas Treatments N and T consistently remained at relatively low levels.

Under NF conditions, POD activity was higher in Treatments N and A (8.92 and 8.59 $U \cdot g^{-1}$, respectively), whereas Treatments B and T exhibited lower baseline activities (Fig. 6B). Under IF conditions, a universal decline in POD activity was observed across all treatments, with Treatments N and A displaying pronounced reductions to 5.18 and 5.37 $U \cdot g^{-1}$, respectively. Under CF conditions, POD activity in Treatment N dropped to its minimum, whereas Treatments A and T experienced significant recoveries, and Treatment B remained largely unaltered.

As the hydrostatic pressure escalated, the SOD activity of all treatments generally displayed a trend of either an initial increase followed by a decrease, or remaining relatively stable (Fig. 6C). Treatment B reached its maximum SOD activity (104.84 $U \cdot g^{-1}$) under IF conditions. For Treatment T, the peak activity was observed under NF conditions (105.61 $U \cdot g^{-1}$); however, it precipitously plummeted by 47.5% under IF conditions and further decreased to its lowest level (46.17 $U \cdot g^{-1}$) under CF conditions. Treatments N and A experienced a continuous decline with the aggravation of flooding, dropping to 60.02 and 61.32 $U \cdot g^{-1}$ under the CF condition, respectively.

3.3.2 Effects of different treatments on membrane lipid peroxidation and osmotic adjustment of *Suaeda salsa*

Two-way ANOVA indicated that MDA, SP, and SS content were all significantly influenced by litter addition, flooding regimes, and their interactive effects (Table 5).

With the intensification of flooding stress, variations in MDA content diverged remarkably depending on the specific litter treatments (Fig. 6D). Under NF conditions, Treatment N exhibited the highest MDA content (3.71$\mu mol \cdot g^{-1}$), which decreased significantly upon flooding, dropping by over 60% to 1.50 and 1.35$\mu mol \cdot g^{-1}$ under IF and CF conditions, respectively. In Treatment A, MDA content increased gradually with flooding, exhibiting minimal fluctuations. Treatment B remained highly stable across all hydrological contexts, maintaining values within a narrow range of 2.70–2.90 $\mu mol \cdot g^{-1}$. Conversely, Treatment T exhibited a distinct “V-shaped” trend: it stood at 1.44 $\mu mol \cdot g^{-1}$ under NF conditions, plummeted to 0.88 $\mu mol \cdot g^{-1}$ under IF conditions, and rebounded sharply to 3.01 $\mu mol \cdot g^{-1}$ under CF conditions.

The developmental trajectory of SP content varied distinctively based on the coupling of flooding regimes and litter treatments (Fig. 6E). Treatments N and A exhibited higher SP contents under NF conditions (14.66 and 12.13 mg/g), which subsequently decreased continuously as flooding intensified, dropping to 9.42 and 9.71 mg/g under CF conditions, respectively. In Treatment B, the SP content was 13.39 mg/g under NF conditions and experienced a pronounced decline under IF and CF conditions, falling to 8.11 and 8.14 mg/g, respectively. In sharp contrast, Treatment T exhibited the minimum SP

content under NF conditions (10.82 mg/g), but increased to 11.77 mg/g under CF conditions, emerging as the maximum value within that specific hydrological environment.

The dynamic variations in SS content are delineated in Fig. 6F. In Treatment N, SS content increased continuously with the aggravation of flooding. Treatment A displayed negligible changes between NF and IF conditions, decreasing slightly to 8.21 mg/g under CF conditions. In Treatment B, SS content decreased with flooding intensity, dropping to 6.74 and 7.21 mg/g under IF and CF conditions, respectively. Completely opposite to these patterns, Treatment T exhibited significant accumulations under IF and CF conditions, representing substantial increases of approximately 68% and 70% compared to its baseline under NF conditions, respectively, thereby constituting the highest values across both flooded environments.

3.4 Correlation analysis between growth indicators and physiological and biochemical characteristics of *Suaeda salsa*

Pearson correlation analysis systematically elucidated the intrinsic coupling relationships among the simulated indicators (Fig. 7). Total biomass exhibited a significant positive correlation with plant height ($r = 0.61$, $p < 0.05$). Morphological traits maintained robust positive associations with P_n, G_s, and stem diameter. Notably, a highly significant positive correlation was detected between P_n and *CE* ($r = 0.88$, $p < 0.05$), while *CE* exhibited a high degree of systematic synergy with both *LUE* and *WUE*. This firmly establishes that *CE*, at the biochemical level, serves as the core driving force modulating carbon assimilation and biomass accumulation in *Suaeda salsa*.

MDA content exhibited a universal negative correlation with most positive physiological indicators. In particular, the prominent negative correlations observed between C_i and both P_n and *CE* further corroborate that the decrement in photosynthetic capacity under severe stress conditions is predominantly driven by non-stomatal limitations rather than stomatal factors. Furthermore, regarding physiological defense mechanisms, the activities of CAT, POD, and SOD demonstrated significant positive correlations with photosynthetic parameters and pigment contents. Specifically, the correlation coefficient between CAT activity and chlorophyll b content reached 0.68 ($p < 0.05$). SP content maintained a stable positive relationship with growth indicators.

3.5 PCA-based comprehensive evaluation of physiological and biochemical response strategies of *Suaeda salsa*

Principal Component Analysis (PCA) was performed to comprehensively evaluate the growth, photosynthetic, and enzymatic indicators across the 36 samples from the 12 treatment combinations. The first two principal components, PC1 and PC2, explained 30.0% and 14.9% of the total variance, respectively, yielding a cumulative explained variance of 44.9% (Fig. 8). This captured the overarching physiological trajectory of *Suaeda salsa* driven by complex environmental factors.

The distribution of sample points within the ordination space exhibited a distinct hydrology-driven pattern, displaying a clear negative shift along the PC1 axis as flooding intensity escalated (Fig. 8A). The NF treatments were significantly clustered on the positive semi-axis of PC1, showing a strong positive correlation with key loading vectors such as P_n, G_s, and stem diameter ($p < 0.05$). Conversely, the CF regime induced a substantial shift of sample points toward the negative region of PC1, aligning closely with the direction of the MDA loading vector.

Furthermore, the 95% confidence ellipses for Treatments B and T shifted significantly toward the positive direction of the PC2 axis (Fig. 8B), exhibiting a distributional trajectory highly congruent with the loading vectors of total biomass and C_i. In contrast, Treatments N and A were primarily aggregated within the regions associated with the antioxidant enzymes SOD, CAT, and *WUE*.

