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Sunflower Photosynthetic Characteristics, Nitrogen Uptake, and Nitrogen Use Efficiency under Different Soil Salinity and Nitrogen Applications

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Abstract: Understanding salinity and fertilizer interaction is of great importance to improve crop production and fertilizer use efficiency in saline areas. To evaluate the interactive effects of different soil salinity levels and nitrogen (N) applications rates on the sunflower photosynthetic characteristics of N uptake and N use efficiency, a two-year field experiment was conducted in Hetao Irrigation District, China. The experiment consisted of three initial salinity (IS) levels expressed as the electrical conductivity of a saturated soil extract (EC_e) (S0: 1.72–2.61 dS/m; S1: 4.73–5.90 dS/m; S2: 6.85–9.04 dS/m) and four N rates (45, 90, 135, and 180 kg/ha), referred as N0–N3, respectively. The results indicated that the net photosynthetic rate (*Pn*) of sunflowers treated with S0 and S1 levels both had a significant decrease in the bud stage, and then reached their maximum at anthesis. However, during the crop cycle, the *Pn* at S2 level only had small fluctuations and still remained at a high level (>40 μmol $CO_2/(m^2\ s)$) at the early mature stage. When increasing IS levels from S0 to S1, the plant N uptake (*PNU*) under the same N rates were only decreased by less than 10% at maturity, whereas the decline was expanded to 17.2–45.7% from S1 to S2. Additionally, though applying the N2 rate could not increase sunflower *PNU* at the S0 and S1 levels, its N use efficiency was better than those under N3. Meanwhile, at the S2 level, the application of the N0 rate produced a higher N productive efficiency (*NPE*) and N uptake efficiency (*NUPE*) than the other N rates. Therefore, our study proposed recommended rates of N fertilizer (S0 and S1: 135 kg/ha, S2: 45 kg/ha) for sunflowers under different saline conditions.

Keywords: sunflower; salt stress; nitrogen application rate; photosynthesis; nitrogen uptake; nitrogen use efficiency

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1. Introduction

Nitrogen (N), as a key component of all nucleic acids and proteins, is crucial for the development of new plant cells and crop growth [1]. In modern cropping systems, high-yield crop production relies heavily on the application of N fertilizers [2]. However, overfertilization with N not only increases production costs, but also causes soil degradation and water eutrophication, and contributes to the emissions of greenhouse gases [3]. On the other hand, soil salinity is another major abiotic stress that limits crop production worldwide, especially in arid and semiarid regions [4]. Salinity has been proved to alter N dynamics in soils, such as mineralization, nitrification, and denitrification [5,6], thus influencing the uptake and utilization of N by crops. At the same time, as a type of salt itself, N fertilizer will aggravate soil salinization and lead to crop yield reduction when applied excessively [7–9].

Hence, the vulnerable saline agroecosystem has posed a major challenge for farmers when selecting the appropriate amount of N fertilizer for saline fields, which can both secure crop yields and minimize adverse environmental impacts.

In recent years, numerous studies have shown that proper management of N fertilizer in saline fields could alleviate the growth inhibition induced by salt stress, depending on plant species and salinity levels [10–13]. For example, Mansour [14] indicated that N might enhance plant salt tolerance by altering the contents of endogenous phytohormones (e.g., cytokinin and kinetin). Likewise, the study by Dong [15] reported that proper N application played not only a nutritional role, but also an osmotic role in enhancing the salt tolerance of cotton via increasing nutrient uptake and decreasing Na^+ accumulation in its tissues. In addition, our previous studies on sunflower [16,17] suggested that applying 135 kg/ha of N fertilizer under low and moderate saline conditions could alleviate the detrimental effects of salt stress through optimizing the root:shoot ratio and promoting the rapid growth of fine roots in early growth stages. However, relevant studies based on phenotypic changes have also shown that the effects of N application on crop growth varied with the development of growth stages, and were quite different at different soil salinity levels. It is necessary to further explain the influence of coupled salt and N stresses on crop growth from the perspective of photosynthesis and N utilization.

The efficient use of N fertilizer is conducive to both food security and environmental quality. The existing studies on crop N use efficiency mainly focused on the effects of different tillage, planting, and water and fertilizer managements under a nonsaline condition [2,18,19], while few studies were reported concerning the coupled effects of N application rates and salt levels. It should be noted that salt stress increased the complexity of plant response to N fertilizers [20,21], which led to controversial results on the process of photosynthesis. For instance, Liu et al. [22] showed that increasing N fertilizer could always increase the chlorophyll content in the leaves of winter wheat during the crop cycle under different degrees of salt stress. However, the study by Pei et al. [23] on sunflower showed that the increase of N application at a high salt level could reduce the chlorophyll content in some growth stages, but higher chlorophyll content was remarkably found in the leaves at a medium salt level. This was also different from the results of Zhang et al. [24], who suggested that the optimal rates of N application at both medium and high salt levels were relatively low (96 kg/ha), based on the chlorophyll fluorescence parameters of tomato. Moreover, the mentioned studies on crop photosynthetic characteristics were mostly conducted at controlled pot or microplot scales, rather than naturally salt-affected field scales.

Sunflower (*Helianthus annuus* L.), which is classified as moderately salt-tolerant [25], has become an important industrial crop planted in salt-affected areas worldwide, especially in the arid northwest of China. The main objectives of this study were: (i) to determine the photosynthetic characteristics, N uptake, and N use efficiency of sunflower varying with different soil salinity and N applications; and (ii) to provide a physiological basis for the accumulation and partitioning rule of sunflower biomass, which has been previously reported at different salt levels and N rates [26]. The information obtained from this study will scientifically and reasonably guide the management of N fertilizer in saline fields.

