

EFFECTS OF SOIL SALINITY AND NITROGEN FERTILIZER APPLICATION ON THE PHOTOSYNTHETIC CHARACTERISTICS AND SUCROSE METABOLISM OF WINTER JUJUBE

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Abstract. The coastal saline-alkali land in the Yellow River Delta region of China is a famous core production area of winter jujube (*Ziziphus jujuba* Mill. cv. Dongzao). In the yield-focused fertilization management practice of winter jujube, excessive nitrogen application has led to a decline in fruit quality. A comprehensive understanding of how salt and nitrogen synergistically affect the fruit quality of winter jujube can provide a theoretical basis for the nutritional management of winter jujube orchards. The results showed that, the interaction between medium salt (2.5 g·L⁻¹ NaCl) and medium nitrogen (5 g·L⁻¹ urea) significantly enhanced the photosynthetic performance, sucrose accumulation, ¹³C assimilation rate, and activities of sucrose-metabolizing enzymes. Conversely, the photosynthetic performance, synthesis of primary sugar components, ¹³C output ratio, and activity of sucrose-metabolizing enzymes were significantly inhibited under the combined influence of high nitrogen (10 g·L⁻¹ urea) and high salt (5 g·L⁻¹ NaCl) conditions. In summary, moderate saline stress combined with appropriate nitrogen application could significantly improve the fruit quality of winter jujube. Under high salt stress, excessive nitrogen application would have a negative impact on photosynthesis and fruit sugar accumulation of winter jujube. Therefore, it is suggested that the amount of nitrogen application should be appropriately reduced in winter jujube orchards with high soil salinity.

Keywords: *Zizyphus jujuba*, salt-nitrogen interaction, ¹³C-photosynthate, translocation and distribution, sucrose metabolism

Introduction

As arable land diminishes worldwide, formerly marginal saline-alkali lands are becoming crucial agricultural resources (You et al., 2021). The Yellow River Delta, located in the northern part of Shandong Province, China, is a newly developed coastal saline-alkali system, and the soil salinization degree in this area is high, which has seriously affected agricultural activities in this region (Zhou et al., 2021). The winter jujube (*Ziziphus jujuba* Mill. cv. Dongzao), as a well-known fresh-eating jujube variety in China, is one of the main cultivated economic crops in the Yellow River Delta region. Driven by the pursuit of high yields, excessive and imbalanced nitrogen application has become a widespread practice in winter jujube cultivation systems, which has ironically lead to yield fluctuations and a decline in fruit quality (Zhang et al., 2023).

Severe salinity stress reduces global crop yield and quality (Roy et al., 2014; Van Zelm et al., 2020). Nitrogen deficiency acts as a key growth-limiting constraint due to its status as the most essential plant macronutrient. In the cultivation of fruit crops in saline-alkali areas, the interplay between salinity and nitrogen fertilization emerges as a pivotal agricultural challenge, as these factors jointly govern both yield parameters and quality attributes (Da Silva et al., 2023; Ahmad et al., 2023).

The effects of salinity and nitrogen on fruit plant growth both showed dose-dependent effects. Severe salinity stress reduces fruit yield and quality (Roy et al., 2014; Van Zelm et al., 2020). In saline-alkali environments, ions such as sodium or chloride can inhibit nutrient absorption in plants and interfere with the assimilation of essential nutrients including ammonium, nitrate, and potassium, thereby disrupting ionic homeostasis (Sánchez-Rodríguez et al., 2011; Ashraf et al., 2018). On the other hand, saline-alkali stress can impair plant photosynthesis and disrupt metabolic processes involving sugars, inorganic ions, and organic acids, thereby affecting plant growth, fruit yield and quality (Balibrea et al., 2000; Chen et al., 2010). However, mild saline-alkali stress has been shown to enhance fruit quality through multiple physiological mechanisms (Dorais et al., 2001; Galli et al., 2016; Vanessa Galli et al., 2016). Mild salt stress can enhance fruit quality by activating plant responses that increase metabolite levels, such as sugars and organic acids, thereby improving sweetness and flavor (Zhu et al., 2001; Keutgen et al., 2008; Coban et al., 2020; Eynizadeh et al., 2023; Zhao et al., 2024b). This "low-dose stress boost" offers a sustainable way to enrich nutrient content in crops. Increasing nitrogen application within certain limits can boost leaf photosynthate production, optimize photosynthate distribution, and fruit quality (Meng et al., 2018; Sha et al., 2020; Khasawneh et al., 2021). However, Over-application of nitrogen promotes excessive vegetative growth at the expense of reproductive development, leading to reduced fruit set, fruit size and quality (Rutkowski et al., 2022; Amin et al., 2024; Chawla et al., 2025).

However, there are complex interactions and coupling effects between salt and nitrogen in saline-alkali habitats, such as synergism, sequential addition, and antagonism (Chen et al., 2010; Murtaza et al., 2017). Salt stress can reduce the accumulation of nitrogen in plants (Ma et al., 2022). Some scholars attribute this inhibition to the antagonistic absorption of chloride ion and nitrate ion, and others believe that salt indirectly affects nitrogen accumulation by reducing water absorption (Lea-Cox et al., 1993; Bar et al., 1997). Many studies have set out to test the hypothesis that the addition of nitrogen fertilisers alleviates, at least partially, the deleterious effects of salinity on plants (Grattan et al., 1999). However, excessive nitrogen application can exacerbate soil salinization and further increase the inhibitory effect of salt on nutrient absorption, utilization, and metabolism in plants (Semiz et al., 2014; Xie et al., 2021).

As mentioned above, numerous experimental investigations have been conducted to examine the impacts of salinity and nitrogen levels on crop growth, development, and C-N metabolic processes. However, under the condition of soil salt stress, how nitrogen and salt synergistically affect the nutrient metabolism process and fruit quality of winter jujube has not been clearly studied.

