# Effects of Salt and Phosphorus on Photosynthesis and Nutrient Characteristics of Acacia confusa Seedlings (Postprint)

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## Abstract

To investigate the effects of combined salt and phosphorus application on leaf photosynthesis and nutrient characteristics of *Acacia confusa* seedlings, an important coastal protection forest tree species, this study established five NaCl solution concentrations of 0% (B0), 0.2% (B1), 0.4% (B2), 0.6% (B3), and 0.8% (B4), and three phosphorus supply levels using calcium superphosphate: no application (P0), 0.5 $g \cdot kg^{-1}$ (P1), and 1.5 $g \cdot kg^{-1}$ (P2). Six combined salt-phosphorus treatments were established based on these parameters, and photosynthetic and nutrient characteristic indices of seedlings were measured. The results demonstrated: (1) Salt stress significantly inhibited the growth and development of *Acacia confusa* seedlings, with the degree of inhibition increasing with salinity level. Phosphorus application under low-salt conditions was detrimental to seedling growth, whereas phosphorus application under medium- and high-salt conditions significantly mitigated the inhibitory effects of salt on seedling growth. (2) Photosynthesis in *Acacia confusa* seedlings was significantly impacted by salt stress. Under low and medium salt conditions, phosphorus application increased stomatal closure, thereby exacerbating the effects of salt stress on seedling photosynthesis; however, appropriate phosphorus application under high-salt conditions significantly enhanced the photosynthetic capacity of *Acacia confusa* seedlings. (3) Salt stress significantly reduced chlorophyll content and caused damage to Photosystem II. Phosphorus application under low-salt stress was unfavorable for chlorophyll synthesis in *Acacia confusa* seedlings, whereas appropriate phosphorus application under high-salt stress could increase chlorophyll synthesis, stabilize cell membrane structure, and enhance leaf potential photosynthetic capacity. (4) Salt stress substantially interfered with leaf content of metal elements including Fe, Mn, Na, and Cu. Phosphorus application on the basis of salt stress effectively promoted seedling absorption of certain elements. Overall, phosphorus application under salt-stress conditions could improve the photosynthetic capacity and nutrient absorption ability of *Acacia confusa* seedlings. These findings provide a theoretical basis for enhancing salt tolerance and phosphorus use efficiency in *Acacia confusa*, and offer guidance for the sustainable management of coastal protection forests.

## Full Text

## Effects of Salt and Phosphorus Fertilization on Photosynthesis and Nutrient Characteristics of Acacia confusa Seedlings

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### Abstract

Acacia confusa is an important species in coastal shelter forests. This study investigated the effects of salt and phosphorus fertilization on leaf photosynthesis and nutrient characteristics of A. confusa seedlings. NaCl solutions were prepared at concentrations of 0% (B0), 0.2% (B1), 0.4% (B2), 0.6% (B3), and 0.8% (B4), and superphosphate solutions at 0 $g \cdot kg^{-1}$ (P0), 0.5 $g \cdot kg^{-1}$ (P1), and 1.5 $g \cdot kg^{-1}$ (P2). Photosynthetic and nutrient characteristics were measured after seedlings were treated with six combined salt-phosphorus solutions. The results showed: (1) Salt stress significantly inhibited seedling growth and development, with greater impacts at higher salinity levels. Phosphorus application under low-salt stress was unfavorable for growth, whereas phosphorus application under medium-to-high salt stress significantly alleviated growth inhibition. (2) Photosynthesis in A. confusa seedlings was significantly affected by salt stress. Phosphorus application under low-to-medium salt stress increased stomatal closure, exacerbating the negative effects on photosynthesis, whereas appropriate phosphorus application under high-salt stress significantly improved photosynthetic capacity. (3) Salt stress significantly reduced chlorophyll content and damaged Photosystem II. Phosphorus fertilization under low-salt stress adversely affected chlorophyll synthesis, whereas appropriate phosphorus application under high-salt stress increased chlorophyll synthesis, stabilized cell membrane structure, and improved leaf potential photosynthetic capacity. (4) Salt stress strongly interfered with leaf contents of Fe, Mn, Na, Cu, and other metal elements. Phosphorus application under salt stress effectively promoted seedling absorption of some elements. Overall, phosphorus application under salt stress conditions enhanced photosynthetic capacity and nutrient uptake in A. confusa seedlings. These findings provide a theoretical basis for improving salt tolerance and phosphorus utilization efficiency in A. confusa and offer guidance for sustainable management of coastal shelterbelts.