2. Materials and Methods

2.1. Experimental Site

The field experiments were conducted at the Yichang experimental station, which is located in the Hetao Irrigation District (40°19′–41°18′ N, 106°20′–109°19′ E) of Inner Mongolia, China. The average annual precipitation of this area is 139 to 222 mm, with approximately 60% falling in the summer from June to August. Annual potential evaporation is approximately 2200 to 2400 mm. The strong evaporation with a high ratio of evaporation and precipitation (E/P > 10) makes the groundwater and soil water migrate upward continuously, bringing a large number of salts from the soil parent materials that then accumulate in the soil surface. Therefore, the problem of soil salinization in the Hetao Irrigation District

is very serious, and it is necessary to carry out such studies in this area. The average annual groundwater depth at the Yonglian experimental station is about 2.21 m, and the groundwater depth in the irrigation period is about 0.6 m, which is a typical representation of the irrigation districts in Northwest China.

2.2. Field Experiments

Two years of field experiments (2015 and 2016) were carried out in six 7.5 × 4.5 m plots, which were established in three nearby fields (40–55 m apart) with naturally varying salinity levels, and each field had two adjacent plots applied with different nitrogen application rates (N rates). A two-factor randomized block design was used in the experiments of these two years, both including three initial salinity (IS) levels and two N rates. The electrical conductivity of 1:5 soil–water extract ($EC_{1:5}$) was measured using a digital conductivity meter (Leici, Yidian Co., Ltd., Shanghai, China), then converted to the electrical conductivity of a saturated-paste extract (EC_e) by an empirical formula ($EC_e = 7.4 \times EC_{1:5}$) [27]. At a 0 to 60 cm soil depth of these three fields, the average EC_e values varied within certain ranges at 10 d before sowing in 2015 and 2016, and could be divided into three soil salinity levels (Table 1): low (S0, EC_e = 1.72–2.61 dS/m), medium (S1, EC_e = 4.73–5.90 dS/m), and high level (S2, EC_e = 6.85–9.04 dS/m). Four N rates were included in the two-year experiments: 45, 90, 135, and 180 kg/ha, referred to as the N0 (extremely low), N1 (low), N2 (moderate), and N3 (high) rates, respectively, which were set based on our previous studies [16,17,28]. As shown in Table 1, the N0 and N2 rates were determined in 2015, and the N1 and N3 rates were determined in 2016. Among them, the N0 and N1 rates were applied basally before sowing, while the N2 and N3 rates were achieved by top-dressing an additional 90 kg/ha at 20 days after sowing, based on N0 and N1, respectively. All the N rates mentioned above were achieved using diammonium phosphate (18% N) as 45 kg/ha of basal N fertilizer, while the rest basal N rate and the top-dressed N rate in Table 1 were all from urea (46% N). Moreover, all plots were basally applied with additional 78.59 kg/ha of P fertilizer as calcium superphosphate (7.86% P) and 62.23 kg/ha of K fertilizer as potassium sulfate (44.8% K), based on local practice.

Table 1. The initial soil salinity (IS) levels and nitrogen application rates (N rates) of different treatments in the field experiments of 2015 and 2016.

Years	Treatments	S †	N Rate	Basal N Rate	Top-Dressed N Rate
		dS/m	kg/ha	kg/ha	kg/ha
2015	S0N0	1.878	45	45	0
	S0N2	1.723	135	45	90
	S1N0	5.017	45	45	0
	S1N2	5.898	135	45	90
	S2N0	8.157	45	45	0
	S2N2	9.035	135	45	90
2016	S0N1	2.613	90	90	0
	S0N3	2.227	180	90	90
	S1N1	4.731	90	90	0
	S1N3	5.515	180	90	90
	S2N1	6.847	90	90	0
	S2N3	7.158	180	90	90

Note: † IS indicates the average EC_e (electrical conductivity of a saturated-paste extract) values at a 0 to 60 cm depth before sowing.

The soil texture in each plot was mainly silty loam, and the basic physical and chemical properties of the soils in the experimental fields can be found in our previous study [17]. The soils were plowed and harrowed around 30 d before sowing, then each plot was mulched with three plastic films (80 cm width, with a 30 cm interval). All the basal fertilizer was applied beneath the plastic films at the same time of film mulching. In addition, all the plots were irrigated (250 mm) around 20 d before sowing in each year, and no irrigation

was provided during the sunflower growth period. When soil moisture was considered acceptable for sowing, two rows of sunflower (GL601) were sown in each plastic film using manual hill-drop planting on 28 May 2015 and 5 June 2016, respectively. The cultivar GL601 was an edible sunflower that was widely planted by local farmers in recent years. Seedlings were thinned to 4.28 plants/m^2 by leaving one vigorous plant per hill at the four-true-leaf stage. The sunflower plants were harvested on 11 September 2015 and 19 September 2016.

2.3. Data Collection

2.3.1. Photosynthetic Characteristics

In the field experiment of 2016, three tagged sunflower plants were selected in each plot, and their photosynthetic characteristics were measured five times by a portable photosynthetic system (LI-6400XT, LI-COR, Lincoln, NE, USA) during the crop cycle at 41 (late seedling stage), 52 (middle bud stage), 64 (anthesis), 71 (early mature stage) and 106 (maturity) days after sowing (DAS). The measured photosynthetic data included the net photosynthetic rate (*Pn*, μmol CO_2/(m^2 s)), stomatal conductance (Stomatal conductance, *Gs*, mmol H_2O/(m^2 s)), intercellular CO_2 concentration (*Ci*, μmol CO_2/mol), and leaf transpiration rate (Transpiration rate, *Tr*, mmol H_2O/(m^2 s)). Each observation was carried out at 9:00–11:00 a.m. on a windless and sunny day, and five repeated measurements were performed on the youngest fully expanded leaf of each tagged sunflower plant. The photosynthetic active radiation (PAR), the CO_2 concentration, the flow rate, and the temperature in the leaf chamber were set to 1700 μmol/(m^2 s), 380 μmol/mol, 500 μmol/s, and 30 °C, respectively.