Understanding nitrogen's effects on winter jujube's nutritional metabolism in saline-alkali soils could establish a theoretical foundation for developing optimized nitrogen fertilization protocols. Through isotopic tracing with ^{13}C labeling, researchers have characterized carbon partitioning mechanisms in fruit crops under salt stress, demonstrating how adaptive sugar metabolism drives carbohydrate accumulation

patterns that directly impact fruit quality parameters (Sami et al., 2016; Beshir et al., 2017; Jeandet et al., 2022). Therefore, this study uses ^{13}C isotope labeling technology to investigate the effects of various concentrations of salt and nitrogen on photosynthetic performance, the transport and distribution of photosynthetic compounds, and the characteristics of sugar accumulation from the perspective of carbon nutrition.

Materials and methods

Experimental sites and materials

The experiment was carried out from April to September 2023, under second-generation solar greenhouse conditions in the Yellow River Delta (Binzhou) National Agricultural Science and Technology Park, Binzhou City, Shandong Province, China (118°4'E, 37°34'N).

Five-year-old *Zizyphus jujuba* 'Zhandong 2' plants were used in this study, and the average yield per plant in the preceding year was 10.38 kg. The plants were cultivated in ceramic basins measuring 38 cm in height and 49 cm in internal diameter, with one plant per basin. The spacing between the basins was 60 cm. The bottom of each basin featured five drainage holes, each approximately 7 mm in diameter, to ensure adequate aeration and drainage. Each basin was filled with 23.5 kg of air-dried soil. The soil utilized in the pot experiment was tidal soil, with the following properties: pH 7.81; bulk density $1.16 \text{ g}\cdot\text{cm}^{-3}$; organic matter content $15.73 \text{ g}\cdot\text{kg}^{-1}$; salt content $1.21 \text{ g}\cdot\text{kg}^{-1}$; and available potassium (K), available phosphorus (P), NO_3^- -N, and NH_4^+ -N at 279.07, 59.40, 33.57, and $7.55 \text{ mg}\cdot\text{kg}^{-1}$, respectively.

Experimental design

In this study, the pot experiment of winter jujube in greenhouse was carried out. The greenhouse has a light transmittance of 60%-80% (arched roof covered with 150-micron transparent low density polyethylene plastic, to allow the passage of light). Winter jujube trees are capable of growing in both heavy and moderately saline soils with a salt content of up to 0.5%. Based on the preliminary test results, a two-factor 3×3 randomized block design was used to analyze the effects of salt-nitrogen interaction, by adding $0.5 \text{ g}\cdot\text{L}^{-1}$, $2.5 \text{ g}\cdot\text{L}^{-1}$, and $5 \text{ g}\cdot\text{L}^{-1}$ NaCl solution (low salt, medium salt, and high salt) and 1, 5, and $10 \text{ g}\cdot\text{L}^{-1}$ urea solution (low nitrogen, medium nitrogen, and high nitrogen) to the planting pots. In the above experiment, 3 replicates were set for each treatment, and a total of 27 pots with winter jujube were arranged, with a five-year-old winter jujube tree planted in each pot. All the 27 winter jujube trees used in the experiment were healthy and of similar size, with a similar number of lateral branches in the canopy, each plant about 1.4 m tall, with a base diameter of about 2.8 cm and a crown spread of about 0.9 m.

Irrigation with a mixed solution of nitrogen and salt was carried out during the growing season, a total of 5 times, each time applying 5 L of the corresponding salt-nitrogen solution per pot. Solutions of NaCl and urea with varying concentrations were prepared using distilled water. Different concentrations of NaCl and urea solutions were applied to the roots of winter jujube trees at five distinct phenological stages: early flowering (May 20), full flowering (June 18), late flowering (July 17), fruit hardening (August 18), and white ripening (September 12). Over the course of five growing

seasons, a total of 5 L of a salt and nitrogen mixture was added to each basin in a single application to ensure that the solution drained from the bottom.

Phosphorus and potassium fertilization were applied to each pot at the germination stage (mid-April), by applying 3.39 g and 4.24 g of soil P_2O_5 and K_2O , respectively, in the forms of single superphosphate and potassium nitrate, per plant as per recommendation. The average temperature inside the greenhouse was $26.4^{\circ}C$ with an average relative humidity of 55.3%. The highest recorded temperature was $39.0^{\circ}C$, with a peak relative humidity of 87.6%, while the lowest temperature and humidity were $10.8^{\circ}C$ and 14.0%RH, respectively. Prior to the experiment, the soil's field water capacity, which serves as the basis for irrigation water requirements, was determined. The freshwater irrigation method employed was drip irrigation, conducted twice weekly with each session lasting one hour. During the treatment process, the positions are regularly adjusted to ensure that each plant is exposed to a consistent environment. Additionally, other cultivation management practices, such as budding and ring stripping, remain consistent in accordance with conventional management practices.

¹³C labeling method

Based on our research group's prior investigations into the dynamic changes in fruit dry matter throughout the annual cycle of winter jujube, mid-September marks the period of most rapid growth in fruit dry matter. This is also the phase when the fruit's demand for photosynthetic compounds is most intense. On September 15, one fruit-bearing secondary branch was selected from each pot of winter jujube for ^{13}C isotope labeling using $Ba^{13}CO_3$ (^{13}C purity 98%) as the marker. Prior to labeling, circumferential stripping was performed at the base of the fruiting branch, which was then wrapped and sealed to prevent the transport of ^{13}C photosynthates to other parts of the plant. Five jujube hangers on the basal branches were selected to ensure uniform numbers of leaves and fruits. These hangers, markers, fans, and reduced iron powder were placed in a sealed marking room made of transparent film. The sunlight transmittance in the labeling chamber was 95% of the natural light intensity. Labeling commenced at 9:00 a.m. with the fan turned on and the chamber sealed. One mL of hydrochloric acid ($1\text{ mol}\cdot\text{L}^{-1}$) was added into the beaker every 0.5 h to maintain carbon dioxide (CO_2) concentration, and the ^{13}C labeling lasted for 4 h. Three additional plants were used as blank controls (natural ^{13}C abundance), destructive samples were collected on the third day after labeling, and ^{13}C was determined (Sha et al., 2020).

