Response of Photosynthetic Characteristics of Desert Plant Bassia dasyphylla to Mixed Saline-Alkaline Stress: Postprint

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Abstract

By mixing two neutral salts (NaCl, Na2SO4) and two alkaline salts (Na2CO3, NaHCO3) at different ratios to simulate varying degrees of salt and alkali stress conditions, we investigated the responses of photosynthetic pigment contents, gas exchange parameters, and chlorophyll fluorescence parameters of the desert plant Bassia dasyphylla to mixed saline-alkali stress. The results showed that under the 30 simulated saline-alkali stress conditions uniformly covering a total salinity range of 50-250 mmol/L and pH range of 7.10-10.19, the chlorophyll a content (Chla), chlorophyll b content (Chlb), carotenoid content (Caro), net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO2 mole fraction (Ci), transpiration rate (Tr), potential activity of PSII (Fv/F0), maximum quantum efficiency of PSII primary reactions (Fv/Fm), quantum efficiency of PSII electron transport (ΦPSII), apparent photosynthetic electron transport rate (ETR), photochemical quenching coefficient (qP), and other indicators of Bassia dasyphylla were all highest in the control group (CK), and all decreased with increasing salt concentration and pH of the treatment solutions, with significant differences between each treatment group and the control group ($P<0.05$); steady-state fluorescence (Fs) initially decreased with increasing salt concentration and pH of the treatment solutions, then exhibited an "M" -shaped variation trend, i.e., increasing then decreasing, then increasing again and decreasing again; water use efficiency (WUE) and non-photochemical quenching coefficient (NPQ) did not show regular variation trends with changes in salt concentration and pH of the treatment solutions. Correlation coefficients between salt composition ions and the above-mentioned photosynthetic characteristic indicators revealed that the inhibitory effects of salt composition on photosynthetic pigments and gas exchange parameters of Bassia dasyphylla followed the order: Na2CO3 > NaHCO3 > NaCl > Na2SO4, while the effects on chlorophyll fluorescence parameters were more complex. The study indicates that saline-alkali

habitats caused certain damage to the photosynthetic system of Bassia dasyphylla, but the plant could reduce the degree of damage through corresponding physiological responses.

Full Text

Response of Photosynthetic Characteristics of *Bassia dasyphylla* to Mixed Salt-Alkaline Stress in Desert Regions

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Abstract

Two neutral salts (NaCl and Na SO) and two alkaline salts (Na CO and NaHCO) were selected and mixed in various ratios to simulate different degrees of salt-alkaline stress, covering a total salinity range of 50–250 mmol/L and pH values of 7.10–10.19. The responses of photosynthetic pigment content, gas exchange parameters, and chlorophyll fluorescence parameters of the desert plant *Bassia dasyphylla* to these mixed salt-alkaline stresses were investigated. The results showed that chlorophyll a (Chla), chlorophyll b (Chlb), carotenoid (Caro) content, net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO concentration (Ci), transpiration rate (Tr), PSII potential efficiency (Fv/Fm), PSII actual quantum yield (ΦPSII), apparent electron transfer rate (ETR), and photochemical quenching coefficient (qP) in all treatment groups were significantly lower than those in the control group (CK), and decreased with increasing solution salinity and pH. Steady-state fluorescence (Fs) exhibited an "M-type" variation trend with increasing salinity and pH, first increasing then decreasing, followed by a similar trend again. Water use efficiency (WUE) and non-photochemical quenching coefficient (NPQ) showed no regular pattern with increasing solution salinity and pH. Correlation coefficients between salt ions and photosynthetic characteristic indices indicated that the inhibitory effect of salt composition on photosynthetic pigments and gas exchange parameters followed the order: Na CO > NaHCO > NaCl > Na SO , while the effect on chlorophyll fluorescence parameters was more complex. Salt-alkaline habitats caused certain damage to the photosynthetic system of *B. dasyphylla*, but the plant could reduce the degree of damage through corresponding physiological responses.

Keywords: *Bassia dasyphylla*; salt-alkaline stress; photosynthetic pigment content; photosynthetic gas exchange parameters; chlorophyll fluorescence parameters

Introduction

Photosynthesis is the foundation of assimilation in all plants, algae, and certain bacteria, and represents the most important link in material cycling in the biosphere. It plays a key role in energy distribution and transformation. Photosynthesis is highly sensitive to environmental stress, with saline-alkaline stress being a crucial external factor affecting photosynthetic processes. Soil salinization is one of the major global ecological environmental problems. Approximately 1.5×10 hm^2 of saline wasteland and 6.67×10 hm^2 of saline-alkaline soil exist worldwide, with 20% of arable land experiencing salinization and 33% experiencing alkalization. Salt content typically ranges from 0.07% to 1.3%, with pH ranging from 6.9 to 10.8, and both the degree and area of salinization show an increasing trend annually. Due to the complex composition and proportions of salts in saline-alkaline soils, mixed salt-alkaline stress is the primary problem faced by plants surviving in these habitats. Differences in salt content and composition across different plots or regions affect normal plant growth and population distribution.