2.3.2. Plant Biomass and Seed Yield

The growth cycle of sunflower can be divided into four growth stages, based on the study of Schneiter and Miller [29]: seedling, bud, flowering, and mature stages. At each sunflower growth stage, three plants were randomly chosen from each plot, and destructive measurements were undertaken at 23, 56, 73, and 106 DAS in 2015; and at 28, 52, 66, and 106 DAS in 2016, respectively. The chosen plants were cut just above the soil surface using hand clippers and separated into leaves, stems, and flower disks. All the samples were placed in paper bags and oven-dried at 70 °C to constant weight. The dry samples were weighed to calculate the shoot biomass. At harvest, 20 mature sunflower plants were also randomly chosen from each plot to obtain all their seeds on the flower disks, and the seed yield (SY) was air-dried to constant moisture (approximately 8%) and measured in each year.

2.3.3. Plant Nitrogen Uptake

To determine sunflower N uptake, the dry samples of each plant part mentioned above were milled with a pulverizer (9FZ-35, Taifeng Machinery Factory, Taizhous, China), mixed, and passed through a 0.5 mm sieve. Total N concentration was determined using the micro-Kjeldahl method [30]. The N concentration was expressed on a dry-weight basis, and total N uptake and accumulation were calculated as the product of concentration and dry weight.

2.4. Data Analysis

2.4.1. Stomatal Limitation Index

The stomatal limitation index (*Ls*) reflects the limitation of stomatal aperture to leaf photosynthesis. The greater the *Ls* value, the stronger the stomatal aperture limited plant photosynthesis. The *Ls* was calculated as follows:

$$Ls = (1 - \frac{Ci}{Ca}) \times 100\% \quad (1)$$

where *Ci* denotes intercellular CO_2 concentration, μmol CO_2/mol; and *Ca* denotes external CO_2 concentration, which was maintained at 380 μmol CO_2/mol using the CO_2 controlling system of LI-6400XT when measuring the photosynthetic characteristics of sunflower leaves in this study.

The factors causing the decrease in the *Pn* value included the partial closure of leaf stomata and a decrease in the photosynthetic activity of mesophyll cells. The former factor was called the stomatal factor, and the latter was called the nonstomatal factor. According to the judgment method proposed by Xu [31], the change direction of *Ci* and *Ls* was a reliable criterion for the decrease in the *Pn* value. A decreasing *Ci* value and increasing *Ls* value indicated that the stomatal factor was the main cause, whereas an increasing *Ci* and decreasing *Ls* indicated the nonstomatal factor was the main reason.

2.4.2. Nitrogen Production, Uptake, and Utilization Efficiency

In this study, three kinds of N efficiency indices were used to evaluate sunflower uptake and utilization of N fertilizer from the soils; these were N productive efficiency (*NPE*, kg/(kg N)), N uptake efficiency (*NUPE*, kg/kg), and N utilization efficiency (*NUTE*, kg/(kg N)). The *NPE*, *NUPE*, and *NUTE* could be calculated as follows:

$$NPE = \frac{SY}{N_{total}} \quad (2)$$

$$NUPE = \frac{PNU}{N_{total}} \quad (3)$$

$$NUTE = \frac{SY}{PNU} \quad (4)$$

where N_{total} denotes the total amount of applied N fertilizer, kg/ha; *SY* denotes the sunflower seed yield, kg/ha; and *PNU* denotes the total N uptake of sunflower plants at maturity, kg/ha.

2.4.3. Photosynthetic Nitrogen Use Efficiency

Photosynthetic nitrogen use efficiency (*PNUE*, μmol CO_2/(mg s)) reflected the instantaneous CO_2 assimilation rate per unit leaf N, and could be expressed as:

$$PNUE = \frac{Pn}{LTNA/LA} = \frac{Pn}{N_{area}} \quad (5)$$

where *Pn* denotes net photosynthetic rate, μmol CO_2/(m^2 s); *LTNA* denotes the amount of total leaf N accumulation, mg/plant; *LA* denotes the total leaf area, cm^2/plant; and N_{area} denotes the leaf N content per unit area, mg/cm^2.

3. Results

3.1. Sunflower Photosynthetic Characteristics in Saline Fields

3.1.1. Net Photosynthetic Rate

As shown in Figure 1, the net photosynthetic rate (*Pn*) of all treatments declined from the seedling stage (41 DAS) to bud stage (52 DAS), and decreased mostly for the S1N1 and S1N3 treatments, by 33.9% and 43.2%, respectively. After that, the *Pn* at S0 and S1 levels (Figure 1a,b) increased significantly in the late bud stage, reached their maximum at anthesis (64 DAS), and then declined again after entering the mature stage. Particularly, only the *Pn* of sunflowers treated with the N3 rate were found to have a significant decline, from 64 to 71 DAS. On the other hand, at the S2 level (Figure 1c), the variations in *Pn* after anthesis (71 and 106 DAS) were less than 2.2% compared with the values at 64 DAS, and they could still remain at a high level of more than 40 μmol CO_2/(m^2 s). At maturity (106 DAS), the *Pn* of each treatment was significantly decreased to a very low level of less than 12.5 μmol CO_2/(m^2 s) due to leaf senescence.

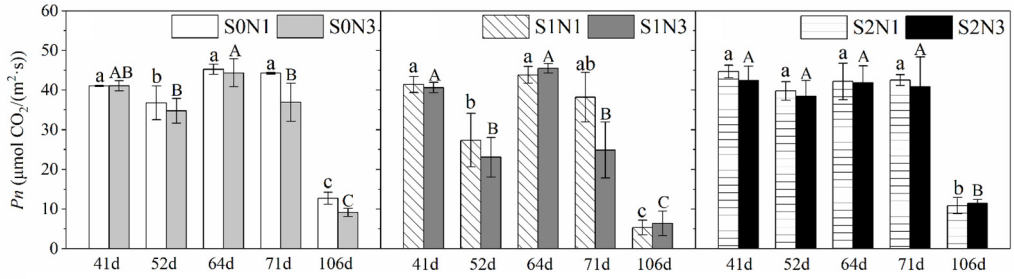

Figure 1. Sunflower net photosynthetic rate (*Pn*) at different observation times under different treatments in 2016. The horizontal coordinate represents days after sowing, the data were averaged measurements from the three fixed sunflower plants (n = 15), and vertical bars indicate the standard error. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N1 and N3 indicate different N application rates (low and high); and their combinations represent different treatments. Different lowercase letters above the bars represent significant differences at 0.05 levels under the N1 level; different uppercase letters above the bars represent significant differences at 0.05 levels under the N3 level.

