Effects of Different Nitrogen Application Rates and Split Application Ratios on Cotton Seedling Growth and Water Use Efficiency, and the Underlying ABA Regulatory Mechanisms: Postprint

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Abstract

This study investigated the changes in plant height, stem diameter, root-shoot biomass, gas exchange parameters, water use efficiency (WUE), total root length, root surface area, and root-sourced abscisic acid (ABA) content in cotton seedlings (variety: Bianmian 5) after experiencing drought stress, under partial root-zone alternating irrigation (APRI) conditions with different nitrogen application rates (high nitrogen HN 200kg/hm2, medium nitrogen MN 120kg/hm2, and low nitrogen LN 80kg/hm2) and split nitrogen application ratios (1:3, 2:2, and 0:4). The objective was to further clarify the physio-ecological effects of root-sourced ABA on the regulation of cotton seedling growth and WUE. The results showed that nitrogen application rate and split nitrogen application significantly enhanced the regulatory role of root-sourced ABA on cotton seedling growth and WUE under drought conditions, but root-sourced ABA had no significant effect on nitrogen use efficiency. Under high nitrogen treatment, cotton seedling growth was least affected by drought, exhibiting the best growth status and the highest root-sourced ABA content, but with the lowest WUE; whereas under low nitrogen treatment, cotton seedlings showed the weakest growth but achieved the highest WUE. Regardless of nitrogen application rate, cotton seedlings with 0:4 split ratio exhibited the weakest growth under drought conditions, while those with 1:3 split ratio showed the best growth and possessed the highest WUE, root-sourced ABA content, total root length, and root surface area; no significant differences were observed in root-shoot growth and leaf area between 2:2 and 1:3 split ratios; differences in stomatal conductance, transpiration rate, WUE, and root-sourced ABA content were not significant between 0:4 and 1:3 split ratios. Therefore, nitrogen application and appropriate split ratios could induce stronger signaling effects of root-sourced ABA, regulating cotton seedlings to reduce water consumption, maintain better root morphology (maintenance and increase of root length, surface area, and fine root proportion), and sustain photosynthetic capacity to maintain better plant growth and higher WUE under drought conditions, particularly under the 1:3 split ratio. Although low nitrogen combined with 1:3 split ratio under drought conditions achieved the highest WUE, medium nitrogen combined with 1:3 split ratio treatment could obtain the highest biomass while achieving relatively high WUE, simultaneously accomplishing high yield, water saving, and nitrogen fertilizer conservation.

Full Text

Regulation of Root-Sourced ABA on Growth and Water Use Efficiency of Cotton Seedlings and Their Response to Different Nitrogen Levels and Distribution Ratios

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Abstract

This study investigated the effects of different nitrogen application levels (high nitrogen, HN 200 kg/hm^2; medium nitrogen, MN 120 kg/hm^2; and low nitrogen, LN 80 kg/hm^2) and nitrogen distribution ratios (1:3, 2:2, and 0:4) on cotton seedlings (variety: B) grown under alternative partial root-zone irrigation (APRI) conditions and subjected to 15 days of drought stress. Parameters measured included plant height, stem width, root and shoot biomass, gas exchange parameters (net photosynthetic rate [P], stomatal conductance [G], transpiration rate [T], and intercellular CO_2 concentration [C]), leaf area, water use efficiency (WUE), total root length, root surface area, nitrogen use efficiency (NUE), and root-sourced ABA concentrations (in both root tissue and root xylem sap). The objective was to elucidate the regulatory effects of root-sourced ABA on cotton seedling growth and WUE under drought conditions.