4 Discussion

4.1 Effects of flooding and litter addition on growth traits of *Suaeda salsa*

Hydrological variation constitutes the primary driver shaping the morphological plasticity of coastal wetland plants, as water level fluctuations directly modulate physiological, morphological, and biomass traits [25, 26]. In this study, plant height, root length, and total biomass of *Suaeda salsa* exhibited a significant gradient-dependent declining trend as flooding intensified. This indicates that rhizosphere hypoxia induced by prolonged submergence severely suppressed vertical elongation and material accumulation, which is consonant with the findings on *S. salsa* in the Yellow River Delta [27]and waterlogging tolerance in landscape plants[28]. However, under IF conditions, plant height and root length in the N treatment were higher than those under NF condition, while stem diameter displayed the opposite trend. This morphological manifestation reflects an “escape strategy” adopted by the plant in response to fluctuating hydrological environments. Previous research has demonstrated that waterlogging stress triggers ethylene accumulation within plant tissues, which subsequently activates the gibberellin signaling pathway to promote cellular elongation [29]. Wet-dry alternations may repeatedly activate this signaling cascade, sustaining the stimulus for vertical extension. Concurrently, prioritizing resource allocation toward cellular elongation restricts lateral stem expansion, resulting in a “tall and slender” phenotype—a trait widely documented in typical escape-strategy plants such as deepwater rice [30].

The regulatory effects of litter additions on plant growth exhibited a pronounced dependency on hydrological conditions. Under CF conditions, the T treatment significantly outperformed the N treatment, exerting a prominent growth-compensatory effect. Under NF and IF conditions, the B treatment displayed a highly significant promotional effect on biomass accumulation, while maintaining robust stem diameters under CF conditions. This corroborates the paradigm that belowground organic matter input optimizes soil structure or provides slow-release nutrients, thereby alleviating the

physiological burdens associated with submergence[31]. Moreover, the optimal mitigation of plant height suppression achieved by Treatment T under CF conditions suggests that the synergistic interaction between aboveground and belowground litter components facilitates the construction of a more resilient micro-habitat ecosystem.

PCA provided robust multidimensional support for the aforementioned assertions. PC1 exhibited a clear negative displacement along the flooding gradient; it correlated positively with stress indices such as MDA and SOD, and negatively with growth and photosynthetic metrics including plant height, total biomass, and P_n. This confirms that the hydrological gradient serves as the primary effect axis governing stress responses, a pattern consistent with population-level insights in the Yellow River Delta [32]. Conversely, PC2 segregated the litter addition treatments and aligned with the loading vectors of total biomass and C_i, indicating that litter configuration constitutes a regulatory axis for resource allocation strategies. This two-dimensional framework of stress intensity and regulatory direction mirrors the conceptual approach of the hydrological risk assessment theory documented previously[33]. In the present study, the introduction of belowground litter successfully guided submerged plants from a passive defense-dominated mode toward an active growth-compensatory mode, a strategic transition closely resembling documented empirical evidence from the drawdown zone of the Three Gorges Reservoir [34].

4.2 Effects of flooding and litter addition on photosynthetic parameters of *Suaeda salsa*

Flooding stress profoundly suppressed the photosynthetic capacity of *Suaeda salsa* leaves, as evidenced by the gradient-dependent declines in P_n, G_s, *CE*, and *LUE* with increasing submergence, aligning with patterns reported in *Populus cathayana* seedlings [35]. The suppression of photosynthesis is typically governed by a dynamic interplay between stomatal and non-stomatal limitations [36], with the dominant restrictive factor shifting from stomatal to non-stomatal constraints as environmental stress exacerbates [37]. Based on the concurrent directional changes of P_n and C_i the precise limitation type can be diagnostic: a decrease in P_n accompanied by reduced C_i and elevated *Ls* denotes a stomatal constraint; conversely, a decline in P_n paired with stable or elevated C_i and diminished *Ls* indicates the predominance of non-stomatal limitations [36, 38]. In our experiment, the reduction in P_n was accompanied by a concomitant increase in C_i and a decrease in *Ls* as flooding intensified, firmly demonstrating that non-stomatal limitations served as the overarching cause for the decline in P_n. Under CF conditions, the synchronized reduction of G_s and C_i in the N treatment superficially resembled stomatal limitation; however, this trend likely reflects a systemic degradation of the photosynthetic apparatus under prolonged hypoxia rather than active stomatal regulation. In contrast, while Treatments B and T exhibited marked reductions in G_s, their C_i values remained high, coupled with a significant recovery in *CE* and *LUE*. This indicates a strategic shift in their photosynthetic constraints from stomatal to non-stomatal factors, suggesting that belowground litter effectively alleviates photosynthetic

attenuation under extreme stress by safeguarding mesophyll cell carboxylation capacity and photosystem II functionality [39].

The degradation of photosynthetic pigments serves as a critical material basis for the decline in photosynthetic performance. In this study, the contents of chlorophyll a, chlorophyll b, and carotenoids decreased significantly under intensified flooding, with the N treatment experiencing a 55.4% drop in chlorophyll a under CF conditions. Litter additions profoundly mitigated this pigment degradation: Treatment B induced a 58.6% recovery in chlorophyll a content, while Treatment T manifested the most optimal protective effect on chlorophyll b and carotenoids while maintaining a low chlorophyll a/b ratio. This low ratio implies an increased proportion of light-harvesting antenna complexes, which is ecologically advantageous for maximizing light capture efficiency in high-water, low-light microenvironments [40]. Furthermore, the preservation of carotenoid content critically aids in quenching reactive oxygen species and dissipating excess excitation energy [41]. In summary, the responses of *Suaeda salsa* photosynthetic indicators to hydrological effects are stress-type dependent: under continuous flooding without litter, photosynthetic constraints are predominantly dictated by stomatal factors; however, the incorporation of belowground litter shifts the limitation toward non-stomatal factors by preserving carboxylation activity and energy conversion efficiency, while simultaneously adapting to low-light stress through the maintenance and compositional optimization of pigment pools.