**Keywords:** salt stress, phosphorus fertilization, photosynthesis, nutrient content, Acacia confusa seedlings

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## Introduction

Soil salinization and phosphorus deficiency in coastal areas threaten the survival of coastal shelter forests and national ecological security. Soil salinization is a critical environmental factor limiting plant productivity, with affected areas increasing globally each year. In China alone, saline soils exceed 34 million hectares, with coastal saline soils typically containing more than 4 $g \cdot kg^{-1}$ salt in the 1 m soil layer, seriously endangering sustainable management of agriculture and forestry, including coastal shelter forests. Salt stress causes osmotic stress and disrupts nutritional ion balance in trees, affecting normal growth by inhibiting and inducing various enzyme systems, while also reducing photosynthetic efficiency by affecting PSII potential activity and primary light energy conversion efficiency. Phosphorus deficiency exacerbates salt damage by causing malnutrition. Coastal soils in southern China are generally phosphorus-deficient, with most containing 0.043%-0.066% phosphorus, which limits the formation of assimilatory power, Calvin cycle enzyme activity, RuBP regeneration, and assimilate transport, thereby affecting photosynthesis and reducing whole-plant accumulation of phosphorus, potassium, calcium, nitrogen, and magnesium, making regeneration of coastal shelter forests difficult. Ignoring the combined effects of high salt and low phosphorus on coastal shelter forest species underestimates the challenges posed by harsh coastal soil conditions and hinders sustainable management.

Acacia confusa is widely distributed in China' s coastal regions and serves as an important, low-maintenance coastal shelter forest species that significantly contributes to soil and water conservation in southern China. Recent studies have shown that A. confusa possesses certain drought resistance, low-temperature tolerance, and strong light stress tolerance, and that combined high-salt and low-phosphorus stress adversely affects seed germination and seedling growth, though the underlying mechanisms remain unclear. Most research on forest tree resistance has focused on single salt or phosphorus stress effects, yet while large-scale desalination is difficult, phosphorus fertilization is relatively simple and feasible. Phosphorus application typically promotes plant growth and photosynthesis under phosphorus-deficient conditions, but whether phosphorus supplementation can mitigate or eliminate salt stress damage remains uncertain. Therefore, this study measured biomass, photosynthetic parameters, chlorophyll content, leaf relative electrical conductivity, chlorophyll fluorescence, and nutrient contents in A. confusa seedlings under different NaCl concentrations and phosphorus fertilization levels to clarify how phosphorus application alters leaf photosynthesis and nutrient characteristics under salt stress, providing theoretical and practical guidance for improving salt tolerance, phosphorus utilization efficiency, and sustainable coastal shelterbelt management.

# 1. Materials and Methods

## 1.1 Study Site Description

The experiment was conducted at the Field Science and Technology Park of Fujian Agriculture and Forestry University in Fuzhou, Fujian Province (119°13 E, 26°05 N). The region has a subtropical monsoon climate with flat terrain, a frost-free period of 326 days, annual sunshine of 1,700–1,980 hours, annual precipitation of 900–2,100 mm, and average relative humidity of approximately 77%. During the experimental period, the minimum temperature was 17 °C, maximum was 38 °C, and average was 24 °C.

## 1.2 Experimental Design

One-year-old A. confusa seedlings with good growth and strong adaptability were obtained from Guangzhou Ruijing Garden Seedling Wholesale Center. Plastic pots (18 cm diameter, 19 cm height) were filled with 4.5 kg of sandy soil substrate (sand:soil = 3:1) with pH 6.30 ± 0.04, salt content 0.03% ± 0.002%, and available nitrogen, phosphorus, and potassium at 0.4 ± 0.05, 0.7 ± 0.05, and 1.8 ± 0.7 $g \cdot kg^{-1}$, respectively.

Seedlings were planted on March 28, 2021 (one per pot) and acclimated until April 29. After measuring initial height and ground diameter, stress treatments were initiated. To simulate coastal saline conditions, NaCl solutions were applied at 0% (B0), 0.2% (B1), 0.4% (B2), 0.6% (B3), and 0.8% (B4) concentrations, added incrementally in four applications at one-week intervals to prevent mortality. Phosphorus fertilizer (superphosphate with $ $16% available phosphorus and $ 11^{-1}$ (P0), 0.5 $g \cdot kg^{-1}$ (P1), and 1.5 $g \cdot kg^{-1}$ (P2). Six salt-phosphorus coupling treatments were established: P1+B2, P1+B3, P1+B4, P2+B2, P2+B3, and P2+B4, with nine pots per treatment (117 pots total). The experiment concluded on August 1, 2021.