3.1.2. Stomatal Conductance

Stomatal conductance (*Gs*) represents the degree of stomatal opening and is proportional to the intensity of photosynthesis and transpiration. As shown in Figure 2, an increased *Gs* was found at the S0 and S2 levels from 41 to 52 DAS, but the increase was only significant in the S0N1 treatment, by 45.7%. Meanwhile, the *Gs* for the S1N1 and S1N3 treatments decreased significantly, by 43.2% and 78.0% during the same period, respectively, and then experienced a rapid rebound from 52 to 64 DAS, which was consistent with the trend of the *Pn* value at the S1 level. After 64 DAS, the Gs for the S0 and S1 levels decreased constantly to a low level of less than 0.12 mmol $H_2O/(m^2$ s) at maturity, while an increased *Gs* could still be found for the S2 level in the early mature stage.

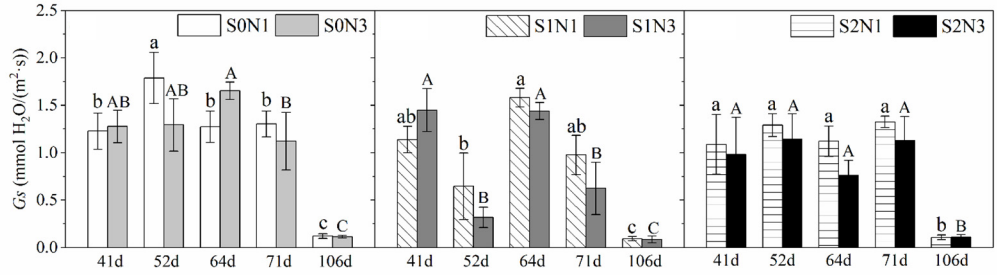

Figure 2. Sunflower stomatal conductance (*Gs*) at different observation times under different treatments in 2016. The horizontal coordinate represents days after sowing, the data were averaged measurements from the three fixed sunflower plants (n = 15), and vertical bars indicate the standard error. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N1 and N3 indicate different N application rates (low and high); and their combinations represent different treatments. Different lowercase letters above the bars represent significant differences at 0.05 levels under the N1 level; different uppercase letters above the bars represent significant differences at 0.05 levels under the N3 level.

3.1.3. Intercellular CO_2 Concentration and Stomatal Limitation Index

As mentioned in Section 2.4.1, the intercellular CO_2 concentration (*Ci*) and stomatal limitation (*Ls*) were important judgment bases for determining the causes of the *Pn* decline. Accordingly, after comparing Figures 3a–c and 3d–f, we proposed that the reasons for the decline in the *Pn* value for different treatments shown in Figure 1 were as follows: (i) in the bud stage, the reason for the significant decline in *Pn* for the S0N1 treatment was the nonstomatal factor, which was due to N deficiency, while the reason for the significant

decline in *Pn* for S1N1 and S1N3 was the stomatal factor; (ii) in the early mature stage, the significant decline in *Pn* for S0N3 and S1N3 were caused by stomatal factors; (iii) during the entire mature stage, the reasons for the decreased *Pn* in all treatments were mainly stomatal factors, which were due to the reduction in and closure of stomata caused by leaf senescence.

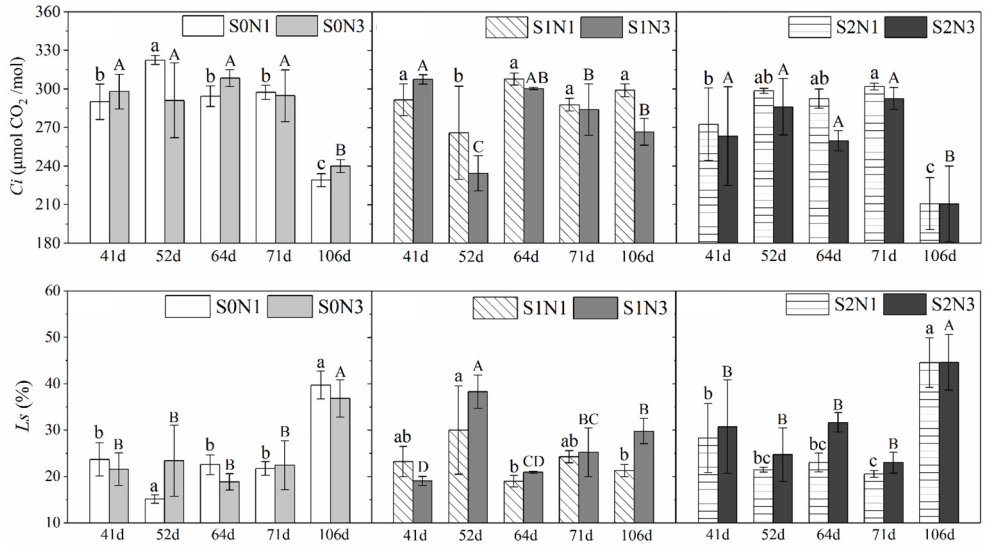

Figure 3. Sunflower intercellular CO_2 concentration (*Ci*) and stomatal limitation index (*Ls*) at different observation times under different treatments in 2016. The horizontal coordinate represents days after sowing, the data were averaged measurements from the three fixed sunflower plants (n = 15), and vertical bars indicate the standard error. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N1 and N3 indicate different N application rates (low and high), and their combinations represent different treatments. Different lowercase letters above the bars represent significant differences at 0.05 levels under the N1 level; different uppercase letters above the bars represent significant differences at 0.05 levels under the N3 level.