4.3 Effects of flooding and litter addition on antioxidant enzyme activities of *Suaeda salsa*

Under flooding stress, the disrupted equilibrium between the generation and scavenging of reactive oxygen species (ROS) is the fundamental cause of cellular oxidative damage, and the antioxidant enzyme system responds in a highly treatment-dependent manner [42]. In this study, the N treatment under CF conditions exhibited the lowest CAT activity alongside the highest MDA accumulation, signaling a catastrophic collapse of the antioxidant defense system and severe lipid peroxidation under prolonged hypoxia, which concurs with the conclusions of Blokhina [42]. Conversely, Treatment B remarkably reversed this detrimental trajectory by maintaining the highest CAT activity and the lowest MDA level, indicating that belowground litter effectively bolstered the H_2O_2 scavenging capacity and mitigated membrane damage. This supports the premise that belowground organic material exerts positive regulatory feedback on antioxidant defenses, parallel to patterns observed in crops under straw incorporation [43]. Under IF conditions, the SOD activity in Treatment B was significantly higher than that in all other treatments, demonstrating that belowground litter effectively induces superoxide anion scavenging within alternating redox environments. In flooding reoxygenation experiments on soybean, a pronounced up-regulation of SOD activity was similarly observed during the reoxygenation phase to counteract the post-flooding ROS burst [44]. This implies that under wet-dry cycling, belowground litter can preemptively activate SOD to buffer oxidative oscillations.

The response of POD activity displayed distinct functional characteristics. Under CF conditions, Treatment T manifested the highest POD activity, which is intimately tied to the functional role of POD in

lignin biosynthesis and cell wall reinforcement [45]. This provides a solid physiological explanation for the structural maintenance of stem diameter observed in Treatment T under continuous flooding. Furthermore, the accumulation of SS and SP was most pronounced in Treatment T, showcasing the strongest osmotic adjustment capacity, which is vital for maintaining cellular turgor pressure and protecting macromolecular structures [46]. This implies that total litter incorporation not only accelerates cell wall fortification via POD enhancement but also sustains cellular homeostasis through the accumulation of osmolytes, thereby synergistically buffering waterlogging stress.

Collectively, flooding stress incited an acute stress response within the antioxidant system, while litter additions further modulated the magnitude and direction of this response. The antioxidant apparatus is highly susceptible to collapse in the N treatment; however, Treatment B successfully eliminated active oxygen through CAT and SOD activation, and Treatment T collaboratively protected cellular integrity via POD enhancement and osmotic adjustment. Nevertheless, this protective efficacy may entail elevated metabolic energy costs: Treatment B channels resources toward antioxidant enzyme synthesis, whereas Treatment T simultaneously invests in cell wall fortification and osmotic synthesis. Such disparities in energy allocation strategies under varying litter regimes could ultimately dictate overall plant growth trade-offs, a dimension that warrants further empirical validation.

4.4 Systemic coupling characteristics of growth, photosynthetic, and physiological indicators

Pearson correlation analysis systematically unveiled the intrinsic coupling mechanisms operating among the simulated parameters. Total biomass was significantly and positively correlated with P_n and *CE* (r = 0.61–0.88), confirming that photosynthetic efficiency is the direct driver of material accumulation. The robust negative correlations of C_i with both P_n and *CE* statistically validated the predominant role of non-stomatal limitations under prolonged submergence, aligning with patterns observed in barley [47]. Additionally, CAT activity was negatively correlated with MDA content and positively associated with chlorophyll b, demonstrating the coordinated contribution of antioxidant defense to membrane integrity and pigment preservation. This conclusion is reinforced by studies showing that organic amendments can significantly enhance crop tolerance to water stress by elevating antioxidant defense levels [48]. The positive response linking SP with growth indicators reflects the role of osmotic adjustment in facilitating vegetative growth. These interlocking relationships are highly congruent with the tightly knit coupling network among antioxidant enzyme systems, photosynthetic pigments, and morphological parameters reported in the halophyte *Capparis spinosa* under stress [49]. Building upon these foundations, the present study further quantifies the statistical coupling strength linking photosynthetic efficiency, biomass accumulation, and antioxidant defenses, thereby providing rigorous quantitative evidence for deciphering the systemic adaptation mechanisms of halophytes under compound environmental stress.

5. Conclusion

(1) Hydrological gradients serve as the dominant ecological factor driving the growth and physiological variations of *Suaeda salsa*, with continuous flooding imposing severe environmental stress. Submergence significantly suppresses growth and photosynthetic capacity; under continuous flooding, photosynthetic constraints are predominantly governed by non-stomatal factors, wherein the degradation of carboxylation efficiency and light use efficiency constitutes the fundamental cause of photosynthetic decay.

(2) The mitigation effects of litter additions on *Suaeda salsa* growth exhibit a distinct dependency on hydrological conditions. Under the CF regime, total component litter or belowground litter additions represent the optimal management strategies. Under NF and IF conditions, Treatment B yields the most superior growth promotion. The underlying mechanism rests on belowground litter optimizing the rhizosphere microenvironment and reinforcing antioxidant enzyme activities to alleviate oxidative stress, while total litter addition further synergistically enhances osmotic adjustment capacity and light capture efficiency.

(3) Correlation and multivariate analyses reveal that photosynthetic efficiency, material accumulation, and antioxidant defense capacity coalesce into a mutually reinforcing, synergistic network. While hydrological conditions dictate the core magnitude of the stress response, litter configuration determines the strategic orientation of plant resource allocation, wherein belowground litter components effectively drive the transition of stressed plants from passive defense to active growth compensation.

In summary, this study decouples the interactive effects of aboveground and belowground ecological processes across varying hydrological contexts. It confirms the feasibility of regulating stress adaptive strategy transitions in wetland vegetation through optimal litter inputs, thereby providing critical theoretical insights and a scientific basis for zoned litter management and community restoration in degraded saline wetlands.

Declarations

Ethics, Consent to Participate, and Consent to Publish declarations: The seeds and litter materials of *Suaeda salsa* used in this study were collected from the Yellow River Delta Wetland Nature Reserve, Dongying, Shandong, China. No specific permits were required for the collection site. All experimental procedures complied with relevant institutional, national, and international guidelines.

Availability of data and materials: The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests: The authors declare that they have no competing interests.

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Authors' contributions: Jingkuan Sun and Runrong Han conceived the experiments. Runrong Han, Qingkai Qi, Ming Jin , Han Xin , Jinzhao Ma and Tian Li performed the experiments and collected the data. Runrong Han and Rui Hu undertook the data analysis. Runrong Han drafted the manuscript. All authors read and approved the final manuscript.