## 1.3 Measurement Methods

**1.3.1 Morphological Measurements** Six seedlings per treatment were selected to measure plant height and ground diameter, then separated into root, stem, and leaf components. Fresh leaf weight was measured before oven-drying at 105 °C for 30 minutes, then at 80 °C to constant weight for dry weight determination. Morphological indices were calculated as:

- Relative height increment = measured height - initial height

- Relative ground diameter increment = measured ground diameter - initial diameter
- Relative water content = (fresh weight - dry weight) / fresh weight

**1.3.2 Physiological Measurements** Experiments were conducted outdoors under natural light and $CO_2$ conditions. Healthy leaves were selected on sunny days (July 7–8) between 9:00–11:00 h to measure net photosynthetic rate, stomatal conductance, intercellular $CO_2$ concentration, and transpiration rate using a LI-6400 portable photosynthesis system (LI-COR, USA). After 20 minutes of dark adaptation, initial fluorescence ($F_0$), maximum fluorescence (Fm), and PSII maximum photochemical efficiency (Fv/Fm) were measured using a portable fluorometer (OS-30P, Li-Cor, USA). Chlorophyll content was determined by extracting leaf samples in acetone-ethanol mixture (5 mL each) in darkness until bleached, then measuring absorbance at 663 nm and 645 nm using a microplate reader. Leaf relative electrical conductivity was measured using a conductivity meter method. For nutrient analysis, dried leaves were ground and passed through a 0.149 mm sieve, digested with nitric acid-hydrogen peroxide in a temperature-controlled digestion furnace, and analyzed using inductively coupled plasma optical emission spectrometry (ICP-OES, PerkinElmer, USA).

### 1.4 Data Analysis

All data are presented as means. Statistical analysis was performed using Excel 2016, figures were prepared using OriginPro, and LSD significant difference tests were conducted using SPSS 25.0 based on one-way ANOVA to determine differences among treatments.

## 2. Results

### 2.1 Effects of Salt and Phosphorus on Seedling Growth and Leaf Biomass

Growth and leaf biomass of A. confusa seedlings decreased significantly with increasing salt stress severity . Under low salt concentration, relative height increment, relative ground diameter increment, leaf fresh weight, leaf dry weight, and leaf relative water content decreased by 40.74%, 4.62%, 24.16%, 21.98%, and 1.47% compared to the control, respectively. Under high salt concentration, these indices decreased by 70.00%, 30.56%, 52.57%, and 58.27%, respectively, with the largest reduction 幅度, while leaf relative water content increased by 4.08% relative to the control. These results indicate that salt stress significantly inhibited A. confusa seedling growth, with greater impacts at higher salinity levels.

Phosphorus application affected seedling biomass differently across salt concentrations [Figure 1: see original paper]. At 0.4% NaCl, P0 treatment showed significantly higher relative height increment, leaf fresh weight, and leaf dry weight than P1 and P2 treatments, with no significant differences in ground diameter or relative water content. At 0.6% NaCl, relative height increment decreased significantly under P1 treatment, and relative water content decreased significantly under P2 treatment, while other parameters showed no significant differences among phosphorus treatments. At 0.8% NaCl, P1 treatment produced greater increases in relative height increment, leaf fresh weight, and leaf dry weight compared to P2 treatment, with smaller increases in leaf relative water content and no significant difference in ground diameter increment. These results suggest that phosphorus application under low salt stress inhibited A. confusa seedling growth, whereas low phosphorus application under high salt stress was more beneficial than high phosphorus application.

### 2.2 Effects of Salt and Phosphorus on Leaf Photosynthetic Parameters

Photosynthetic parameters of A. confusa seedlings were significantly affected by salt stress, with greater impacts at higher salinity . Under low salt concentration, net photosynthetic rate and transpiration rate decreased by 1.08% and 4.15% compared to the control, while stomatal conductance and intercellular $CO_2$ concentration increased by 16.67% and 5.60%, respectively. Under high salt concentration, net photosynthetic rate, stomatal conductance, intercellular $CO_2$ concentration, and transpiration rate decreased by 69.40%, 83.33%, 28.72%, and 77.86%, respectively, indicating severe photosynthetic inhibition.