3.1.4. Leaf Transpiration Rate

Leaf transpiration rate (*Tr*) refers to the amount of water transpired from per unit leaf area in a certain period of time. As shown in Figure 4, the leaf *Tr* showed an overall upward trend from the seedling to early mature stage at the S0 and S1 levels. Among them, the leaf *Tr* of sunflowers treated at the N1 rate reached their maximum at the early mature stage (71 DAS), while the maximum *Tr* appeared earlier—at anthesis (64 DAS) at the N3 rate. At the S2 level (Figure 4c), a rapid increase of about 250% in *Tr* was found from 41 DAS to 52 DAS, and then followed by a fast decline of more than 50% after entering the flowering stage (64 DAS). At maturity (106 DAS), the leaf *Tr* of each treatment was significantly decreased to a very low level of less than 3.3 mmol $H_2O/(m^2\ s)$ due to leaf senescence.

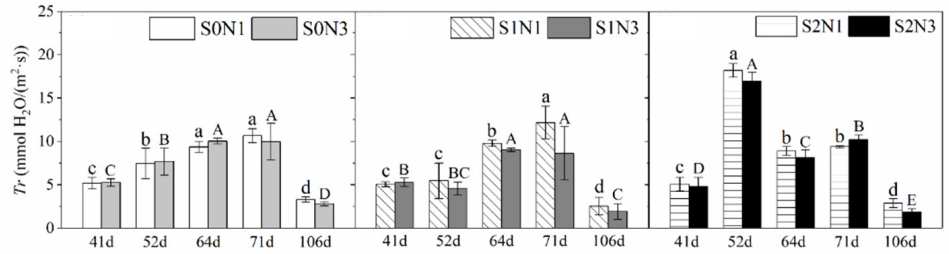

Figure 4. Sunflower leaf transpiration rate (*Tr*) at different observation times under different treatments in 2016. The horizontal coordinate represents days after sowing, the data were averaged measurements from the three fixed sunflower plants (n = 15), and vertical bars indicate the standard error. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and

high); N1 and N3 indicate different N application rates (low and high); and their combinations represent different treatments. Different lowercase letters above the bars represent significant differences at 0.05 levels under the N1 level; different uppercase letters above the bars represent significant differences at 0.05 levels under the N3 level.

3.2. Nitrogen Uptake and Utilization of Sunflowers in Saline Fields

3.2.1. Plant Nitrogen Uptake

The plant nitrogen uptake (*PNU*) of sunflower measured at four different growth stages in 2015 and 2016 were shown in Figure 5. Overall, sunflower *PNU* decreased with an increase in soil salinity under the same N rate. Compared with the sunflowers grown at the S1 level, the *PNU* at the S0 level was only decreased by less than 10% under the same N rate. However, when the IS level increased from S1 to S2, the *PNU* was decreased by 32.3%, 17.2%, 45.7%, and 43.5% under the N0, N1, N2, and N3 rates, respectively. In addition, at the S0 and S1 levels, applying different amounts of N fertilizer had different effects on sunflower *PNU.* In 2015, compared with N0, the application of the N2 rate had no promotion effect on sunflower *PNU* during the crop cycle, whereas a slight increase in sunflower *PNU* could be found under the N3 rate in 2016, compared with those under N1. Nevertheless, at the S2 level, applying the N2 rate of fertilizer in 2015 could decrease the *PNU* of sunflower at each growth stage, compared with N0, whereas the *PNU* of the S2N3 treatment was also lower than that of S2N1 by 18.5% at maturity in 2016. Moreover, the *PNU* of each treatment at maturity in 2015 and 2016 (n = 36) were combined, as shown in Figure 6, and showed a strong linear relationship with their seed yield (R^2 close to 0.7).

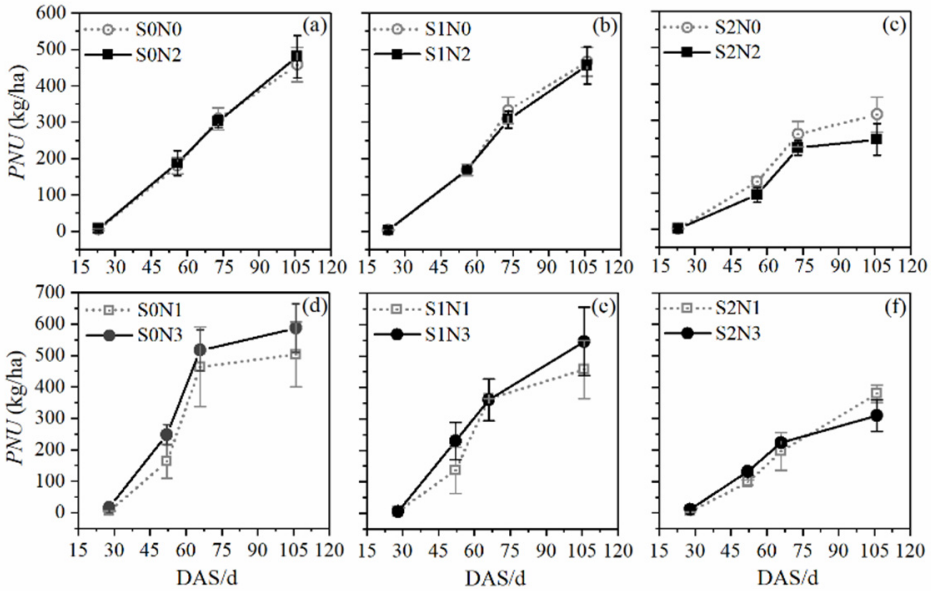

Figure 5. Plant nitrogen uptake (*PNU*) of sunflower at different growth stages: (**a**–**c**) in 2015; (**d**–**f**) in 2016. DAS = days after sowing. The data were averaged measurements from three sampled sunflower plants (n = 3), and the vertical bars indicate the standard error. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N0, N1, N2, and N3 indicate different N application rates (extremely low, low, moderate, and high); and their combinations represent different treatments.

