Delayed Nitrogen Application Promotes Root Morphology Recovery and Improves Post-Anthesis Photosynthetic Performance in Waterlogged Summer Maize (Postprint)

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Abstract

The Jianghuai region is affected by the plum rain season, during which waterlogging stress readily occurs in the seedling stage of corn; investigating how to achieve stress alleviation effects through rational nitrogen fertilizer management is therefore of research significance. Using the summer corn variety 'Longping 206' as experimental material, this study examined the effects of different nitrogen fertilizer management strategies [100% basal nitrogen application (N1), 70% basal + 30% jointing stage fertilizer (N2), 50% basal + 50% jointing stage fertilizer (N3), and 30% basal + 50% jointing stage + 20% large trumpet stage fertilizer (N4)] on root morphology and post-anthesis photosynthetic performance recovery in summer corn subjected to waterlogging at the seedling stage, aiming to provide a theoretical basis for rational fertilization of waterlogged summer corn. The results showed that 7 days of waterlogging at the seedling stage inhibited root growth, with root weight, root length, root surface area, and root diameter all decreasing significantly; the inhibitory effect of waterlogging on root morphological indices was manifested as: root length > root surface area > root diameter. Delayed nitrogen application exerted a significant compensatory effect on root growth after waterlogging; as the proportion of delayed nitrogen increased, root weight, root length, and root surface area increased significantly. At 18 days after waterlogging stress relief, root length in N1-N4 treatments increased by 1.9-5.1 times compared with pre-waterlogging levels, root surface area increased by 6.3-10.3 times, and root diameter increased by 0.7-1.0 times; the magnitude of the compensatory growth effect of delayed nitrogen application on root morphological indices was manifested as: root surface area > root length > root diameter. Waterlogging reduced the canopy leaf area index by 9.3%-22.5%; delayed nitrogen application could increase the canopy leaf area index by 3.2%-20.7% compared with the all-basal application treatment. Seven days of waterlogging at the seedling stage significantly reduced the photosynthetic capacity of ear leaves during the grain filling period, with decreased net photosynthetic rate; net photosynthetic rate decreased by 16.1% and 28.9% at the middle and late grain filling stages, respectively, with the decline in photosynthetic capacity at the late grain filling stage being greater than that of the control; non-stomatal limitation was the primary cause of decreased net photosynthetic rate under waterlogging stress. Under waterlogging stress, delayed nitrogen application treatments improved the photosynthetic performance of ear leaves, with photosynthetic capacity being superior to that of early nitrogen application treatments. In regions prone to waterlogging damage during the seedling stage, appropriately reducing the proportion of basal fertilizer and delaying nitrogen application to the jointing and large trumpet stages can produce favorable compensatory growth effects in waterlogged summer corn.

Full Text

Postponed Nitrogen Application Enhances Root Morphology Recovery and Photosynthetic Characteristics of Summer Maize Waterlogged at Seedling Stage

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Abstract: Maize is one of the main summer crops in Anhui Province. However, maize production in this region is often subjected to waterlogging stress at seedling stage. Nitrogen (N) is a key nutrient that influences growth, yield and quality of maize, but what role it plays in relieving waterlogging stress on summer maize remains unclear. Thus field experiments were carried out to determine the effect of N application on the recovery of root morphology and photosynthetic characteristics of summer maize cultivar 'Longping 206' after waterlogging stress at seedling stage. Under both waterlogging and control (normal water) conditions, four treatments of different N application rates at land preparation, jointing stage, and big flare stage (N1: 10 0 0; N2: 7 3 0; N3: 5 5 0 and N4: 3 5 2) were set with a total N amount of 240 kg · hm ². The results showed that waterlogging stress at seedling stage significantly inhibited maize root growth. Root weight, length, surface area and diameter significantly decreased compared with those of the control. The degree of inhibiting effect on root morphology was in the order of total root length > root surface area > root diameter. Delayed N application had a compensation effect on root growth after waterlogging. Eighteen days after waterlogging, total root length of N1 to N4 treatments increased by 1.9–5.1 folds that before waterlogging. Root surface area and diameter increased by 6.3–10.3 folds and 0.7–1.0 folds, respectively. The degree of compensation effect of delayed N application on root morphology was in the order of root surface area > total root length > root diameter. Waterlogging stress at seedling stage significantly decreased leaf area index (LAI) at spinning stage by a range of 9.3%-22.5%. Compared with N1 treatment, N2, N3 and N4 treatments increased LAI within 3.2%-20.7% under waterlogging treatment. Waterlogging induced a noticeable decline in Pn, respectively by 16.1% and 28.9% compared with the control at mid grain-filling and late grain-filling stages. At late grain-filling stage, Pn decreased faster than that of control. Under waterlogging stress, non-stomatal restriction was the main factor driving the decline of photosynthetic capacity. Moreover, delayed N application improved photosynthetic capacity of ear leaf, which photosynthetic capacity was better than basal N application. In conclusion, the morphological characteristics of root and leaf along with the photosynthetic characteristics of maize under waterlogging responded positively to delayed N supplication. Therefore to improve the growth of maize in the study area (which could be affected by waterlogging at seedling stage), it was recommended to apply N at jointing and big-flare stages.