Measurement of photosynthetic indexes

Photosynthetic indexes were measured using a LI-6800 photosynthetic instrument from 9:00 to 11:00 a.m. on September 18 under standardized climatic conditions. Intact functional leaves from the central part of the branch of winter jujube were selected to measure net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (T_r), and intercellular carbon dioxide (CO_2) concentration (C_i). Measurements were repeated three times for each leaf, and averages were calculated. The light-saturation point was set to $1200\text{ }\mu\text{mol (photon)}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the leaf chamber temperature ($2\text{ cm} \times 3\text{ cm}$) was maintained at $(25 \pm 1)^{\circ}C$, CO_2 concentration was $400\text{ }\mu\text{mol (CO}_2\text{)}\cdot\text{mol}^{-1}$, relative humidity was 60%–65%, and airflow was $500\text{ }\mu\text{mol}\cdot\text{s}^{-1}$. Water use efficiency (WUE) and stomatal limitation (L_s) were calculated as follows (Zhao et al., 2015).

$$WUE = P_n/T_r \quad (\text{Eq.1})$$

$$L_s = 1 - C_i/C_a \quad (\text{Eq.2})$$

Measurement of physiological characteristics in leaf

A portion of the leaf, whose photosynthetic parameters were measured, was placed on A3 paper with a 25 cm² green cardboard as the control. Images were captured digitally, and leaf area was calculated using Image-Pro Plus 6.0 software. Another part of the leaf, excluding the midvein, was cut into 0.2 g samples, soaked in 95% ethanol for 48 h, and measured the light absorption values at 665 nm and 649 nm to calculate chlorophyll a, chlorophyll b, chlorophyll (a + b), and the chlorophyll a/b ratio.

Measurement of sugar components and the enzyme activity of sugar metabolism in the fruit flesh

On September 21, 30 fruits were randomly selected from the middle of secondary jujube branches located in four directions (east, west, south, and north) outside the crown of each sampling tree and stored in a laboratory refrigerator at -80 °C. The activities of sucrose phosphate synthase (SPS), acid invertase (AI), neutral invertase (NI), sucrose synthetase of synthetic direction (SS-s) and sucrose synthase of cleavage direction (SS-c) in winter jujube fruits was measured using the method modified by Ma et al. (2021). Accurately weigh 0.1 g of the frozen sample and placed in a 2 mL centrifuge tube. The enzyme activity was measured with a sucrose phosphate synthase kit (SPS), a acid convertase kit (S-AI), a neutral translate kit (NI), a Sucrose synthase of synthetic direction kit (SS-s), and a Sucrose synthase of cleavage direction kit (SS-c).

The content of the sucrose, fructose and glucose in the fruits was determined using an Agilent 1260 high-performance liquid chromatograph. Chromatographic conditions were as follows: Waters XBridge™ Amide column (4.6 mm × 250 mm, 5 μm); mobile phases were ultra-pure aqueous solution A (0.2% triethylamine (TEA)) and solution B (0.2% TEA and acetonitrile) in a 35:65 ratio. The column temperature was 35°C, the atomizing tube temperature was 60°C, the drift tube temperature was 60°C, the gas flow rate was maintained at 1.6 L·min⁻¹, and the gain value was 1.0.

Contents and calculation of ¹³C

The fruit-bearing branches were divided into labeled leaves, labeled jujube hangers, labeled fruits, unlabeled leaves, unlabeled annual branches, unlabeled perennial branches, and unlabeled fruits. The samples were washed sequentially with clear water, detergent, clear water again, and 1% hydrochloric acid, followed by three washes with deionized water. The samples were dried at 105°C for 30 min, followed by 80°C for 3 d. The dried samples were ground using an electric grinder and filtered through a 0.25 mm mesh screen (Wang et al., 2020). The δ¹³C values were measured using a ZHT-03 mass spectrometer from the Beijing Analytical Instrument Factory (Chinese Academy of Agricultural Sciences). Three replicates were conducted for each treatment.

The ¹³C calculation formula, based on the modified methods described by Lu et al. (2002) and Wu et al. (2009), is as follows:

$$\text{Abundance of } ^{13}\text{C}: F_i (\%) = \frac{(\delta^{13}\text{C} + 1000) \times R_{\text{PDB}}}{(\delta^{13}\text{C} + 1000) \times R_{\text{PDB}} + 1000} \times 100\% \quad (\text{Eq.3})$$

where R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$. The δ values represent the ratio of heavy and light isotopes in the samples compared with the standard reference material, Vienna PeeDee Belemnite (PDB) carbonate ($R_{\text{PDB}} = 0.0112372$)

$$\text{Carbon content of each organ: } C_i = \frac{\text{amount of dry matter (g)}}{\text{total carbon content (\%)}} \quad (\text{Eq.4})$$

The ^{13}C incorporated into apple plants was calculated based on the difference in atom% ^{13}C of plants in the labeled and non-labeled samples as follows:

$$\text{Content of } ^{13}\text{C} \text{ of each organ: } ^{13}\text{C}_i (\text{mg}) = \frac{C_i \times (F_i - F_{nl})}{100} \times 1000 \quad (\text{Eq.5})$$

where F_{nl} : no ^{13}C labeling, natural abundance of ^{13}C of each organ.

The percentage distribution of ^{13}C into plants was calculated as follows:

$$^{13}\text{C} \text{ partitioning rate: } ^{13}\text{C}(\%) = \frac{^{13}\text{C}_i}{^{13}\text{C}_{\text{net absorption}}} \times 100\% \quad (\text{Eq.6})$$

Statistical analysis

Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA, USA) was used for data processing and graphical representation. SAS statistical software was utilized to perform variance analysis and multiple comparisons of the data. Specifically, ANOVA was conducted for variance analysis, while Duncan's method ($p=0.05$) was applied for the multiple comparison tests.

Results

Effects of salt-nitrogen interaction on physiological characteristics of winter jujube leaves

According to the summary of the analyses of variance (*Table 1*), there was a significant interaction ($p \leq 0.01$) between the salinity treatment and the nitrogen fertilization combinations for the chlorophyll content and leaf nitrogen content. Compared with low and medium salt treatments, high salt stress significantly reduced the chlorophyll a, chlorophyll b, chlorophyll (a + b), leaf nitrogen concentration, and leaf area in plants irrigated with an equivalent nitrogen concentration. This detrimental effect was particularly pronounced under the combined influence of high nitrogen and high salt conditions.