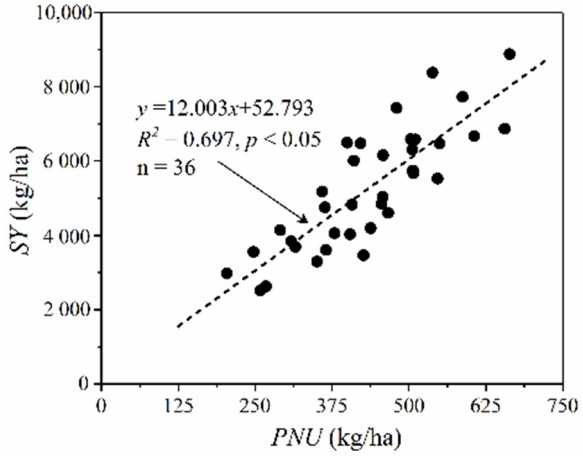

Figure 6. The relationship between the plant nitrogen uptake (*PNU*) at maturity and sunflower seed yield (*SY*) of all the collected data in 2015 and 2016 (n = 36).

3.2.2. Photosynthetic Nitrogen Use Efficiency

In the five photosynthetic observations in 2016, the dry matter and N content of sunflower leaves were simultaneously measured three times. Therefore, the N content per unit leaf area (N_{area}) and photosynthetic nitrogen use efficiency (*PNUE*) of sunflower were calculated using Equation (5) at three different times (52, 64, and 106 DAS). The results showed that the N_{area} of each treatment increased significantly from the bud to flowering stage (52–64 DAS), and their maximum values both appeared in the S1N3 treatment. In particularly, when the N_{area} of S1N3 was increased to 0.484 mg/cm^2 at 64 DAS (Figure 7b), it was significantly higher than all the treatments at the S0 and S2 levels. After entering the mature stage, the N_{area} at the S1 level declined sharply, by more than 60%, while the N_{area} of S0N1 was only decreased by 6.5%, and that of S2N1 even had an increase of 4.6%.

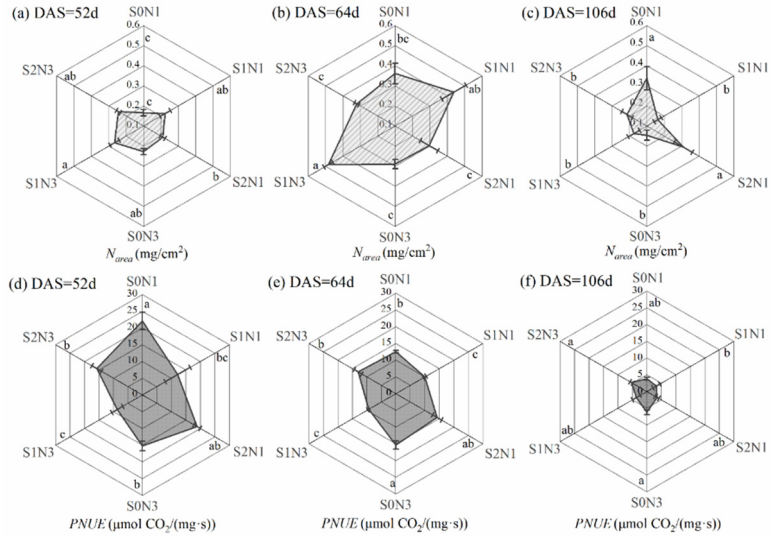

Figure 7. Nitrogen content per unit leaf area (N_{area}) and photosynthetic nitrogen use efficiency (*PNUE*) of sunflower at different growth stages in 2016: (**a**–**c**) the N_{area} at 52, 64, and 106 days after sowing (DAS); (**d**–**f**) the *PNUE* at 52, 64, and 106 DAS. In the legends, S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N1 and N3 indicate different N application rates (low and high); and their combinations represent different treatments. The data were averaged measurements from three sampled sunflower plants (n = 3), the vertical bars indicate the standard error, and different letters located at the end of the radial lines represent significant differences at 0.05 levels between the corresponding treatments measured at the same time.

As can be seen in the radar charts in Figure 7d–f, the *PNUE* values under the N1 rate at 52 DAS were higher than those under the N3 rate. Subsequently, the *PNUE* values generally declined from 52 to 64 DAS, which were 43.4%, 17.8%, and 24.6% at the S0, S1, and S2 levels, respectively. Meanwhile, the *PNUE* of S1N1 and S2N1 were still slightly higher than those of S1N3 and S2N3 at 64 DAS. In addition, at both 52 and 64 DAS, the *PNUE* values for the S0 and S2 levels were significantly higher than those at the S1 level under the same N rate (except for S2N1), while no significant difference in *PNUE* values could be found between different IS levels at 106 DAS.

3.2.3. Nitrogen Use Efficiency

The seed yield (*SY*), N production efficiency (*NPE*), N uptake efficiency (*NUPE*), and N utilization efficiency (*NUTE*) of sunflower under different treatments in 2015 and 2016 are shown in Table 2. Among them, the variation in sunflower *SY* was analyzed in our previous study [26]. The *NPE* and *NUPE* of sunflowers grown at the same IS level decreased significantly with increasing N rates. On the other hand, the *NPE* values under the same N rate also decreased with increasing IS levels. However, the *NUPE* of sunflowers treated with the same N rate varied only within 10.0% when the soil salinity was aggravated from the S0 to S1 level. Additionally, the application of the N2 rate at the S0, S1, and S2 levels in 2015 increased the *NUTE* values by 15.1%, 7.8%, and 23.0% compared with those under N0, respectively. However, the increases in *NUTE* values by applying the N3 rate at different IS levels in 2016 were obviously lower than those by N2 in 2015. Among them, the average *NUTE* of the S0N3 treatment was only increased by 0.1 kg/(kg N) compared with that of S0N1, whereas the S1N3 even had a lower *NUTE* than S1N1 by 0.9 kg/(kg N).

Table 2. Sunflower seed yield (SY), N productive efficiency (*NPE*), N uptake efficiency (*NUPE*), and N utilization efficiency (*NUTE*) in the field experiments of 2015 and 2016.