Keywords: Summer maize; Waterlogging; Delayed nitrogen application; Root growth; Photosynthetic characteristics

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Maize (*Zea mays*) is a grain crop with high yield potential in the Jianghuai region of Anhui Province. However, the seedling stage coincides with the rainy season in this region, making waterlogging stress a common occurrence. Continuous rainfall or flooding during the seedling stage creates soil waterlogging conditions that affect normal plant growth and development, representing a major abiotic stress factor constraining high and stable maize yields. Waterlogged soils create hypoxic conditions that reduce root vigor, decrease mineral element absorption, and substantially decline dry matter accumulation. Previous research has shown that waterlogging induces stomatal closure, reduces transpiration rate, and lowers photosynthetic rate. As waterlogging duration extends, chlorophyll content and photosynthetic enzyme activities decline, PSII photochemical efficiency decreases, and leaves undergo premature senescence.

Nitrogen is crucial for maize organ development, with significant yield increases observed after nitrogen application. Studies indicate that rational fertilization contributes 28-30% to maize yield enhancement. Since soil nitrogen and applied fertilizer must be absorbed through the root system, root growth characteristics are closely related to nutrient uptake. Research has demonstrated that localized high nitrate treatment can increase lateral root length and enhance nitrogen absorption. Under combined water and nitrogen stress, resupplying nitrogen can restore root nitrogen absorption rates both temporally and spatially. Waterlogging reduces photosynthetic performance, but rational nitrogen management can improve crop photosynthetic characteristics. Higher nitrogen levels can maintain post-silking leaf photosynthetic rates and total nitrogen content in low-nitrogen sensitive varieties, while nitrogen deficiency reduces chlorophyll content and accelerates leaf senescence. Supplemental nitrogen under nitrogen-deficient conditions can improve leaf photosynthetic performance and alleviate stomatal limitations, increasing PSII actual photochemical quantum yield and mitigating photoinhibition and photodamage caused by waterlogging. Previous studies have also shown that postponed nitrogen application can mitigate the impact of seedling-stage waterlogging on summer maize yield. While most root research has focused on drought stress, the changes in root characteristics of summer maize under seedling-stage waterlogging and the effects of delayed nitrogen application on root and photosynthetic traits remain inadequately understood. Therefore, this study conducted field experiments to investigate the effects of different nitrogen management strategies on root characteristics and photosynthetic physiology of waterlogged summer maize, aiming to clarify the regulatory effects of nitrogen on root and canopy growth and development under waterlogging stress.

1.1 Experimental Site Conditions

Field experiments were conducted during 2014–2015 at the Gangji Experimental Base of Anhui Academy of Agricultural Sciences in Hefei (31°57 27.7 N, 117°11 51.81 E). The soil was a clayey yellow-cinnamon soil. The 0–20 cm soil layer contained organic matter 21.6 $g \cdot kg^{1}$, hydrolyzable nitrogen 118.4 $mg \cdot kg^{1}$, available potassium 269.6 $mg \cdot kg^{1}$, and available phosphorus 25.4 $mg \cdot kg^{1}$. From June to September, mean temperature was 23.5 °C with 734 mm precipitation in 2014, and 25.7 °C with 794 mm precipitation in 2015.

1.2 Experimental Design

The summer maize cultivar ‘Longping 206’ was planted at a density of 75,000 $plants \cdot hm^{2}$. A waterlogging treatment was imposed at the 4-5 leaf stage for 7 days, maintaining a 1-2 cm water layer on the soil surface without precipitation during this period. A non-waterlogged control was also established.

Both waterlogging and control treatments included four nitrogen management regimes: (N1) 100% nitrogen as basal fertilizer; (N2) 70% basal + 30% at jointing stage; (N3) 50% basal + 50% at jointing stage; and (N4) 30% basal + 50% at jointing stage + 20% at big flare stage. The jointing-stage fertilizer was applied 2 days after waterlogging stress was relieved, while the big flare-stage fertilizer was applied at the big flare stage (applied in furrows and covered with soil). Total nitrogen application was 240 $kg \cdot hm^{2}$ as urea. All plots received 112.5 $kg \cdot hm^{2}$ P O and 112.5 $kg \cdot hm^{2}$ K O before planting, which was incorporated into the soil through tillage.