Under identical salt stress conditions, the chlorophyll a, chlorophyll b, chlorophyll (a + b) content, leaf nitrogen content, and leaf area initially increased and subsequently decreased with the rise in nitrogen application levels. All three parameters reached their highest values in plants under medium nitrogen treatment. There were statistically significant differences ($p \leq 0.05$) in chlorophyll content across different nitrogen treatments while maintaining a constant salinity level.

Table 1. Leaf chlorophyll content, total nitrogen content, and leaf area of winter jujube at different concentrations of salinity and nitrogen

Nitrogen (g L ⁻¹)	NaCl (g L ⁻¹)	Chlorophyll a (mg·g ⁻¹ FW)	Chlorophyll b (mg·g ⁻¹ FW)	Chlorophyll (a+b) (mg·g ⁻¹ FW)	Chlorophyll a/b	Nitrogen content (mg·g ⁻¹)	Leaf area (cm ²)
1 (Low)	0.5(Low)	1.70d	0.59d	2.30d	2.88c	30.55d	13.16c
	2.5(Medium)	1.61e	0.56d	2.18e	2.88c	30.31e	13.14c
	5(High)	1.36g	0.44f	1.80g	3.09b	25.97g	10.29de
5 (Medium)	0.5(Low)	1.96a	0.83a	2.79a	2.36g	34.87a	16.02a
	2.5(Medium)	1.89b	0.81ab	2.70b	2.33g	33.68bc	15.90ab
	5(High)	1.42f	0.50e	1.92f	2.84d	26.48f	10.37d
10 (High)	0.5(Low)	1.92b	0.79b	2.71b	2.43f	34.54b	15.96a
	2.5(Medium)	1.82c	0.72c	2.54c	2.53e	33.59c	15.85b
	5(High)	1.25h	0.40g	1.65h	3.13a	23.14h	10.11e
NaCl	A	***	***	***	***	***	*
Nitrogen	B	***	***	***	***	***	**
Their interaction	A × B	***	***	***	***	***	*

Nitrogen concentration was 1, 5, and 10 gL⁻¹, respectively. NaCl concentration was 0.5, 2.5, and 5 gL⁻¹, respectively. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Different lowercase letters in the same column indicate the significant difference among different salinity and nitrogen combination concentrations at $P < 0.05$. The same as below

Effects of salt-nitrogen interaction on photosynthetic characteristics of winter jujube

As depicted in *Figure 1*, when comparing the other salinity treatments under the identical nitrogen level, high salt treatment resulted in a significant decrease in the plant's net photosynthetic rate (P_n) (*Fig. 1A*), stomatal conductance (g_s) (*Fig. 1B*), transpiration rate (T_r) (*Fig. 1C*), and stomatal limiting value (L_s) (*Fig. 1E*). Furthermore, high salt treatment produced the most significant inhibition on photosynthetic performance when paired with the high nitrogen treatment. In contrast, the intercellular CO₂ concentration (C_i) (*Fig. 1D*) of plants exhibited an inverse trend relative to the aforementioned photosynthetic indices.

When comparing various combination treatments under the identical salinity level, the medium nitrogen treatment demonstrates a more significant enhancement in the plant's P_n , g_s , T_r and L_s . Significant differences ($p \leq 0.05$) were observed among various combinations of salinity and nitrogen treatments.

Water use efficiency (WUE) (*Fig. 1F*), a holistic indicator of plant photosynthetic and transpirational attributes, achieved its highest values with the combination containing medium salt and medium nitrogen treatments. Under low and medium salt stress conditions, no significant differences in plant WUE were observed between medium and high nitrogen treatments. However, the WUE of plants subjected to high salt stress was significantly lower than that of other treatment combinations.

Effects of salt-nitrogen interaction on the accumulation of photoassimilates in winter jujube fruit

Under identical NaCl concentrations, as the nitrogen application rate increased, the fructose (*Fig. 2A*), glucose (*Fig. 2B*), sucrose (*Fig. 2C*) and total sugar (*Fig. 2D*) contents in winter jujube fruits initially rose and subsequently declined, reaching their highest values under medium nitrogen treatment and their lowest values under high

nitrogen treatment. Additionally, under medium salt conditions, significant differences were observed in the fructose, sucrose, and total sugar contents across different nitrogen levels ($p \leq 0.05$).

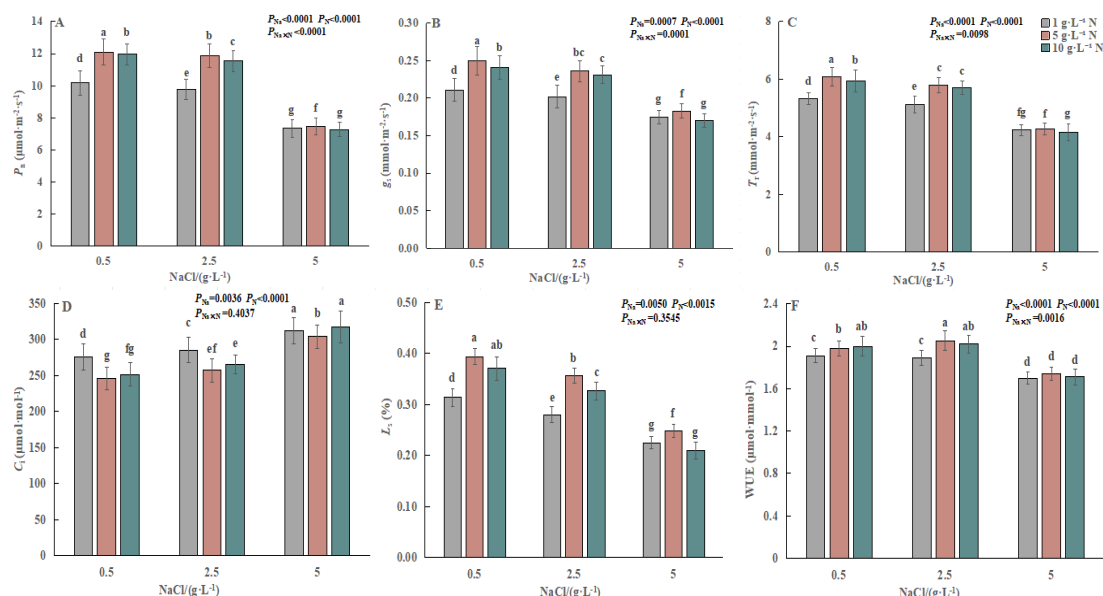


Figure 1. Photosynthetic parameters of winter jujube at different concentrations of salinity and nitrogen. P_n : Net photosynthetic rate; g_s : Stomatal conductance; T_r : Transpiration rate; C_i : Intercellular carbon dioxide concentration; L_s : Limiting value of stomata; and WUE : Water use efficiency. Different lowercase letters on the column indicate significant differences among different salinity and nitrogen combination concentrations at $P < 0.05$. The same as below