Years	Treatments	N Rate	*SY*	*NPE*	*NUPE*	*NUTE*
		kg/ha	kg/ha	kg/(kg N)	kg/kg	kg/(kg N)
2015	S0N0 ‡	45	6161.6 ± 172.5 ^{ab} †	136.9 ± 3.3 ^{a}	10.2 ± 1.1 ^{a}	13.5 ± 1.1 ^{b}
	S0N2	135	7436.3 ± 1119.7 ^{a}	55.1 ± 7.0 ^{c}	3.6 ± 0.4 ^{c}	15.5 ± 0.1 ^{a}
	S1N0	45	4608.5 ± 1342.2 ^{b}	102.4 ± 25.4 ^{b}	10.4 ± 0.9 ^{a}	9.9 ± 1.6 ^{c}
	S1N2	135	4853.4 ± 966.4 ^{b}	36.0 ± 6.1 ^{cd}	3.4 ± 0.4 ^{c}	10.7 ± 0.6 ^{c}
	S2N0	45	3693.0 ± 1249.6 ^{b}	82.1 ± 23.6 ^{b}	7.0 ± 1.1 ^{b}	11.7 ± 1.6 ^{c}
	S2N2	135	3558.5 ± 685.5 ^{b}	26.4 ± 4.3 ^{d}	1.8 ± 0.3 ^{d}	14.4 ± 0.2 ^{ab}
2016	S0N1	90	6589.9 ± 87.5 ^{ab}	73.2 ± 1.0 ^{a}	5.6 ± 1.1 ^{a}	13.1 ± 2.6 ^{a}
	S0N3	180	7734.9 ± 1148.5 ^{a}	43.0 ± 6.4 ^{bc}	3.3 ± 0.4 ^{bc}	13.2 ± 0.2 ^{a}
	S1N1	90	5037.8 ± 1433.1 ^{b}	56.0 ± 16.0 ^{b}	5.1 ± 1.0 ^{a}	11.0 ± 1.0 ^{ab}
	S1N3	180	5533.2 ± 1338.1 ^{b}	30.7 ± 7.4 ^{cd}	3.0 ± 0.6 ^{bc}	10.1 ± 0.5 ^{b}
	S2N1	90	4061.3 ± 766.8 ^{b}	45.1 ± 8.5 ^{bc}	4.2 ± 0.3 ^{ab}	10.7 ± 1.2 ^{ab}
	S2N3	180	3849.5 ± 1330 ^{b}	21.4 ± 7.4 ^{d}	1.7 ± 0.3 ^{c}	12.5 ± 2.3 ^{ab}

Notes: † The data are means ± standard errors. Different letters next to standard errors in each column of the same year indicate significant differences at 0.05 levels. ‡ S0, S1, and S2 indicate different levels of initial soil salinity (low, medium, and high); N0, N1, N2, and N3 indicate different N application rates (extremely low, low, moderate, and high); and their combinations represent different treatments.

4. Discussion

Nitrogen is an essential macronutrient for plant growth and basic metabolic processes, such as the synthesis of chlorophyll and various enzymes [32,33]. Meanwhile, a high content of salt ions reduces the activity of PSII and loosens the binding between chlorophyll and the chloroplast protein, which results in more chlorophyll decomposition and a decreased photosynthetic rate [34,35]. In this study, the photosynthetic capacity of sunflower fluctuated during the crop cycle, and different levels of soil salinity resulted in different degrees of variation. At the S1 level, after bud initiation, the indicators reflecting the photosynthetic capacity (*Pn*, *Gs*, *Ci*) were all significantly decreased due to stomatal

limitation, while the decline at the S2 level was much smaller during the same period. This phenomenon was also reported by Zeng et al. [28] in sunflowers grown in saline fields. The reason might be explained from two aspects, which were the enhanced salt tolerance and the insufficiency of the leaf area. Firstly, after entering the bud stage, the sunflowers treated with moderate soil salinity showed improved salt tolerance faster than those with high soil salinity. This was supported by the findings of Ma et al. [17] and Zhang et al. [36], who reported significant increases in fine root growth and the uptake of water and nutrients during this period. Secondly, our previous study on sunflower [26] indicated that moderate salt stress obviously reduced the development of the leaf area in the bud stage, and the inhibition could not be alleviated until entering the flowering stage, which meant that the growth rate of sunflower leaves lagged behind the enhancement of the salt tolerance under moderate saline condition. Thus, the relatively lagging growth of the leaf area at the S1 level resulted in a large accumulation of N in sunflower leaves (highest N_{area} in Figure 7), and the number of stomata was insufficient to maintain the high demand of photosynthesis in the meantime. As a result, the sunflower plants had to temporarily reduce their photosynthetic capacity at the bud stage.

After developing into the mature stage, the photosynthetic capacity of sunflowers at the S0 and S1 levels decreased to varying degrees, but could still be maintained at a high level when treated with the S2 level, indicating that sunflowers still ensured a certain assimilation rate at the early mature stage to compensate for the insufficiency of vegetative growth induced by severe salt stress. This change rule of photosynthetic indicators also provided a reasonable explanation for the compensatory vegetative growth of sunflower that occurred after entering the mature stage under a high saline condition, which was reported in our previous studies [16,21,26,37]. Moreover, the studies of Zeng et al. [28] on sunflower and Pei et al. [38] on maize both showed that the stage when the maximum leaf *Tr* occurred had no correlation with the salt levels, and they always occurred at the flowering stage and tasseling stage, respectively. However, in the present study, the occurrence of the maximum *Tr* was advanced to the middle bud stage at the S2 level, compared with those at the S0 and S1 levels. Meanwhile, the peak value of leaf *Tr* at the S2 level was much higher than for those treated at other IS levels. Our observation of root dynamics in the same experiment [17] could explain this phenomenon, which showed a rapid growth of fine roots under a high saline condition that could significantly improve the water absorption capacity of sunflower plants during the same period.