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Figures

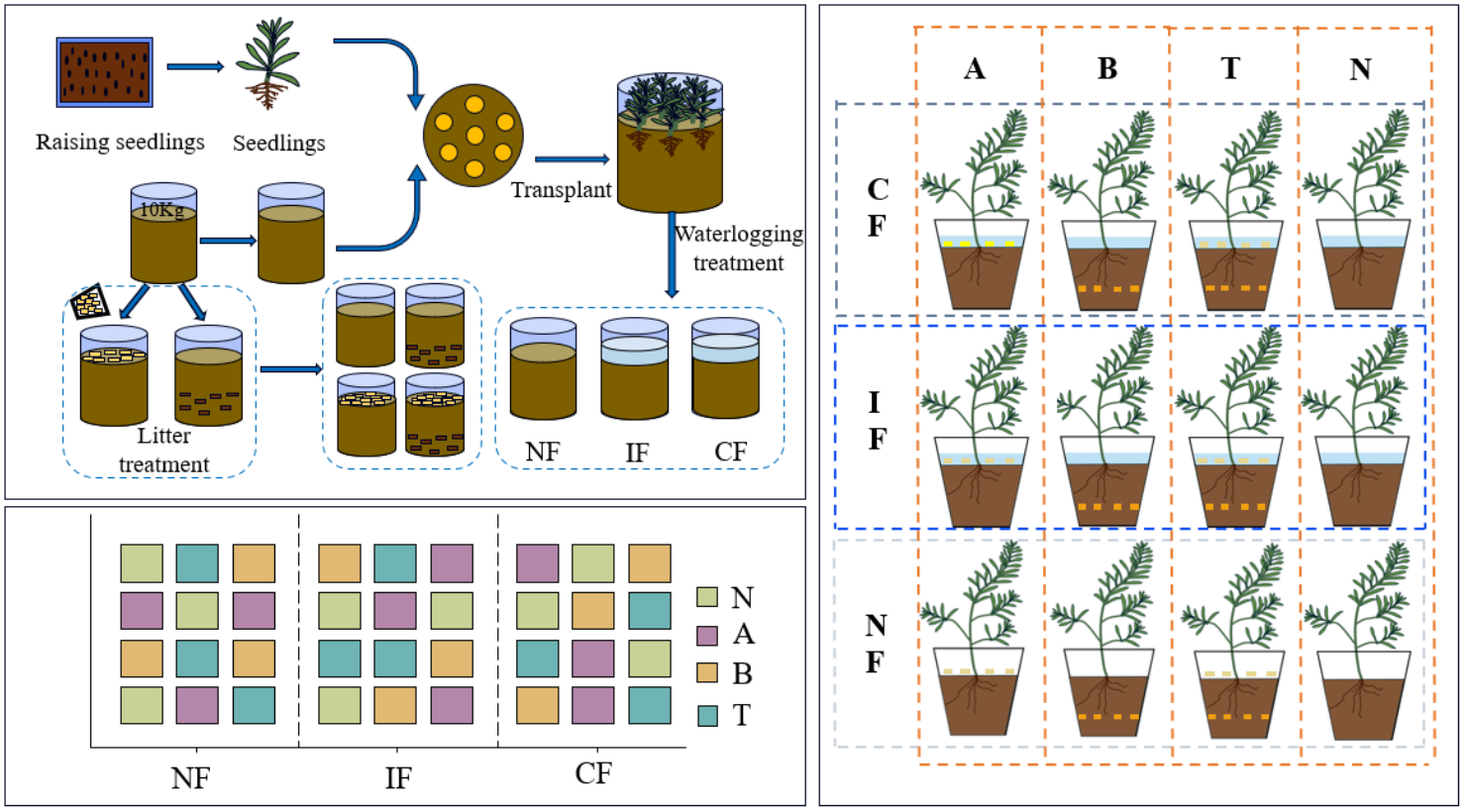

Figure 1

Two-factor experimental design of flooding stress and litter addition on *Suaeda salsa*.