The results demonstrated that nitrogen application with an appropriate distribution ratio enhanced the regulatory capacity of root-sourced ABA on seedling growth and WUE under drought stress, although NUE was not significantly correlated with root-sourced ABA. HN-treated seedlings exhibited the most vigorous growth and highest biomass, along with the greatest root-sourced ABA concentrations and NUE, but the lowest WUE. Conversely, LN-treated seedlings showed the weakest growth and lowest biomass, yet achieved the highest WUE. Regardless of nitrogen level, seedlings with the 0:4 distribution ratio performed poorest, while those with the 1:3 ratio performed best, displaying the highest

NUE, WUE, and root-sourced ABA concentrations. No significant differences in growth, root/shoot morphology, or leaf area were observed between 1:3- and 2:2-distributed seedlings. C was unaffected by either nitrogen level or distribution ratio, and differences in gas exchange parameters, WUE, and root-sourced ABA concentrations between 0:4- and 1:3-distributed seedlings were not significant.

Root-sourced ABA, directly or indirectly, stimulated reduced water consumption (lower stomatal conductance and transpiration rate) and enhanced root morphology (greater total root length, root surface area, and fine root proportion) to maintain better growth and higher WUE under drought stress, particularly at the 1:3 nitrogen distribution ratio. Although the 1:3-distributed seedlings under LN exhibited the highest WUE, those under MN demonstrated greater NUE and biomass while maintaining relatively high WUE. This treatment combination could simultaneously achieve higher production, reduced water consumption, and efficient nitrogen application.

Keywords: nitrogen distribution ratio; root-sourced ABA; nitrogen level; growth; water use efficiency (WUE); drought stress

Introduction

Cotton is a crucial economic crop worldwide. However, the emergence of ecological and environmental problems such as soil acidification [1] has severely hindered the achievement of high-yield goals with reduced water and fertilizer inputs in cotton production. Currently, agricultural water resources are scarce, nitrogen fertilizer application is excessive, and associated environmental issues pose significant challenges. The theoretical importance of partial root-zone irrigation technology in production practice has been demonstrated. Alternative partial root-zone irrigation (APRI) has been successfully implemented in various crops including cotton [2-10], grape [11-13], potato [14], tomato [15], apple [16], and maize [17-22], enabling efficient water use without yield reduction—i.e., improved water use efficiency (WUE).

Nitrogen fertilization experiments have shown that appropriate nitrogen application can effectively promote photosynthesis, regulate root growth, optimize dry matter distribution, and simultaneously increase cotton yield and WUE [10, 23-28]. However, insufficient or excessive nitrogen application accelerates root senescence and restricts root growth due to nitrogen deficiency or inhibition, thereby compromising efficient water-fertilizer utilization and yield formation [26-27]. While research on nitrogen application effects on cotton growth and WUE is relatively mature, studies on split-root nitrogen application remain limited. Zhou et al. [11] investigated the effects of nitrogen forms and supply locations under simulated water stress on cotton seedling growth, finding that heterogeneous nitrogen application benefited plant growth, but this study lacked data under sustained soil drought conditions and did not report interaction effects between treatment factors. Other research confirmed that partial root-zone irrigation promotes nitrogen absorption in maize but did not address whether different nitrogen application rates affect this response [19]. The theoretical foundation of APRI technology lies in root-sourced signaling theory [29-31] and root compensation effects [29, 32]. Under drought conditions, root-sourced ABA signals are transported via the xylem to regulate stomatal aperture, maintain plant water balance, and subsequently regulate plant growth and development [32, 36-37]. The increase in WUE resulting from ABA regulation of stomatal behavior has been confirmed in cotton [33].

This study combines irrigation methods with split-root nitrogen application to investigate the regulatory effects of root-sourced ABA on cotton seedling growth and WUE under sustained drought conditions, aiming to provide a theoretical basis for developing water-saving, high-yield cotton cultivation techniques.

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1. Materials and Methods

1.1 Experimental Materials and Treatments Cotton (*Gossypium hirsutum* L., cv. B) was used as the experimental material. Seedlings were cultivated in tubes following the method of Du et al. [3]. Each tube (25 cm height) was longitudinally divided into two equal compartments with plastic film, with a 1.5 cm square opening cut at the root collar region to allow root penetration. After germination in darkness, cotton seeds were sown at the center of the tube, directly below the opening. Two seeds were sown per tube, and uniform seedlings were selected 6-8 cm tall, leaving one plant per tube.