In recent years, many scholars have investigated the effects of saline-alkaline stress on growth, physiological changes, and photosynthesis in plants such as alfalfa, sunflower, poplar, cotton, spiraea, oat, grape, and grasses. These studies have demonstrated strong damaging effects of saline-alkaline stress. However, most research has focused on artificially cultivated plant varieties, with few reports on native saline-alkaline plants. Annual plants are important components of global desert flora, with high species richness and important ecological functions in various desert ecosystems. As pioneer or constructive species, annual plants are widely distributed in sandy, rocky, and saline-alkaline areas of desert regions. Through long-term evolution and natural selection, they have adapted well to biotic and abiotic factors in desert environments, developing a complete set of survival strategies to cope with the randomness and uncertainty of desert habitats. Based on their unique biological characteristics, annual plants serve as excellent experimental materials for many key ecological questions.

Bassia dasyphylla is an annual herb of the Chenopodiaceae family and *Bassia* genus, a pioneer plant in semi-fixed or fixed dunes, and frequently scattered or clustered in sandy, rocky, or gravelly saline-alkaline soils in grassland, semi-desert, and desert regions of northern China. Previous research on *B. dasyphylla* has been limited to community structure, spatial distribution patterns, and bioindicator functions. However, studies on its environmental adaptability as a saline-alkaline pioneer plant have not been conducted. This study used sand-cultured *B. dasyphylla* seedlings as experimental material, mixing two alkaline salts (Na CO , NaHCO) and two neutral salts (NaCl, Na SO) in different ratios to create 30 different saline-alkaline conditions with varying salinity and alkalinity levels. The objective was to explore the response mechanisms of its photosynthetic characteristics to mixed salt-alkaline stress, elucidate its adaptation mechanisms from a photosynthetic physiology perspective, and accumulate scientific data for saline-alkaline land management and restoration of sand-fixing vegetation.

1. Materials and Cultivation

B. dasyphylla seeds were collected in October 2015 from saline-alkaline land near the Linze Inland River Basin Research Station of the Chinese Ecosystem Research Network. The seeds were sown in plastic pots (30 cm diameter and depth) filled with washed fine river sand and vermiculite at a 3:1 volume ratio. Pots were placed outdoors under natural conditions. After germination, seedlings were irrigated weekly with Hoagland nutrient solution. Daily water loss per pot was determined by weighing, and distilled water was added to compensate. Before stress treatment, seedlings were thinned to ensure uniform growth.

2. Simulation of Mixed Salt-Alkaline Stress

Based on salt composition and distribution ranges in saline-alkaline soils of the Hexi Corridor, two neutral salts (NaCl and Na SO) and two alkaline salts (Na CO and NaHCO) were mixed in different proportions. Six treatment groups (A, B, C, D, E, F) were designed with progressively increasing proportions of alkaline salts. Each group contained five concentration gradients (50, 100, 150, 200, 250 mmol/L), with double-distilled water at 0 mmol/L as the control (CK). This design simulated stress conditions similar to natural saline-alkaline soils in terms of salt composition and variation patterns .

3. Salt-Alkaline Stress Treatment

Uniform *B. dasyphylla* seedlings were selected and treated with the corresponding mixed salt-alkaline solutions. The 30 treatments were labeled A1–A5, B1–B5, C1–C5, D1–D5, E1–E5, and F1–F5. Each pot received 500 mL of treatment solution per irrigation between 17:00–20:00. To prevent salt loss, equal amounts of double-distilled water were applied daily, with trays placed under each pot to collect leachate, which was returned to the pots. Starting the day after treatment, daily water loss was measured by weighing, and distilled water was added to maintain the stress conditions. Photosynthetic pigment content, gas exchange parameters, and chlorophyll fluorescence parameters were measured after treatment.

4. Parameter Measurements

4.1 Photosynthetic Pigment Content Chlorophyll (Chl) and carotenoid (Caro) contents in leaves were determined according to Li Hesheng' s method.

4.2 Photosynthetic Gas Exchange Parameters On a clear day after treatment, gas exchange parameters were measured between 9:00–11:00 using a LI-6400 portable photosynthesis system (LI-Cor, Inc.) at a light intensity of 1000 mol · m ^{2} · s ^{1}. Parameters measured included net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO concentration (Ci), and transpiration rate (Tr). Water use efficiency (WUE) was calculated as the ratio of Pn to Tr (WUE = Pn/Tr). Environmental conditions during measurement were: air temperature (22.45 ± 2.31)°C, relative humidity (57.13 ± 2.45)%, and CO concentration (379.51 ± 13.25) mol/mol. Three replicates were measured per treatment.