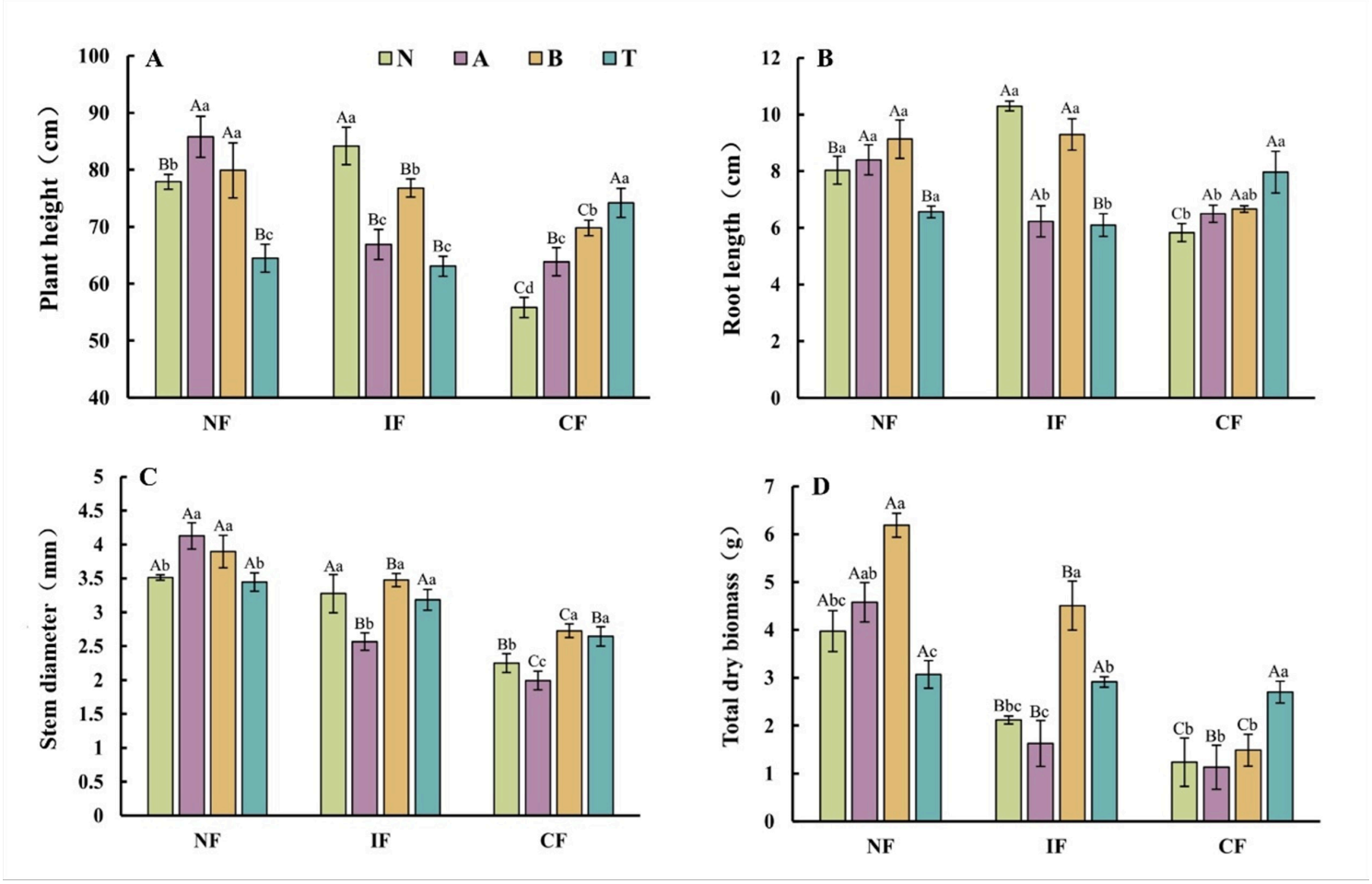

Figure 2

Effects of different treatments on growth indicators of *Suaeda salsa.* Different lowercase letters indicate significant differences among different litter additions under the same water stress condition ($p < 0.05$), and different uppercase letters indicate significant differences among different water stress conditions under the same litter addition ($p < 0.05$).

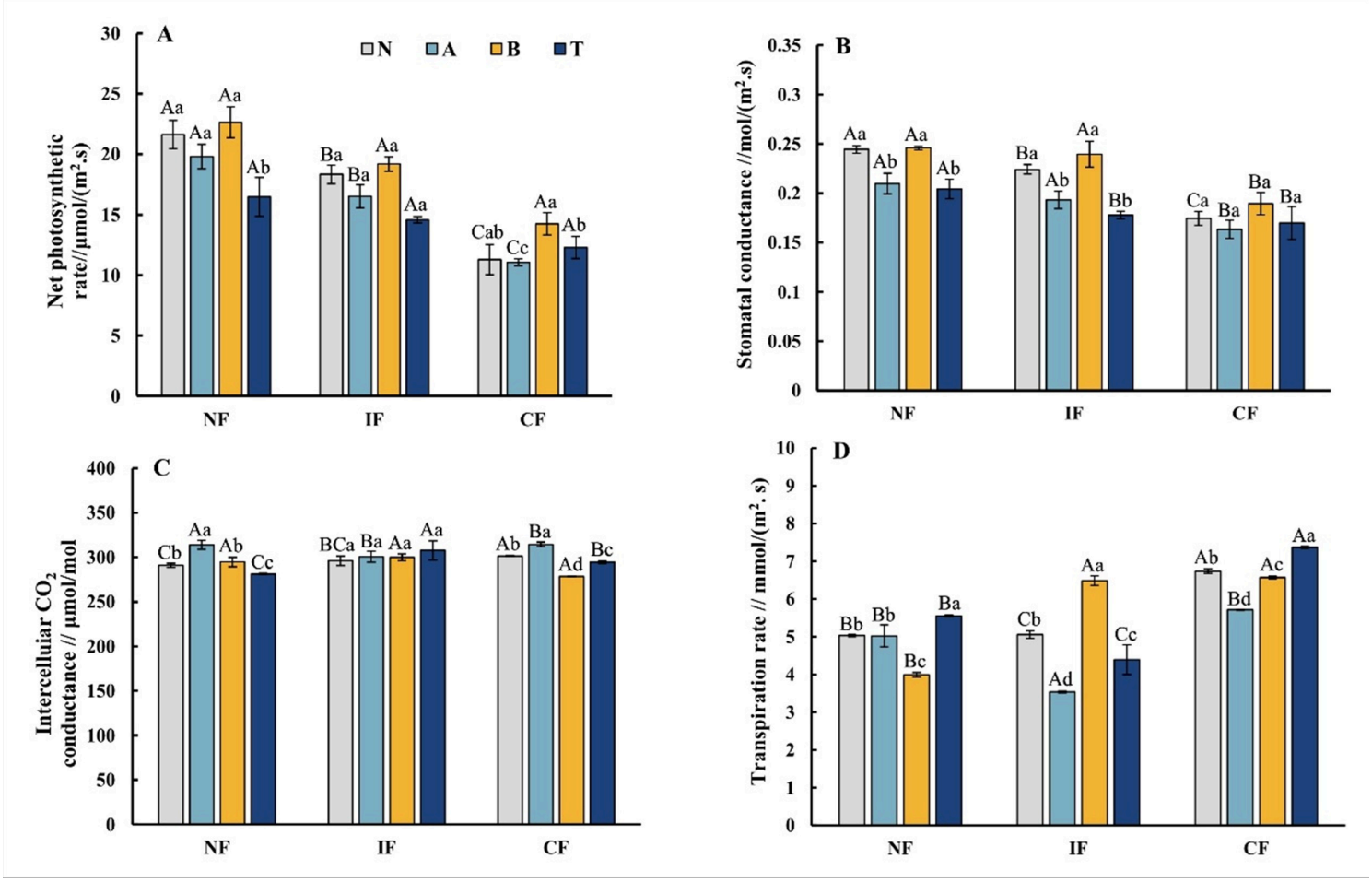

Figure 3

Effects of different treatments on P_n, G_s, C_i, and T_r of *Suaeda salsa*. Different lowercase letters indicate significant differences among different litter additions under the same water stress condition ($p < 0.05$), and different uppercase letters indicate significant differences among different water stress conditions under the same litter addition ($p < 0.05$).