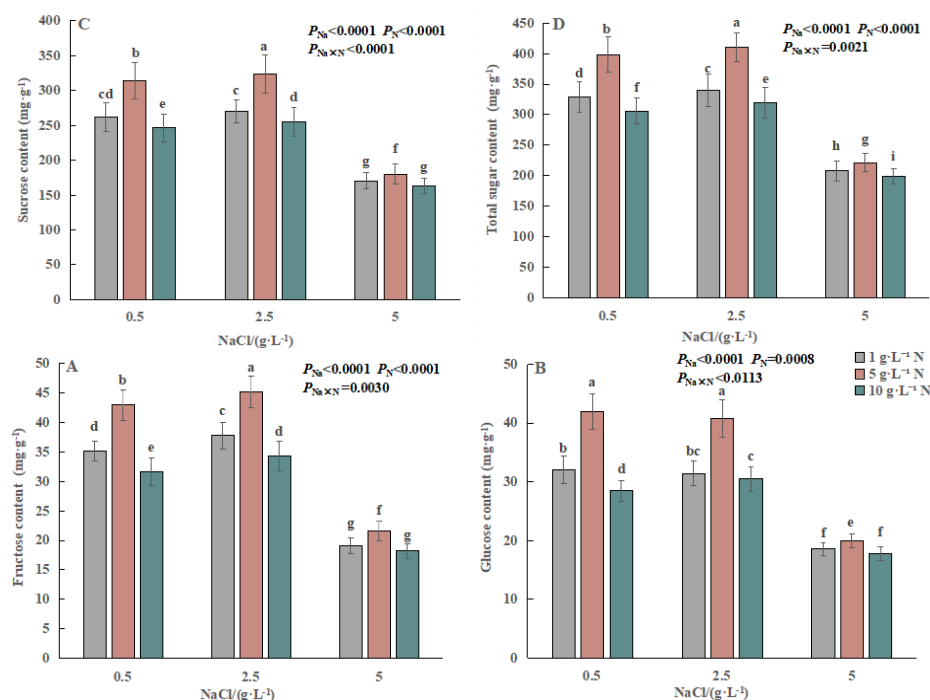


Figure 2. The content of major sugar components in winter jujube fruit at different concentrations of salinity and nitrogen

Medium salt stress showed the highest fruit fructose, sucrose, and total sugar content at equivalent nitrogen levels, differing statistically from other salt treatments ($p \leq 0.05$). However, treatment with high concentrations of salt significantly inhibited the accumulation of sugar components.

Through a comprehensive analysis, it was concluded that the interaction between medium salt and medium nitrogen treatments was the most favorable for sugar accumulation in winter jujube fruit. This was succeeded by the interaction between low salt and medium nitrogen treatments. In contrast, the combination of high nitrogen and high salt stress was found to be the least favorable for sugar accumulation (Figure 2).

Effects of salt-nitrogen interaction on sucrose metabolizing enzyme activity in fruit flesh

The type, quantity, and accumulation rate of sugar components in fruits are regulated by sucrose-metabolizing enzymes (Han et al., 2024). When comparing the other salinity treatments under the same nitrogen level (Figure 3), medium salt stress significantly increased the activities of fruit sucrose phosphate synthase (SPS) (Fig. 3A), acid invertase (AI) (Fig. 3B) and sucrose synthase of cleavage direction (SS-s) (Fig. 3D). Furthermore, there were significant differences ($p \leq 0.05$) in the activities of SPS, AI, and SS-s across different salt treatment conditions when subjected to medium nitrogen conditions. However, high salt stress significantly inhibited the activity of enzymes associated with sucrose metabolism in plants. Notably, under high nitrogen conditions, compared to medium salt treatment, the activities of SPS, AI, and SS-s under high salt treatment decreased by 92.34%, 65.28%, and 76.49%, respectively.