Phosphorus application inhibited photosynthetic parameters under low-to-medium salt stress but enhanced them under high salt stress, with low phosphorus showing greater promotional effects than high phosphorus [Figure 2: see original paper]. At 0.4% and 0.6% NaCl, P0 treatment generally showed higher photosynthetic parameter values than P1 and P2 treatments, with P2 treatment showing the greatest decreases. At 0.8% NaCl, photosynthetic parameter values increased under both P1 and P2 treatments, demonstrating that phosphorus supplementation under high salt stress substantially improved photosynthetic capacity.

### 2.3 Effects of Salt and Phosphorus on Chlorophyll Content and Fluorescence

Chlorophyll content decreased significantly with increasing NaCl concentration, while leaf relative electrical conductivity increased and Fv/Fm showed an initial increase followed by a decrease . At 0.2% NaCl, chlorophyll a, chlorophyll b, and total chlorophyll contents decreased by 23.95%, 18.33%, and 22.03%, respectively, while leaf relative electrical conductivity and Fv/Fm increased by 28.34% and 2.78%, respectively. Fv/Fm reached its maximum at 0.4% NaCl. At 0.6% NaCl, chlorophyll a, chlorophyll b, and total chlorophyll contents decreased by 65.27%, 55.00%, and 62.56%, respectively, while leaf relative electrical conductivity and Fv/Fm increased by 82.14% and 1.39%, respectively. These results indicate that salt stress significantly inhibited chlorophyll synthesis and damaged PSII under high salt stress.

As shown in [Figure 3: see original paper], at 0.4% NaCl, P0 treatment showed higher chlorophyll content and leaf relative electrical conductivity than P1 and P2 treatments, with Fv/Fm reaching its maximum under P1 and minimum under P2. At 0.6% NaCl, chlorophyll content gradually increased and leaf relative electrical conductivity gradually decreased with increasing phosphorus concentration, while Fv/Fm reached its minimum under P2 treatment with no significant difference between P0 and P1. At 0.8% NaCl, P1 treatment showed higher chlorophyll content and leaf relative electrical conductivity than P2 treatment, but lower Fv/Fm. These results demonstrate that phosphorus supplementation after salt stress slowed chlorophyll decomposition and improved PSII photochemical properties.

### 2.4 Effects of Salt and Phosphorus on Leaf Nutrient Characteristics

Under low salt concentration, P, Fe, and Cu contents decreased while Mn, Ca, Na, and K contents increased compared to the control, with no significant differences in Mg and Al contents . Under medium salt concentration, P, Fe, and Al contents reached minima while Mn, K, and Cu contents reached maxima. Under high salt concentration, Mg and Al contents decreased by 5.88% and 20.00%, respectively, while Fe, Mn, Na, K, and Cu contents increased by 47.87%, 20.00%, 669.31%, 18.50%, and 111.11%, respectively, with no significant differences in P and Ca contents. These results indicate that high $Na^+$ concentrations caused salt damage and interfered with absorption of other elements.

As shown in [Figure 4: see original paper], at 0.4% NaCl, P, Fe, Mn, Mg, Ca, Al, K, and Cu contents increased with phosphorus concentration, while Na content was lowest under P1 and highest under P2. At 0.6% NaCl, P, Mg, Ca, Al, and Na contents initially decreased then increased with phosphorus concentration, with P, Mg, and Ca maxima under P0 and Al and Na maxima under P2, while Fe, Mn, K, and Cu contents increased with phosphorus concentration. At 0.8% NaCl, all nutrient contents except Mg and K (which peaked under P1) reached maxima under P2 treatment. These results demonstrate that phosphorus supplementation after salt stress alleviated salt damage and facilitated absorption of other elements.