Growth conditions during the seedling period were: temperature 30°C/23°C (day/night), 14/10 h photoperiod, maximum supplemental light intensity of 800 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and relative humidity of 75%-80%. The soil was cultivated loam from Kaifeng with bulk density 1.12 g/cm^3, total nitrogen content 0.042%, and field capacity 80%.

Each tube contained 800 g of sieved air-dried soil mixed with potassium dihydrogen phosphate as the phosphorus and potassium source. Nitrogen was applied as urea at three levels: 200 kg/hm^2 (HN, 3.309 g/tube), 120 kg/hm^2 (MN, 2.035 g/tube), and 80 kg/hm^2 (LN, 1.356 g/tube). Within each nitrogen level, three distribution ratios were established by dividing the total nitrogen amount: 1:3, 2:2, and 0:4. Nitrogen was applied as a basal fertilizer once before sowing, with the amount calculated by subtracting soil nitrogen content. Each treatment combination had 8 replicates.

Before sowing, water was added to reach 75%-80% of field capacity. The soil surface was covered with perlite to prevent ineffective evaporation. During alternate irrigation and recovery, the gravimetric method was used to control soil moisture at 40%-50% of field capacity, with daily water consumption recorded. Half the materials were used for the following measurements after 15 days of drought, while the other half were rewatered to 75%-80% of field capacity to record stomatal conductance and leaf water potential recovery time.

1.2 Biomass Measurement Plants were divided at the root collar, with aboveground portions as shoot biomass and belowground portions as root biomass. Samples were oven-dried at 105°C for 30 minutes, then at 75°C to constant weight to obtain dry weights of shoots and roots.

1.3 Plant Height, Stem Width, and Leaf Area Plant height (natural height above soil surface) and stem width (below cotyledons) were measured using a ruler and vernier caliper. Total functional leaf area per plant was determined using a leaf area meter (WYD-500A).

1.4 Gas Exchange Parameters and Water Use Efficiency Gas exchange parameters were measured with a portable photosynthesis system (LI-6400) on the second fully expanded leaf from the top between 9:00-11:00. Light intensity was set to 800 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and temperature to 25°C according to actual growth chamber conditions. Measurements included net photosynthetic rate (P), stomatal conductance (G), transpiration rate (T), and intercellular CO$_2$ concentration (C). Instantaneous water use efficiency (WUE) was calculated as P /T . Biomass water use efficiency (WUE) was calculated as the ratio of individual plant biomass to total transpiration water consumption during the experimental period.

1.5 Nitrogen Use Efficiency Nitrogen content was determined using the Kjeldahl method with an automatic Kjeldahl nitrogen analyzer (K1100). Dried plant samples were digested with H_2SO_4-H_2O_2 until colorless. Nitrogen use efficiency (NUE) was calculated as: NUE = (plant nitrogen increment / nitrogen fertilizer input) × 100%.

1.6 Root Morphology Measurements After severing at the root collar, roots were washed clean. During washing, roots were placed in nylon mesh to prevent loss of fine roots. Intact root samples were placed in a transparent root tray with water, and roots were adjusted with tweezers to avoid overlap. Root systems were scanned (EPSON PERFECTION 4900 PHOTO) and analyzed using WinRHIZO Pro software to obtain total root length, root surface area, and other morphological parameters.

1.7 Root Xylem Sap Collection and ABA Determination Following the method of Li et al. [34], whole plants were placed in a pressure chamber. After cutting the stem 2-3 cm above the root collar and rinsing the cut surface, pressure was applied at 0.2 MPa above root water potential. Xylem sap was collected in 1.5 mL tubes and immediately frozen in liquid nitrogen. Root tips were also collected and frozen. ABA concentrations in root tissue and xylem sap were determined by enzyme-linked immunosorbent assay [35]. Freeze-dried root tissue samples (0.02 g) were extracted overnight at 4°C in 200 L PBS. After centrifugation, the supernatant was used for analysis. For xylem sap or root tissue extracts, 50 L samples were used, followed by sequential addition of 100 L ABA, 100 L H-(+)-ABA solution, 200 L PBS, and saturated $(NH_4)_2SO_4$. After 60 minutes, radioactivity was read in a scintillation counter (Ls6500) and concentrations were calculated from standard curves.