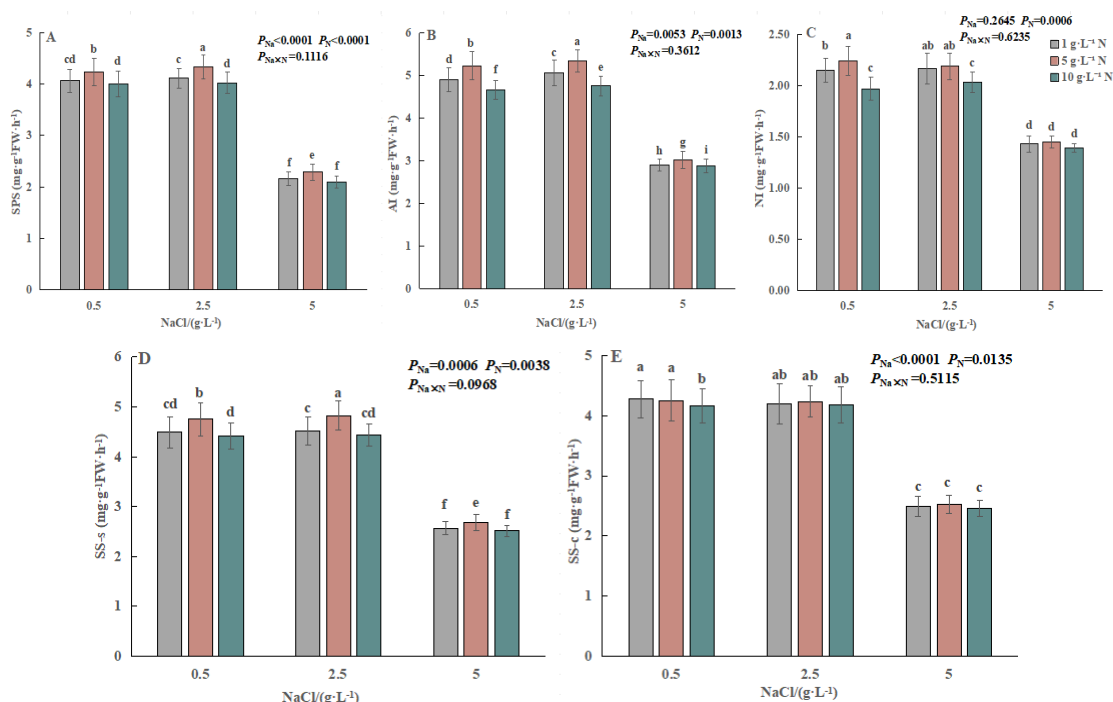


Figure 3. Activity of sucrose metabolizing enzymes of winter jujube fruit at different concentrations of salinity and nitrogen. SPS: Sucrose phosphate synthase; AI: Acid invertase; NI: Neutral invertase; SS-s: Sucrose synthase of synthetic direction; and SS-c: Sucrose synthase of cleavage direction

Under identical salt stress conditions, the activities of SPS, AI, and SS-s in winter jujube fruit reached their highest and lowest values under medium and high nitrogen treatments, respectively, and the AI activity exhibited significant differences ($p \leq 0.05$) across various nitrogen levels.

The activities of neutral invertase (NI) (Fig. 3C) and sucrose synthase of cleavage direction (SS-c) (Fig. 3E) in winter jujube fruit showed no significant difference between low and medium salt treatments at equivalent nitrogen levels, but exhibited a significant decrease under high salt stress.

Effects of salt-nitrogen interaction on accumulation and distribution of ^{13}C in winter jujube

^{13}C assimilation, ^{13}C assimilation capability, and percentage of self-retention and output of ^{13}C of winter jujube leaves

Salt and nitrogen treatments, as well as their interactions, significantly influenced the assimilation, assimilation capability, self-retention, and output of ^{13}C assimilates in winter jujube leaves (Table 2). There was no significant difference in the ^{13}C assimilation capability (ΔF) of winter jujube leaves between low and medium salt treatments when the plants were subjected to medium nitrogen fertilization. However, when comparing the other salinity treatments under identical nitrogen conditions, high salt stress significantly diminished both the ^{13}C assimilation and ^{13}C assimilation capability (ΔF) of leaves. Specifically, under high nitrogen conditions, compared to low salt treatment, the ^{13}C assimilation and ^{13}C assimilation capability (ΔF) of leaves under high salt treatment decreased by 238.30% and 475.00%, respectively.

Table 2. *^{13}C assimilation, ^{13}C assimilation capability, percentage of self-retention, and output of ^{13}C winter jujube leaves at different concentrations of salinity and nitrogen*

Nitrogen (g L ⁻¹)	NaCl (g L ⁻¹)	^{13}C assimilation (mg·g ⁻¹)	^{13}C assimilation capability (ΔF)	Self-retention of ^{13}C (%)	Output of ^{13}C (%)
1 (Low)	0.5 (Low)	2.19d	0.14d	77.76e	24.80b
	2.5 (Medium)	2.06e	0.12e	78.48de	23.71c
	5 (High)	1.13f	0.05g	85.95ab	15.79ef
5 (Medium)	0.5 (Low)	3.29a	0.25a	71.74f	29.92a
	2.5 (Medium)	3.12bc	0.24ab	71.91f	29.39a
	5 (High)	1.22f	0.06f	85.25b	16.28e
10 (High)	0.5 (Low)	3.18b	0.23b	78.70cd	23.25c
	2.5 (Medium)	3.05c	0.21c	79.26c	21.96d
	5 (High)	0.94g	0.04g	86.31a	15.43f
NaCl	A	**	**	**	**
Nitrogen	B	***	***	***	***
Their interaction	A × B	**	**	**	**

Under low and medium salt stress conditions, the ^{13}C assimilation and ^{13}C assimilation capability (ΔF) reached their highest values when the plants were subjected to medium nitrogen fertilization, followed by high nitrogen treatment, and the differences among various nitrogen treatments were statistically significant ($p \leq 0.05$).

The combined application of high salt and high nitrogen exerted the most pronounced inhibitory effect on the accumulation and synthesis of photosynthetic products in plants.

For the low and medium salt treatments, despite the absence of a significant difference in the proportion of ^{13}C self-retention in winter jujube leaves (including labeled leaves and labeled jujube suspensions) at a constant salinity level, there were higher proportion of ^{13}C assimilate output in relation to the high salt treatment.

The plants fertilized with medium nitrogen was most effective in promoting ^{13}C output while maintaining a constant salinity level, whereas the high nitrogen treatment resulted in the highest ^{13}C retention ratio and the lowest ^{13}C output ratio. Under low and medium salt treatments, there were statistically significant differences ($p \leq 0.05$) in the proportions of ^{13}C retention and output across different nitrogen treatments.

Distribution of ^{13}C in different organs

As shown in Table 3, when comparing the high salt treatment at a constant nitrogen level, the ^{13}C distribution rate in both labeled leaves and labeled bearing shoot was significantly reduced under low and medium salt treatments. While there was no statistically significant difference in the ^{13}C distribution rate of labeled leaves and labeled bearing shoots between the low and medium salt treatments for plants fertilized with medium nitrogen.