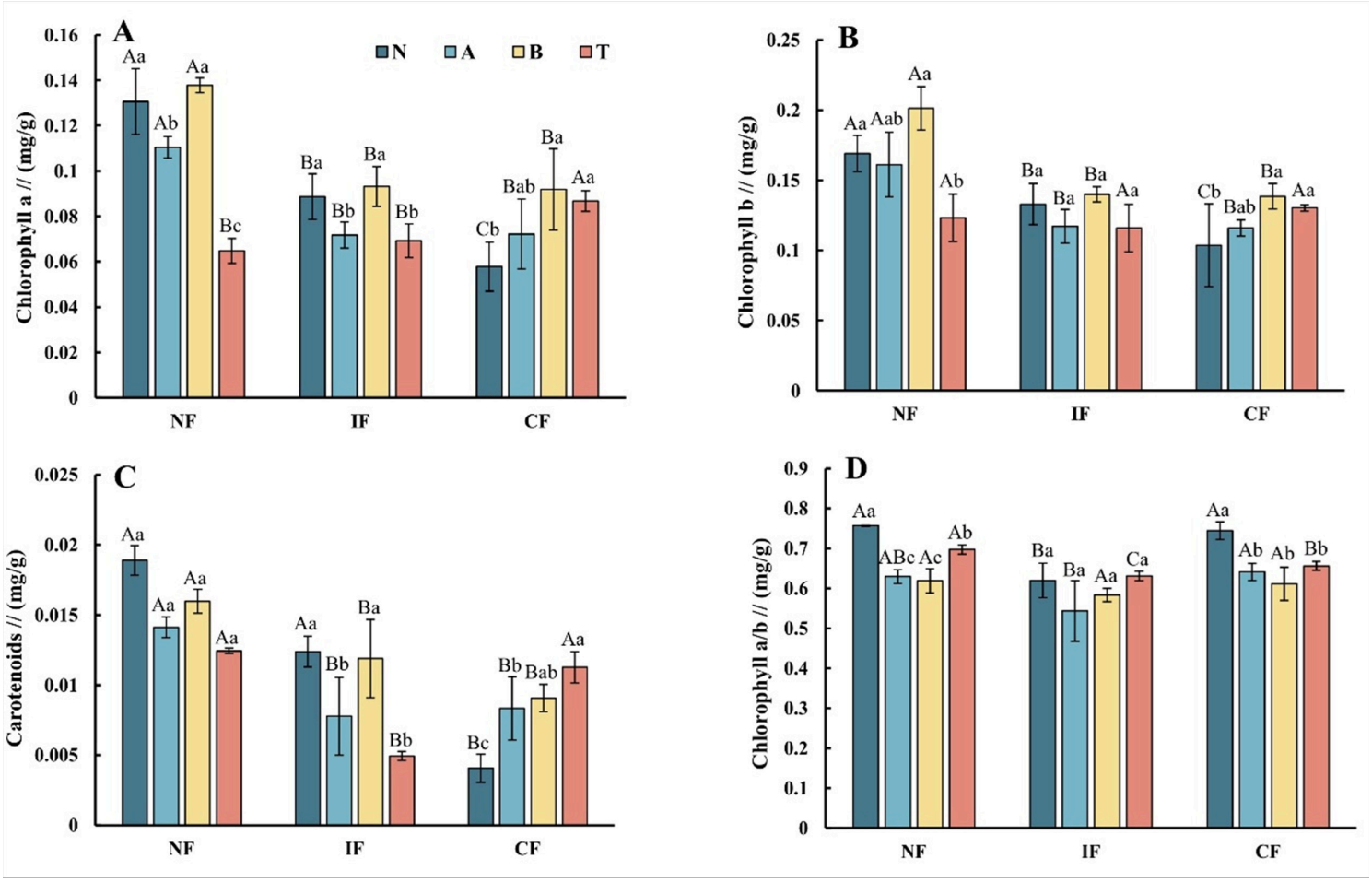

Figure 4

Fig. 5 Effects of different treatments on photosynthetic pigments of Suaeda salsa. Different lowercase letters indicate significant differences among different litter additions under the same water stress condition ($p < 0.05$), and different uppercase letters indicate significant differences among different water stress conditions under the same litter addition ($p < 0.05$).