4.3 Chlorophyll Fluorescence Parameters On a clear day after treatment, chlorophyll fluorescence parameters were measured between 9:00-11:30 using an FMS-2 modulated fluorometer (Hansatech). Parameters measured included initial fluorescence (Fo), maximal fluorescence (Fm), steady-state fluorescence (Fs), minimal fluorescence (Fo'), and maximal fluorescence (Fm'). The following parameters were calculated using Roháček' s formulas: PSII potential efficiency (Fv/Fm), maximal quantum efficiency of primary photochemistry (Fv/Fm), PSII actual quantum yield (ΦPSII), apparent electron transfer rate (ETR), photochemical quenching coefficient (qP), and non-photochemical quenching coefficient (NPQ). Three replicates were measured for both control and treatments.

5. Data Analysis

Data were analyzed using Microsoft Excel 2010 and SPSS 19.0 software. Differences among treatments were compared using Duncan' s multiple range test. Correlation coefficients were calculated, and multiple regression analysis was performed.

Results and Analysis

1. Salinity and pH of Treatment Solutions

Due to the alkaline salts Na CO and NaHCO in each treatment group, pH increased with increasing salt concentration within groups. The 30 treatments covered salinity from 50–250 mmol/L and pH from 7.10–10.19. At the lowest salt concentration (50 mmol/L), Na concentration was 66.7 mmol/L, increasing to 333.5 mmol/L at the highest concentration (250 mmol/L). SO ² concentration ranged from 16.7–83.5 mmol/L, CO ² from 1.7–83.5 mmol/L, and HCO from 16.6–166.5 mmol/L. This successfully simulated stress conditions similar to natural saline-alkaline soils [Figure 1: see original paper].

2. Response of Photosynthetic Pigment Content to Salt-Alkaline Stress

All salt-alkaline treatments reduced chlorophyll and carotenoid contents compared to the control (double-distilled water, 0 mmol/L, pH 7.00). Maximum pigment contents were observed in the control: Chla (240.25 ± 5.75) mg/g, Chlb (155.91 ± 5.22) mg/g, Caro (42.90 ± 5.10) mg/g, and total chlorophyll (396.16 ±

10.97) mg/g. Within each treatment group, pigment contents decreased with increasing solution salinity, with greater reductions at higher salt concentrations. At the same salt concentration, Chla, Chlb, and total chlorophyll first increased then decreased with increasing alkaline salt proportion, while carotenoid content continuously decreased. The Chla/Chlb ratio was higher than control in low-salt, low-pH treatments but lower in high-salt treatments, particularly in groups D, E, and F, which showed a decreasing-then-increasing-then-decreasing pattern. The smallest changes occurred in groups B, D, and F.

3. Response of Photosynthetic Gas Exchange Parameters to Salt-Alkaline Stress

All stress treatments reduced gas exchange parameters compared to the control [Figure 2: see original paper]. Maximum values occurred in the control (0 mmol/L, pH 7.00): Pn (16.79 ± 0.93) mol · m ^{2} · s ^{1}, Tr (13.54 ± 0.42) mmol · m ^{2} · s ^{1}, Gs (394.22 ± 11.84) mmol · m ^{2} · s ^{1}, and Ci (184.06 ± 6.77) mol · mol ^{1}. Within treatment groups, Pn, Tr, Gs, and Ci decreased with increasing salinity, with more pronounced declines at higher concentrations. At the same salt concentration, these parameters also decreased with increasing alkaline salt proportion. Water use efficiency (WUE) showed no regular pattern with increasing salinity and pH, though it tended to increase at the lowest salt concentration (50 mmol/L). Groups A, B, and D exhibited a decreasing-then-increasing-then-decreasing trend, while groups C, E, and F showed an increasing-then-decreasing pattern.

4. Response of Chlorophyll Fluorescence Parameters to Salt-Alkaline Stress

All stress treatments affected chlorophyll fluorescence parameters [Figure 3: see original paper]. Steady-state fluorescence (Fs) showed an "M-type" pattern across the 0–250 mmol/L salinity range, first decreasing then increasing, then decreasing again. All treatment groups showed Fs minima at 50 mmol/L salinity. PSII potential efficiency (Fv/Fm) and maximal quantum efficiency of primary photochemistry (Fv/Fm) showed identical trends, decreasing with increasing salinity. Maximum values occurred in the control (0 mmol/L, pH 7.00): Fv/Fm (0.84 ± 0.01) and Fv/Fm (5.22 ± 0.12). PSII actual quantum yield (ΦPSII), apparent electron transfer rate (ETR), and photochemical quenching coefficient (qP) showed consistent patterns, decreasing with increasing salinity. At the same salt concentration, these parameters showed no clear pattern across different alkaline salt proportions. Non-photochemical quenching coefficient (NPQ) increased with increasing salinity and pH, first decreasing then increasing then decreasing again at the same salt concentration, with maximum values at 0 mmol/L, pH 7.00 (1.84 ± 0.09).