Table 3. Distribution rate of ^{13}C winter jujube at different concentrations of salinity and nitrogen (%)

Nitrogen (g L ⁻¹)	NaCl (g L ⁻¹)	Labeled leaves	Labeled bearing shoots	Labeled fruits	Unlabeled leaves	Unlabeled one-year- old branches	Unlabeled perennial branches	Unlabeled fruits
1 (Low)	0.5 (Low)	39.28e	35.92d	7.76b	2.43b	5.23b	6.26b	3.12b
	2.5 (Medium)	40.05d	36.24c	7.43bc	2.30b	5.05bc	6.01c	2.92c
	5 (High)	44.85a	39.36a	4.86f	1.73d	3.22e	3.92ef	2.06e
5 (Medium)	0.5 (Low)	35.73f	34.35e	9.66a	2.82a	5.94a	7.34a	4.16a
	2.5 (Medium)	36.11f	34.49e	9.54a	2.76a	5.74a	7.26a	4.09a
	5 (High)	44.54b	39.18a	5.03e	1.81d	3.26e	4.05e	2.13e
10 (High)	0.5 (Low)	40.36d	36.39bc	7.29c	2.21b	4.97c	5.90c	2.88c
	2.5 (Medium)	41.38c	36.66b	6.86d	2.01c	4.73d	5.73d	2.63d
	5 (High)	45.03a	39.54a	4.70f	1.67d	3.19e	3.86f	2.01e

The ^{13}C distribution rate in both labeled leaves and labeled bearing shoot reached its highest values under high nitrogen treatment and its lowest values under medium nitrogen treatment while maintaining a constant salinity level. Under low salt and medium salt conditions, the ^{13}C distribution rates in labeled leaves and bearing shoot exhibited significant differences among various nitrogen levels at the same salinity level ($p < 0.05$).

Following the application of medium nitrogen, the ^{13}C distribution rate in fruits (both labeled and unlabeled) significantly increased under low, medium, and high salt treatments (13.8%, 13.6%, and 7.2%, respectively). Conversely, high nitrogen led to a

significant reduction in the ^{13}C distribution rate in fruits (both labeled and unlabeled) under low, medium, and high salt treatments (10.2%, 9.5%, and 6.7%, respectively).

Compared to other nitrogen treatments, medium nitrogen showed greater efficacy in improving the proportion of ^{13}C assimilates allocated to unlabeled leaves and branches under low, medium, and high salt conditions, with respective proportions of 16.1%, 15.8%, and 9.1%. Conversely, under high nitrogen treatment, these proportions were significantly lower, at 13.1%, 12.5%, and 8.7% under low, medium, and high salt conditions, respectively.

The aforementioned findings suggest that under low and medium salt stress, the application of medium nitrogen significantly enhanced the ^{13}C output capacity and the competitive ability of fruits for photosynthetic products. However, under high salt stress, the transport capacity of photosynthates from source to sink was markedly diminished, and even an increased nitrogen fertilizer application could not mitigate this adverse effect (*Table 3*).

Discussion

Chlorophyll content serves not only as an indicator of the photosynthetic capacity of plants (Van Wallendael et al., 2020), but also as a crucial physiological parameter for assessing plant stress resistance (Zhang et al., 2006). With the intensification of salt stress, the chlorophyll content in grapes (Sun et al., 2018) and *Magnolia wufengensis* grafted seedlings (Zhao et al., 2024) initially increased before subsequently decreasing. In contrast, blueberries (Jia et al., 2023) and *Elaeagnus angustifolia* (Jia et al., 2018) exhibited a continuous decline in chlorophyll content. In this study, under conditions of low and medium salt stress, plants fertilized with medium nitrogen levels demonstrated a significant increase in leaf nitrogen content. This enhancement facilitated chlorophyll synthesis, thereby maintaining elevated concentrations of both chlorophyll a and chlorophyll b. However, high salt stress not only severely suppresses nitrogen uptake in winter jujube but also induces ion toxicity as a result of elevated salt concentrations. This may compromise chloroplast morphology, diminish the activity of chloroplast pigment synthase (He et al., 2014; Muhammad et al., 2021; Pan et al., 2022), impair chlorophyll synthesis, accelerate chlorophyll degradation, and ultimately cause a substantial decline in chlorophyll content. The response mechanisms of chlorophyll content in various crops to salt stress vary, and this variation is attributed to the distinct regulatory pathways involved in chlorophyll metabolism (Zhou et al., 2023).

There is a significant interaction effect between soil salinity and nitrogen application rate. Under moderate salt stress, the absorption of ions such as Na^+ and K^+ is enhanced, which in turn stimulates protoplasmic streaming in plant cells and enhances plant photosynthesis (Ahmad and Anjum, 2023). This process facilitates more efficient nitrogen uptake by plants. However, the excessive accumulation of soil salinity can not only result in the degradation of physical properties, such as soil aeration and bulk density, but also decrease the activity of nitrate reductase, thereby reducing the nitrogen absorption and utilization efficiency of crops (Chen et al., 2010). Furthermore, physiological and metabolic alterations lead to nitrogen stress in plants under high nitrogen conditions (Han et al., 2015). The residual excess nitrogen fertilizer in the soil exacerbates salt stress. Consequently, the inhibitory impact of dual stresses salt and nitrogen on plant nutrient uptake and growth becomes increasingly pronounced. This

also explains why the adverse effects of the interaction between high salt and high nitrogen on leaf function were most evident in this study.

The factors contributing to the decline in photosynthetic efficiency under salt stress conditions vary significantly among different plant species (Chen et al., 2011; Hussain et al., 2017; Lekklar et al., 2019; Li et al., 2022). For instance, in switchgrass (Zhao et al., 2015) and *Elaeagnus angustifolia* seedlings (Liu et al., 2014), salt stress significantly increased stomatal limitation, thereby impeding CO₂ diffusion into the leaves and reducing transpiration. This indicates that stomatal limitation may be a critical factor inhibiting photosynthesis in these plants. On *Magnolia grandiflora* (Zhao et al., 2024) and *Betula halophila* (Van Zelm et al., 2020), under salt stress conditions, no consistent correlation was observed between the intercellular CO₂ concentration and the net photosynthetic rate or stomatal conductance. The reduction in photosynthesis was primarily attributed to non-stomatal limitations. In tomato plants (Xin et al., 2024) and *Gymnocarpus przewalskii* seedlings (Zhou et al., 2023), the reduction in net photosynthetic rates was primarily attributed to stomatal limitations under low salt concentrations, whereas at high salt concentrations, stomatal limitations became less significant.