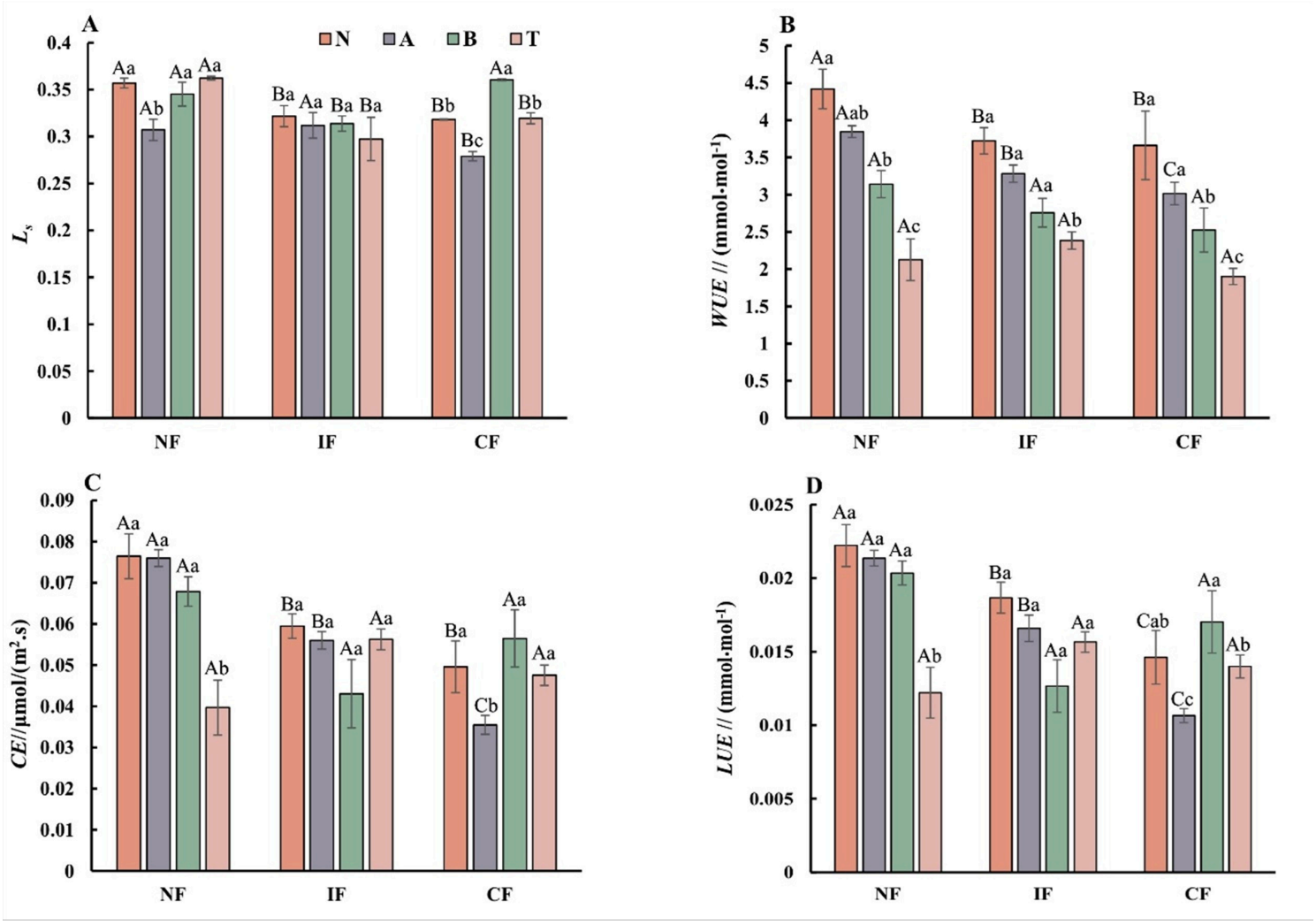

Figure 5

Fig. 4 Effects of different treatments on L_s, *WUE*, *CE*, and *LUE* of *Suaeda salsa*. Different lowercase letters indicate significant differences among different litter additions under the same water stress condition ($p < 0.05$), and different uppercase letters indicate significant differences among different water stress conditions under the same litter addition ($p < 0.05$).

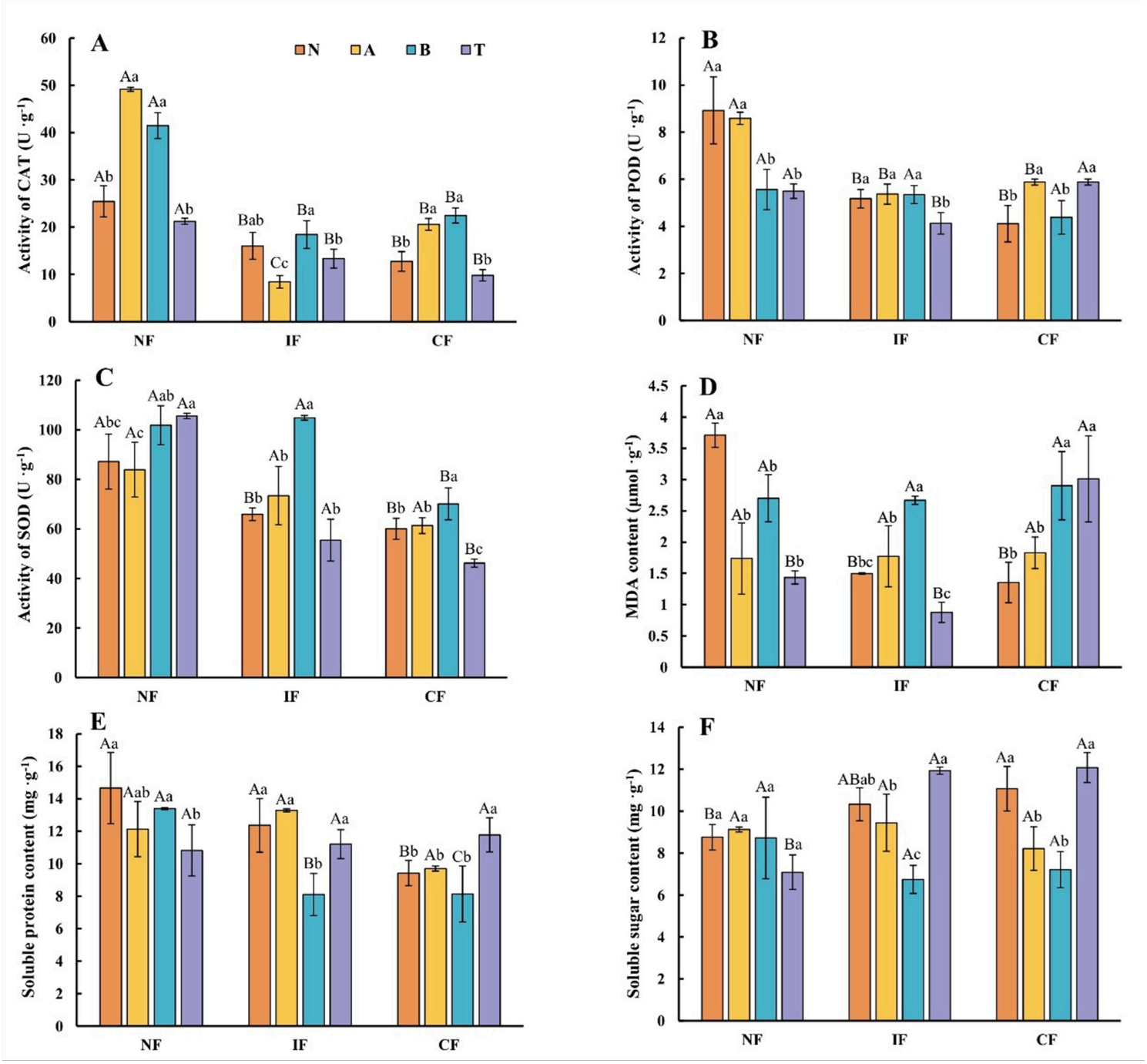

Figure 6

Effects of different treatments on plant enzymes of *Suaeda salsa.* Note: Different lowercase letters indicate significant differences among different litter additions under the same water stress condition ($p < 0.05$), and different uppercase letters indicate significant differences among different water stress conditions under the same litter addition ($p < 0.05$).