5. Correlations Between Salt Ion Composition and Photosynthetic Indices

Correlation analysis revealed relationships between salt ions and photosynthetic indices . Na , CO ^{2} , and HCO showed extremely significant negative correlations with photosynthetic pigment content (except HCO with carotenoids). Cl and SO ^{2} showed non-significant negative correlations with pigment indices. For gas exchange parameters, Na , CO ^{2} , and HCO showed extremely significant negative correlations (except HCO with Ci and SO ^{2} with WUE). Cl showed non-significant correlations with gas exchange parameters. For chlorophyll fluorescence parameters, Na , CO ^{2} , and HCO showed extremely significant negative correlations with most indices, while SO ^{2} showed extremely significant positive correlations with Fs. The inhibitory effects of salt composition on pigments and gas exchange parameters ranked as: Na CO > NaHCO > NaCl > Na SO , while effects on fluorescence parameters were more complex.

Discussion

Photosynthetic pigments are the material basis for photosynthesis. Chlorophyll, as the primary carrier for light energy absorption, transfer, and conversion, plays a crucial role in photosynthesis. This study demonstrated that chlorophyll and carotenoid contents in *B. dasyphylla* decreased under salt-alkaline stress, with greater reductions at higher stress intensities. At the same salt concentration, chlorophyll content first increased then decreased with increasing alkaline salt proportion, while carotenoid content continuously decreased. This aligns with results from Parida et al. on *Bruguiera parviflora* treated with 100–500 mmol/L NaCl solution. The decline in pigment content may be due to high pH reducing metal ion solubility, preventing adequate absorption of essential elements. Alkaline salts can also enhance chlorophyll degradation enzyme activity, accelerating pigment decomposition in chloroplasts.

The Chla/Chlb ratio reflects light energy utilization capability and thylakoid membrane stacking. In *B. dasyphylla*, Chla/Chlb ratios were higher than control under low salinity and pH but lower under high stress, indicating some resistance to salt-alkaline conditions. Carotenoids function as both accessory pigments and endogenous antioxidants, protecting against membrane peroxidation by scavenging reactive oxygen species and dissipating excess light energy through the xanthophyll cycle. The reduction in pigment content contributed to decreased photosynthesis under mixed salt-alkaline stress.

Typically, net photosynthetic rate (Pn) decreases with increasing environmental stress. Under mixed salt-alkaline stress, Pn reduction in plants relates to both photosynthetic capacity damage/stomatal conductance (Gs) reduction and mineral element imbalance. When both Pn and Gs decrease simultaneously, the reduction is caused by stomatal limitation. This study showed that Pn, Gs, and other gas exchange parameters in *B. dasyphylla* decreased with increasing solution salinity and pH, consistent with results from Jerusalem artichoke studies.

The decline in Pn resulted from both stomatal and non-stomatal limitations, as well as their synergistic effects under high stress intensity.

Photosynthetic electron excitation energy capture and conversion are performed by PSII and PSI. When excitation energy capture and conversion become imbalanced between the two photosystems, electron transfer or excitation state imbalance occurs, affecting photosynthetic efficiency. Fv/Fm is an important indicator of photoinhibition. Under non-stressed conditions, plants show high Fv/Fm values for efficient energy assimilation. When stressed by nutrient deficiency or salinity, PSII complexes are damaged, inhibiting electron transfer rates and photochemical quantum efficiency. This study showed that Fv/Fm, ΦPSII, and other fluorescence parameters in *B. dasyphylla* decreased with increasing stress, indicating damage to chloroplast reaction centers and reduced photosynthetic activity.

Non-photochemical quenching coefficient (NPQ) reflects excess excitation energy dissipation. In *B. dasyphylla*, NPQ showed a decreasing-then-increasing-then-decreasing trend with increasing salinity and pH, while increasing at the same salt concentration. This suggests *B. dasyphylla* can maintain high NPQ to enhance thermal dissipation and adapt to salt-alkaline stress. Alkaline salt stress caused greater damage than neutral salt stress, consistent with results from *Nitraria sibirica*.

Correlation analysis revealed that the inhibitory effects of different salt compositions on photosynthetic pigments and gas exchange parameters ranked as: Na CO > NaHCO > NaCl > Na SO . However, effects on chlorophyll fluorescence parameters were more complex, with different ranking orders for different indices. This complexity requires further investigation. The mechanisms underlying these differential effects of salt composition on various photosynthetic indices need to be elucidated in future studies.

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