In this study, as the NaCl concentration increased to 5 g·L⁻¹, a significant decline was observed in the net photosynthetic rate, stomatal conductance, transpiration rate, and stomatal limitation values. Conversely, the intercellular CO₂ concentration exhibited an inverse trend relative to the net photosynthetic rate and stomatal conductance (*Figure 1*). In conjunction with the substantial reduction in chlorophyll content observed in winter jujube under high salinity conditions (*Table 1*), it can be inferred that the decrease in net photosynthetic rate under high salt stress is predominantly influenced by non-stomatal factors. Specifically, the excessive accumulation of Na⁺ and Cl⁻ ions leads to damage to the membrane system (Zhao et al., 2024a), impairs the leaf photosynthetic apparatus, and diminishes the carboxylation capacity of mesophyll cells as well as the activity of photosynthetic enzymes (Li et al., 2010; He et al., 2014). These factors primarily contribute to the decreased net photosynthetic rate.

Under salt stress, application of nitrogen improves photosynthetic pigments and leaf area, enhances plant tolerance against salinity by decreasing photo-inhibition and injury and improving Fv/Fm (Wu et al., 2008; Yang et al., 2023). Under low and medium stress conditions, plants fertilized with medium nitrogen exhibited a significant improvement in the water use efficiency of winter jujube leaves (*Figure 1*). Additionally, this treatment led to a substantial increase in both the intercellular CO₂ diffusion rate and the net photosynthetic rate (*Figure 1*). Therefore, appropriate nitrogen application holds promise for enhancing the formation of assimilatory power and promoting the accumulation of assimilates. When subjected to high salt stress, the photosynthetic capacity of winter jujube was significantly inhibited (*Figure 1*), and the accumulation and transportation of photosynthetic products were substantially impeded (*Table 2*). This detrimental effect was particularly pronounced under the combined influence of high salt and high nitrogen conditions, which hindered efforts to enhance yield and quality (Semiz et al., 2014).

The accumulation of sugar in fruit not only requires robust photosynthetic capacity in the leaves but also depends on the amount of photosynthate transported to the fruit (Álvarez et al., 2008; Desnoues et al., 2018). Under the combined influence of medium salinity and nitrogen conditions, the ¹³C assimilation rate in winter jujube leaves demonstrated a significant increase. Simultaneously, the activities of enzymes involved

in sucrose metabolism within the fruits were markedly enhanced, and the transport of ^{13}C assimilates from the leaves to the fruits exhibited a substantial rise. The activity of sucrose-metabolizing enzymes is not only closely associated with the ability of fruits to unload assimilates (Yamaki, 2010), but also affects how different organs compete for carbon sources to adapt to stress environments (Balibrea and Dell'Amico, 2000). It is evident that the combination of moderate salt stress and appropriate nitrogen fertilizer not only maintains relatively high photosynthetic productivity but also enhances the fruit's 'sink' capacity by increasing the activity of enzymes involved in sucrose metabolism. Consequently, this promotes the transport and distribution of photosynthetic assimilates to fruits. Furthermore, experimental validation across various fruit crops, including grapes (Sun et al., 2018), apple (Zheng et al., 2013), and citrus (Grieve et al., 2007), has demonstrated that under moderate salt stress conditions, plants can enhance the expression of sucrose synthase and acid invertase genes. This enhances cellular osmotic pressure stability through the accumulation of fructose and glucose (Lu et al., 2009; Rahimi et al., 2011), thereby improving stress tolerance. To some extent, this process also promotes sugar accumulation in winter jujube fruits. However, under conditions of high salt stress, particularly when nitrogen application is either insufficient or excessive, plants may experience nutrient deficiencies, ion imbalances, and a diminished capacity for osmotic regulation. Furthermore, the photosynthetic performance of plants is impaired (*Figure 1*), which results in a reduced rate of ^{13}C assimilation (*Table 2*), as well as significant declines in both the rate of ^{13}C assimilate output (*Table 3*) and the activities of enzymes involved in sucrose metabolism (*Figure 3*). Collectively, these factors impede sugar accumulation in fruits.

In this study, the interaction between salt and nitrogen fertilizer demonstrated significant concentration-dependent effects on the translocation and distribution of photosynthetic products. However, certain studies have reported that salt stress inhibits the export of photosynthetic products at the 'source' end and obstructs the 'sink' flow (Hu et al., 2019), thereby preventing effective translocation and degradation of these products. This ultimately leads to a reduction in the soluble sugar content within fruits. It is evident that the 'source-sink' relationship is influenced by species, stress intensity, and duration. In addition, it was observed that high nitrogen treatment led to a significant reduction in the content of major sugar components and the activity of sucrose invertase in winter jujube fruit. Sucrose invertase catalyzes the hydrolysis of sucrose into glucose and fructose, indicating that high nitrogen levels may inhibit this enzymatic activity. This inhibition could prevent the establishment of an adequate sucrose concentration gradient between the fruit and phloem, thereby impeding the transport of photosynthates from the 'source' to the 'sink'. Under identical salt stress conditions, the proportion of ^{13}C output in winter jujube leaves under high nitrogen conditions was significantly lower compared to low nitrogen treatment, further corroborating the detrimental effects of high nitrogen on the source-sink relationship. This finding aligns with previous research showing that high nitrogen reduces the accumulation of sugar in fruits in non-saline environments (Wang et al., 2021), which may contribute to the adverse impact of high nitrogen on fruit sugar metabolism.

Conclusions

Under the experimental conditions, the interaction between $2.5\text{ g}\cdot\text{L}^{-1}$ NaCl and $5\text{ g}\cdot\text{L}^{-1}$ nitrogen fertilizer improved the leaf function of winter jujube, maintained high

photosynthetic production capacity, and provided sufficient carbon sources for fruit sugar metabolism. Simultaneously, the increased activity of sucrose-metabolizing enzymes enhanced the capacity of the fruit to accumulate sugars by promoting the transport and distribution of photosynthates to the fruit. This interaction proved most beneficial for sugar accumulation, improving fruit quality and stress resistance in winter jujube. Conversely, 5 g·L⁻¹ NaCl stress impaired the osmotic regulation and leaf function of winter jujube, severely inhibiting photosynthetic performance. This stress condition significantly reduced the activity of sucrose-metabolizing enzymes, weakened fruit sugar metabolism, and disrupted the effective transport and distribution of photosynthates to the fruits, resulting in lower fruit sugar content. This negative effect was especially obvious when 5 g·L⁻¹ NaCl was combined with 1 or 10 g·L⁻¹ nitrogen fertilizer.

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