Previous studies on sunflower [16,39], cotton [11,36], and some other crops [8,10] proved that the detrimental effects induced by moderate salt stress could be alleviated by applying additional N fertilizer properly. However, our present study found that applying a high N rate of 180 kg/ha at the S0 and S1 levels had no beneficial effects on the photosynthetic capacity of sunflower during the vegetative growth stages; instead, it resulted in an earlier and larger decline at the early mature stage, compared with those under lower N rates. The analysis of limiting factors showed that stomatal closure was the main reason for the decline in *Pn* during this period, which suggested that applying additional N fertilizer could accelerate the senescence of sunflower leaves under low and moderate saline conditions. In addition, the uptake and utilization of N by crops is an important factor that affects physiological processes such as photosynthesis and yield formation. It has been proved that the yield had a strong correlation with its *PNU* in many crops under a nonsaline condition [40–43], but there has been little evidence to support the theory in saline fields. Our study demonstrated that there was also a significant correlation between the *SY* and *PNU* for the sunflowers cultivated in salt-affected soils. Meanwhile, it is generally accepted that an increase in N fertilizer can significantly increase the *PNU* within a certain range [44,45]. However, under the interactive effects of salt and N stress, Chen et al. [11] showed that the *PNU* was mainly correlated with the salt level, and was not significantly affected by the N rate. Moreover, Zhang et al. [36] indicated that soil salinity levels, N rates, and their interactions all had significant effects on N accumulation in cotton. The present study on sunflower suggested that the effects of N applications on

the uptake and utilization of N varied under different saline conditions. At the S0 and S1 levels, although the N2 rate could not increase the *PNU* of sunflower, it had better economic and ecological benefits than the N3 rate with the same yield-increasing effect (higher *NUTE* in Table 2). At the S2 level, the application of N2 and N3 rates could also improve the *NUTE* of sunflower, but it was mainly due to the excessive dissolved N in soils aggravating the adverse effects of salt stress on sunflower, limiting the uptake of N by roots (Figure 5), and forcing it to improve the utilization efficiency of absorbed N, which could be regarded an adaptation mechanism of crops themselves to adversity [46,47]. Therefore, considering the variation in sunflower *SY* shown in Table 2, our study suggested that it was not necessary to increase the amount of N fertilizer at the S2 level; instead, directly applying the N fertilizer at the N0 rate could not only alleviate the decline in sunflower *SY* caused by salinity, but also was superior to the N1 rate in terms of N efficiency indices.

The photosynthetic apparatus in plant leaves is the largest sink of N in the plant [48–50]. However, little is known about the effects of salt stress on plant *PNUE*, and, to the best of our knowledge, the only prior studies found that salt stress led to a decreased *PNUE* [51,52]. Meanwhile, such studies were carried out for halophytes under indoor hydroponic conditions, while relevant studies should also be conducted on field crops in salt-affected fields. The present study found that in the bud and flowering stages with vigorous vegetative growth, the S1 level induced a greater decrease in sunflower *PNUE*, indicating that although the N_{area} of sunflower at the S1 level was higher than those at other IS levels (Figure 7), the proportion of N that could be used for photosynthesis might be lower. This reason also indirectly led to partial closure of leaf stomata at the S1 level, resulting in a significant decrease in *Pn*, as mentioned above for the same period. On the other hand, this study also showed that when the N supply was limited at the bud stage, the N_{area} was relatively low, but it could force the sunflowers to improve their *PNUE* under a lower N rate. Similar findings were reported by Dinh et al. [53] under a drought stress condition; they suggested that sugarcane treated with drought stress also had a higher PNUE at 90 kg/ha of the N rate, compared with those at 180 and 270 kg/ha. After entering the flowering stage, with the increase in N accumulation in leaves, this promotion effect on the *PNUE* was weakened, but the *PNUE* value for the S2N1 treatment was still second only to that of S0N3, which also indicated that not increasing the N fertilizer at the S2 level was more conducive to the role of N in photosynthesis. Nevertheless, the present study only proved that the effects of salt, N, and their interactive stress on the *PNUE* of sunflower varied at different growth stages. The specific reasons for this difference remain to be further studied.

5. Conclusions

Our study illustrated that at low and medium soil salinity levels (S0 and S1), the net photosynthetic rate (*Pn*) of sunflowers reached their peaks at anthesis, but they decreased significantly in the bud stage in advance, and the decrease was found to be largest at the S1 level. Additionally, applying a high N rate of 180 kg/ha (N3) accelerated the senescence of sunflower leaves at the S0 and S1 levels, resulting in their photosynthetic indicators having an earlier and larger decline after anthesis due to stomatal factors. Thus, although a moderate N rate of 135 kg/ha (N2) could not increase the plant nitrogen uptake (*PNU*) of sunflowers, their N efficiency indexes (*NPE*, *NUPE*, *NUTE*) were higher than those under the N3 rate, which meant better economic and ecological benefits. Moreover, at a severe soil salinity level (S2), although sunflower *PNU* was obviously inhibited, their photosynthetic nitrogen use efficiency (*PNUE*) was not affected, and the *Pn* values were relatively stable from the seedling to flowering stages. After entering the mature stage, their *Pn* values were maintained at a high level of more than 40 μmol CO_2/(m^2 s); thus, the sunflower plants could still have some compensatory growth before maturity. Meanwhile, applying an extremely low N rate of 45 kg/ha (N0) could not only alleviate the decline in sunflower seed yield (*SY*) under severe saline condition (S2), but those plants also comprehensively outperformed those under the N1 rate (90 kg/ha) in terms of N efficiency indices. Therefore, our study led us to recommend the application of 135 kg/ha of N fertilizer in the saline

fields at the S0 and S1 levels, and we proposed that 45 kg/ha of N fertilizer was sufficient for the fields affected by the S2 level of salt stress. In a future study, we will conduct additional experiments to reveal the physiological mechanism of the significant decrease in the sunflower *Pn* in bud stage, especially at the S1 level, as well as the variable *PNUE* of sunflower at different growth stages in saline fields.

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