1.8 Statistical Analysis Data were analyzed using two-way and one-way ANOVA with statistical software. Multiple comparisons were performed using the least significant difference (LSD) test at $P < 0.05$. SigmaPlot 8.0 was used for figure preparation. Significant differences are indicated by different letters in tables and figures.

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2. Results

2.1 Effects of Split-Root Nitrogen Application on Cotton Seedling Growth Both nitrogen application rate and distribution ratio, as well as their interaction, significantly affected root and shoot biomass ($P < 0.05$), while only nitrogen rate and its interaction with distribution ratio significantly influenced plant height and stem width (Table 1). With decreasing nitrogen application, seedling growth gradually weakened. Under LN conditions, plant height, stem width, shoot biomass, root biomass, and root/shoot ratio decreased by 52.63%-61.54%, 36.36%-44.17%, 10.73%-13.27%, 8.82%-13.07%, and 11.11%-21.05%, respectively, compared to MN. HN treatment increased these parameters by 9.32%-14.07%, 10.07%-13.54%, 12.89%-17.54%, 9.73%-16.99%, and 11.11%-21.05%, respectively, compared to MN.

Regardless of nitrogen level, seedlings at the 0:4 distribution ratio showed the most significant growth reduction, with plant height, stem width, shoot biomass, root biomass, and root/shoot ratio decreasing by 14.19%-18.23%, 6.49%-13.59%, 26.67%-31.58%, 15.13%-24.45%, and 7.36%-11.90%, respectively, compared to 1:3-distributed seedlings. No growth differences were observed between 1:3- and 2:2-distributed seedlings at any nitrogen level.

After rewatering, leaf water potential and stomatal conductance in HN-treated seedlings recovered to control levels 1-2 days earlier than those under MN and LN. Recovery time for 1:3- and 2:2-distributed seedlings was similar under HN and MN, but under HN, 0:4-distributed seedlings recovered 1-2 days later than 1:3-distributed seedlings (Table 2).

Table 1 Individual and interactive effects of nitrogen application rate and distribution ratio on parameters of cotton seedlings under drought stress (ANOVA)

Table 2 Effect of split-root nitrogen application on growth of cotton seedlings under drought stress

2.2 Effects on Gas Exchange Parameters and Instantaneous Water Use Efficiency Nitrogen rate and distribution ratio significantly affected P , G , T , and WUE , but no significant interaction effects were observed (Table 1). Neither treatment independently or interactively affected C (data not shown), indicating that changes in P were due to stomatal limitation.

Increased nitrogen application significantly promoted P (11.03%-14.34%), G (14.57%-18.12%), and T (5.11%-7.87%), but decreased WUE (2.25%-4.42%). Decreased nitrogen application reduced P (9.78%-14.33%), G (5.16%-14.94%), and T (5.76%-17.84%), but significantly increased WUE (12.59%-21.71%), particularly under LN conditions.

The 1:3 distribution ratio decreased G and T by 4.24%-13.00% and 4.44%-16.95%, respectively, compared to 2:2 and 0:4 ratios, but did not alter P . No significant differences in gas exchange parameters were observed between 1:3- and 2:2-distributed seedlings (Figure 1).

Figure 1 [Figure 1: see original paper] Effect of split-root nitrogen application on gas exchange parameters and instantaneous water use efficiency (WUE) of cotton seedlings under drought stress

2.3 Effects on Leaf Area, Nitrogen Use Efficiency, and Biomass Water Use Efficiency Nitrogen rate, distribution ratio, and their interaction significantly affected leaf area ($P < 0.05$). Increased nitrogen application enhanced leaf area by 9.61%-20.86%, while decreased nitrogen reduced it by 10.53%-17.21%. The 1:3 distribution ratio increased leaf area minimally under HN but decreased it maximally under LN (1.23%-2.63%). The 0:4 ratio decreased leaf area by 5.62%-14.50% under HN and LN.