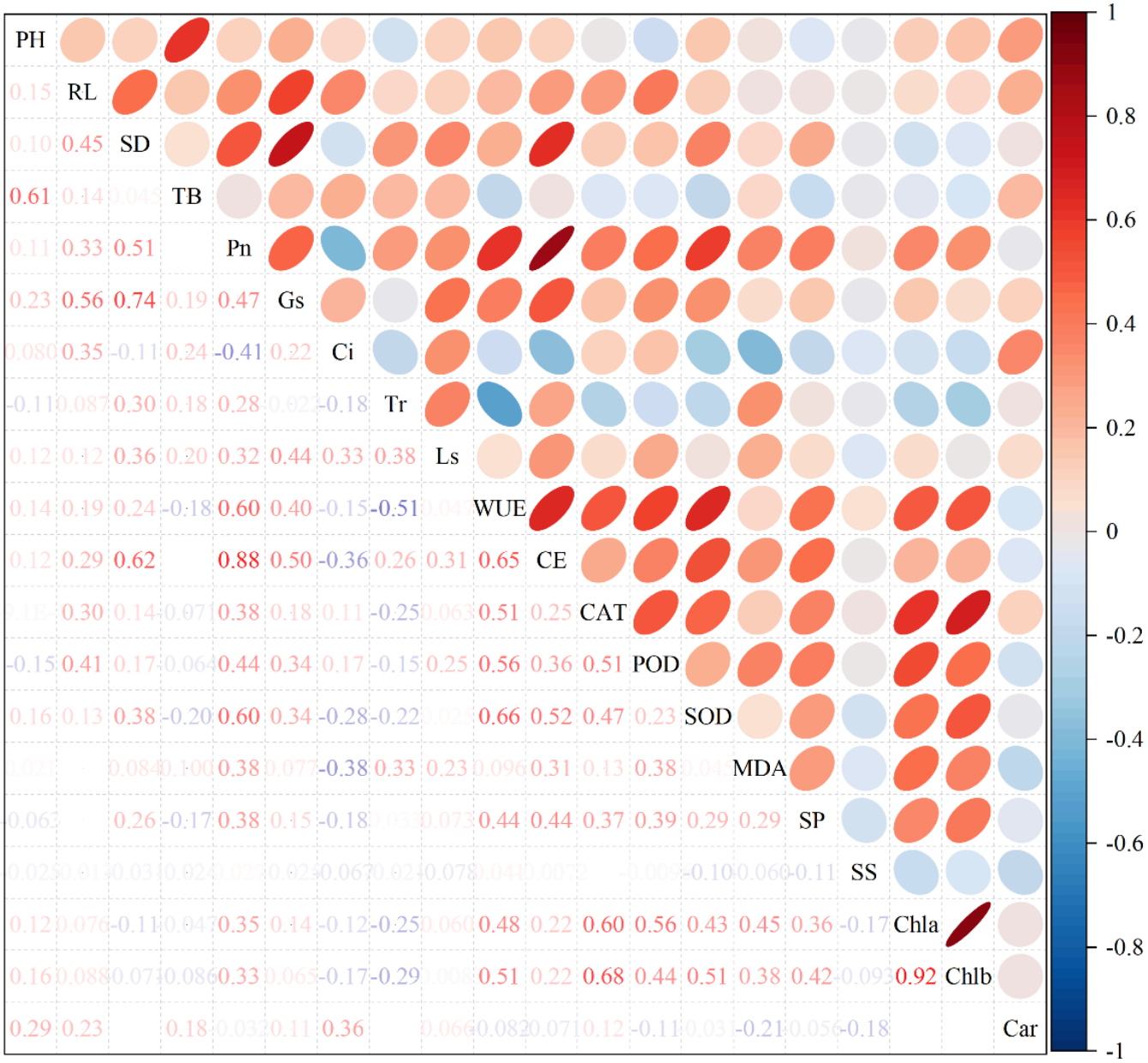

Figure 7

Correlation analysis of photosynthetic physiology and growth traits of *Suaeda salsa*. under different treatments Note: PH, plant height; RL, root length; SD, stem diameter; TB, total biomass; Pn, net photosynthetic rate; Gs, stomatal conductance; Ci, intercellular carbon dioxide concentration; Tr, transpiration rate; LS, stomatal limitation value; WUE, instantaneous water use efficiency; CE, carboxylation efficiency; CAT, catalase; POD, peroxidase; SOD, superoxide dismutase; MDA, malondialdehyde; SP, soluble protein; SS, soluble sugar; Chla, chlorophyll a; Chlb, chlorophyll b; Car, carotenoid

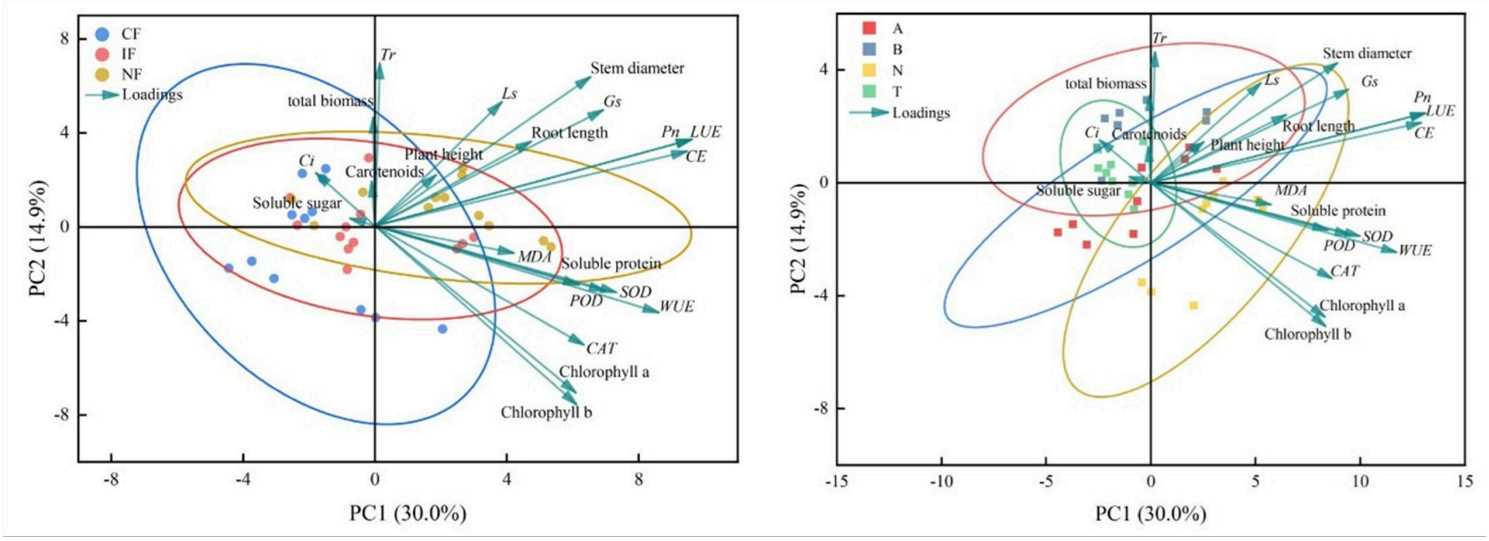

Figure 8

PCA evaluation of *Suaeda salsa* under different treatments.