## 3. Discussion

Changes in growth status represent the most direct response mechanism of plants to environmental stress. The physiological mechanisms underlying growth inhibition under salt stress are multifaceted, including disrupted nutritional ion balance, altered endogenous hormone levels, and affected genetic material. This study found that salt stress significantly inhibited A. confusa seedling growth, with inhibition intensifying at higher salinity levels, consistent with most salt stress research. Although high salt stress can activate water regulation and retention capabilities, these adjustments must occur within certain limits, as unrestricted absorption, transport, and translocation of salt ions inevitably disrupt ionic balance and damage plant resistance. Phosphorus application under salt stress reduced salt tolerance improvement, consistent with previous research, possibly because phosphorus enhanced upward $Na^+$ transport in the xylem, affecting seedling salt tolerance. Excessive phosphorus application during salt-sensitive periods may aggravate salt stress impacts. Additionally, entry of salt and phosphorus ions into cells altered cellular water potential and composition, affecting cell growth, biomass accumulation, and photosynthesis.

Photosynthesis, a crucial physiological process for organic matter production, is highly vulnerable to environmental stress. Salt stress reduces photosynthetic rates by affecting $CO_2$ diffusion to carboxylation sites, altering structure and function of photosynthetic organelles, modifying dark reaction chemistry, and inhibiting assimilate translocation. In this study, fluctuations in net photosynthetic rate, transpiration, stomatal conductance, and intercellular $CO_2$ concentration under low salt stress indicated non-stomatal limitations, whereas inverse relationships between these parameters and salt concentration under medium-to-high salt stress suggested stomatal limitations. The delayed response of aboveground parts to salt stress occurs because salt primarily enters through roots, requiring time for transport to leaves. Chlorophyll, the primary photosynthetic pigment, showed decreased synthesis and increased decomposition with rising salt concentration due to enhanced chlorophyllase activity, affecting light energy absorption and conversion. Increased leaf relative electrical conductivity reflected greater plasma membrane permeability and ion leakage, exacerbating ion damage to photosynthesis. The initial increase followed by decrease in Fv/Fm indicated that PSII damage occurred only under high salt stress, reducing leaf potential activity. Phosphorus supplementation under low-to-medium salt stress may have increased stomatal closure to maintain root ionic balance, reducing leaf water content and impeding photosynthesis. Under high salt stress, improved phosphorus nutrition substantially increased stomatal conductance and chlorophyll a and b contents, reducing salt-induced chlorophyll catabolism, improving PSII photochemical efficiency, and stabilizing cell membrane structure. The smaller Fv/Fm increase under low phosphorus compared to high phosphorus may reflect that appropriate phosphorus levels under high salt stress enhance PSII photochemical properties, seedling potential activity, and primary light energy conversion efficiency.

Mineral element absorption forms the basis of biomass accumulation and is essential for proper growth and development. Soil NaCl under salt stress alters ionic balance, changing salt ion-to-nutrient ratios and affecting normal physiological metabolism. This study showed that salt stress inhibited absorption of P, Fe, Mg, Al, and Cu while increasing Mn, Ca, Na, and K uptake, likely because high $Na^+$ concentrations disrupted ionic balance, causing single-salt toxicity that interfered with uptake of P, Fe, Mg, Al, and Cu. These elements influence growth rate, photosynthetic rate, chlorophyll synthesis, and stress resistance, indicating that long-term salt stress adversely affects these physiological processes. Phosphorus supplementation under salt stress alleviated $Na^+$ toxicity and promoted absorption of other elements. Under medium salt concentration, phosphorus application enhanced Fe, Mn, K, and Cu uptake. Under high salt concentration, low phosphorus was more effective than high phosphorus for Mg and K absorption, while high phosphorus better promoted absorption of other elements, possibly because plants urgently require specific metal ions during salt resistance. Metal ions are highly active, and both salt stress and phosphorus application cause substantial changes in the rhizosphere ionic environment. To maintain nutrient balance and normal physiological activity, metal ion concentrations must fluctuate, though patterns vary due to differences in ion charge and concentration.

In conclusion, different salt levels inhibited A. confusa seedling growth, photosynthetic capacity, and nutrient acquisition to varying degrees, with phosphorus application effects depending on concentration. A. confusa seedlings tolerated low salt concentrations, but higher salinity intensified inhibition of photosynthesis and nutrient uptake, impairing normal growth. Under high salt stress, phosphorus application effectively promoted seedling growth, photosynthetic capacity, and nutrient acquisition. This study revealed the effects of salt and phosphorus on leaf photosynthesis and nutrient characteristics, though the physiological and molecular mechanisms of their interaction and the underlying patterns of ion fluctuations require further investigation.

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*Note: Figure translations are in progress. See original paper for figures.*