Both nitrogen rate and distribution ratio significantly affected NUE and WUE under drought conditions (Figure 2). Compared to MN, HN promoted NUE (4.61%-6.87%) but decreased WUE (2.43%-6.63%), while LN decreased NUE (2.43%-6.63%) but increased WUE (5.34%-9.23%). Regardless of nitrogen level, the 1:3 distribution ratio produced the maximum WUE (1.65%-8.86%), except under HN. The 0:4 ratio decreased WUE by 1.64%-2.90% (except under MN). Changes in WUE mirrored those in WUE .

Figure 2 [Figure 2: see original paper] Effect of split-root nitrogen application on nitrogen use efficiency (NUE), biomass water use efficiency (WUE), and leaf area of cotton seedlings under drought stress

2.4 Effects on Root Morphological Characteristics Nitrogen rate, distribution ratio, and their interaction significantly affected total root length and surface area (Table 1, Figure 2). Increased nitrogen application significantly promoted total root length (18.5%-30.7%) and root surface area (15.76%-20.09%), while increasing the proportion of roots >2.0 mm diameter (9.80%-15.52%). Decreased nitrogen application inhibited total root length (16.11%-19.28%) and root surface area (15.76%-20.09%).

Regardless of nitrogen level, the 1:3 distribution ratio produced the maximum total root length and surface area, increasing them by 4.17%-10.33% and 1.83%-7.34%, respectively, compared to 2:2, while the 0:4 ratio decreased them by 4.29%-9.86% and 2.97%-8.89% (Table 3).

Table 3 Effect of split-root nitrogen application on root morphological characteristics of cotton seedlings under drought stress

2.5 Changes in Root and Xylem Sap ABA Content Figure 3 shows that HN conditions produced the greatest accumulation of root-sourced ABA and xylem sap ABA, while LN produced the least. After drought stress, root ABA and xylem sap ABA increased in all treatments compared to non-stressed seedlings. Under HN, root ABA and xylem sap ABA increased by 8.71%-9.91% and 9.20%-12.42%, respectively, compared to MN, while under LN they increased by 6.75%-10.61% and 19.58%-21.25%.

Regardless of nitrogen level, the 1:3 distribution ratio produced the highest root and xylem sap ABA concentrations, while the 0:4 ratio produced equal or slightly lower values.

Figure 3 [**Figure 3: see original paper**] Effect of split-root nitrogen application on root ABA and root xylem sap ABA concentrations of cotton seedlings under drought stress

Regression analysis (Table 4) revealed significant positive correlations between root ABA/xylem sap ABA concentrations and growth parameters (plant height, biomass, leaf area), P , and root morphological parameters (total root length and surface area). Significant negative correlations were observed with G and T . The correlation trends were consistent between root ABA and xylem sap ABA, though correlation coefficients were generally higher for xylem sap ABA.

Table 4 Correlation of root ABA concentration and root xylem sap ABA concentration with other parameters of cotton seedlings under drought stress

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3. Discussion

Previous studies have confirmed that under APRI conditions, alternating wet and dry soil in root zones induces root-sourced signaling substances, and changes in nitrogen availability in root zones also induce corresponding changes in ABA [15, 30-35]. ABA can be transported upward through the xylem with the transpiration stream to leaves to control stomatal aperture, maintain plant water balance under adverse conditions, and subsequently regulate plant growth and development [32, 36-37].

3.1 Regulation of Root-Sourced ABA on Cotton Seedling Growth Under Split-Root Nitrogen Application Under our experimental conditions, root and xylem sap ABA concentrations in drought-stressed cotton seedlings accumulated with increasing nitrogen application, with HN treatment (especially at 1:3 distribution ratio) showing the highest accumulation. Even with low nitrogen supply or slight distribution bias, split nitrogen application promoted ABA accumulation. The 1:3 distribution ratio produced the highest root and xylem sap ABA concentrations, indicating that increased nitrogen application and split application favor ABA accumulation under drought conditions.

Water stress is the most critical environmental factor inhibiting photosynthesis. The regulation of plant water absorption and utilization by ABA is closely related to nitrogen rate and distribution ratio [28, 33]. Nitrogen application ensures nitrogen supply and ABA signal sources in xylem sap under drought conditions. Sufficient nitrogen promotes enhanced photosynthesis and greater accumulation of photosynthetic products, leading to larger root/shoot ratios and leaf area [38-39]. Our data confirm the positive correlation between ABA concentration and root morphological characteristics (root length and surface area), indicating that under split-root nitrogen conditions, ABA regulation promotes root growth and water absorption, thereby enhancing root vitality and drought tolerance.

The compensation effect is a key theoretical basis for APRI technology. ABA can stimulate root compensation for absorption [19, 32], which is related not only to ABA content from different root sides but also to maintaining relatively stable sap flow, facilitating ABA signal function. The 1:3 distribution ratio likely creates mild nitrogen deficiency that enhances nitrogen absorption capacity, indirectly increasing ABA concentration in xylem sap. Even small nitrogen amounts can significantly enhance nitrogen assimilation capacity and promote key enzyme activities (nitrate reductase, glutamine synthetase) under drought [36-39]. However, as drought intensifies, the compensation effect under nitrogen deficiency becomes limited, and the 0:4 distribution ratio significantly reduces nitrogen availability and utilization, decreasing root growth rate and water absorption capacity.

The negative correlation between ABA and G /T is primarily regulated by distribution ratio. Through direct and indirect regulation of P , gas exchange behavior, and leaf area, root-sourced ABA enables cotton seedlings to cope with water limitation while maintaining photosynthetic capacity, resulting in larger leaf area and improved WUE.

3.2 Regulation of Root-Sourced ABA on Water Use Efficiency Under Split-Root Nitrogen Application Stomata are the primary channels for gas exchange between leaves and the atmosphere, determining the intensity of photosynthesis and transpiration. ABA is recognized as the main regulator of stomatal behavior [23, 32]. In this study, ABA concentrations increased significantly under drought compared to non-drought conditions, consistent with previous findings that ABA induces stomatal closure to reduce ineffective water loss [33-38].

The 1:3 distribution ratio promoted the highest WUE by regulating stomatal behavior and root morphology. Increased nitrogen application enhanced nitrogen absorption and assimilation, providing adequate nitrogen sources for photosynthesis and organic matter synthesis, and promoting greater photosynthate transport to roots. This enhanced root growth and nitrogen utilization, improving canopy growth under drought. The resulting larger root system and leaf area provided stronger ABA sources [33, 38-39], promoting ABA accumulation [32-36], stimulating stomatal closure, and reducing ineffective water loss.

Skinner et al. [19] confirmed that under partial root-zone irrigation, split nitrogen application in dry furrows reduces nitrogen leaching losses and increases nitrogen uptake and biomass in maize. In contrast, the 0:4 distribution ratio creates severe nitrogen deficiency, reducing nitrogen effectiveness and root growth rate, resulting in minimal root length and surface area increase and weakened water absorption. Although the 0:4 ratio increased WUE compared to 1:3, this was primarily due to greater inhibition of canopy growth than root growth and water absorption [3, 19, 33].

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4. Conclusion

Under drought conditions, nitrogen rate and distribution ratio affected the regulatory effects of root-sourced ABA on cotton seedling growth and WUE. HN-treated seedlings showed the most vigorous growth and highest ABA accumulation but the lowest WUE, while LN-treated seedlings grew weakest with the highest WUE. Regardless of nitrogen level, the 1:3 distribution ratio produced better growth, greater ABA accumulation, and higher WUE than other ratios. Although the 1:3 ratio under LN produced the highest WUE, the combination of MN with 1:3 distribution ratio achieved greater biomass and NUE while maintaining relatively high WUE. This treatment combination can simultaneously realize higher production, reduced water consumption, and efficient nitrogen application—achieving high yield, water savings, and nitrogen conservation.

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