A split-plot design was used with waterlogging treatment as the main plot and nitrogen treatment as the subplot, with four replications. Each plot measured 3.6 m × 6.0 m with 50 cm spacing between plots. During waterlogging treatment, impermeable plastic sheets were buried 50 cm deep between plots to prevent water movement. Other cultivation management practices followed high-yield field standards.

1.3 Measurement Methods

1.3.1 Root Morphology Characteristics

Root samples were collected one day before waterlogging, on the 3rd and 7th days of waterlogging, and on the 7th and 18th days after waterlogging relief. Sampling involved digging 40 cm deep and 40 cm from the plant center, with four plants per plot and four replications. After excavation, roots were washed with gentle water flow, dead roots and debris were removed, and roots were rinsed with distilled water. Samples were then killed at 105 °C for 30 minutes and dried at 80 °C to constant weight. A desktop scanner and WinRHIZO root analysis system were used to determine root length (cm), root surface area (cm^2), and root diameter (mm) per unit volume.

1.3.2 Leaf Area Index Determination

At the silking stage, leaf area index (LAI) was measured by randomly selecting one plant per plot with four replications. Leaf length and maximum width were measured with a ruler, and leaf area was calculated as: leaf area = maximum length × maximum width × 0.75.

1.3.3 Leaf Photosynthetic Rate Measurement

Using a Li-6400 portable photosynthesis system with artificial light intensity set at 1500 mol · m ^{2} · s ^{1}, net photosynthetic rate [Pn, mol(CO) · m ^{2} · s ^{1}], stomatal conductance (Gs, mmol · m ^{2} · s ^{1}), intercellular CO concentration (Ci, mol · mol ^{1}), and transpiration rate [Tr, mmol(H O) · m ^{2} · s ^{1}] of ear leaves were measured during mid and late grain-filling stages on clear days between 9:00–11:30. Plants with consistent growth progression and direction were selected, with two plants per plot and four replications.

1.4 Data Processing and Statistical Analysis

Data were calculated using Microsoft Excel 2003 and analyzed using SPSS.

2.1 Effects of Nitrogen Management on Root Morphology of Waterlogged Summer Maize

2.1.1 Root Weight

Seedling-stage waterlogging significantly inhibited maize root growth, with waterlogged treatments showing significantly lower root weight than the control. During waterlogging, no significant differences in root weight were observed among N1–N4 treatments. However, after waterlogging relief when jointing fertilizer was applied, N2–N4 treatments showed significantly higher root weight than N1. Seven days after waterlogging relief, root weight in waterlogged N1–N4 treatments decreased by 68.6%, 41.1%, 39.1%, and 44.9% compared with the control, respectively [Figure 1: see original paper].

2.1.2 Root Length

Under control conditions, N1 and N2 treatments had significantly higher root length than N3 and N4 before jointing fertilizer application. However, 16 days after jointing fertilizer application (18 days after waterlogging relief), N3 and N4 treatments showed significantly higher root length than N1. Seven days of seedling-stage waterlogging inhibited root growth, with the reduction in root length increasing as waterlogging duration extended. After 3 days of waterlogging, root length in N1–N4 treatments decreased by 16.9%, 13.2%, 0.6%, and 1.1% compared with pre-waterlogging values, respectively. After 7 days, decreases were 55.4%, 55.4%, 24.9%, and 34.6%, respectively. Following waterlogging relief and jointing fertilizer application, N3 and N4 treatments recovered faster than N1 and N2. Seven days after relief, root length in N3 and N4 exceeded pre-waterlogging values, and by 18 days after relief, all treatments had recovered, with increases of 1.9-fold, 2.3-fold, 4.4-fold, and 5.1-fold for N1–N4, respectively, indicating that post-waterlogging nitrogen application facilitated rapid root length recovery.

Among nitrogen treatments, N1 showed significantly higher root length than N3 and N4 before waterlogging. After 7 days of waterlogging, no significant differences existed among treatments. Seven days after relief, N4 root length was 13.4%, 12.9%, and 5.4% higher than N1, N2, and N3, respectively. Eighteen days after relief, N4 root length was 15.6%, 8.2%, and 18.0% higher than N1, N2, and N3, respectively, demonstrating that delayed nitrogen application promoted compensatory growth in root length after waterlogging.

2.1.3 Root Surface Area

Seven days of seedling-stage waterlogging reduced root surface area, following a similar trend as root length but with smaller reduction magnitude. The reduction increased with waterlogging duration. After 3 days, root surface area in N1–N4 treatments decreased by 9.2%, 10.0%, 11.8%, and 10.7% compared with pre-waterlogging values. After 7 days, decreases were 35.6%, 39.9%, 12.8%, and 30.4%, respectively. After waterlogging relief and jointing fertilizer application, root surface area recovered faster than root length. By 18 days after relief, root surface area increased by 6.3-fold, 7.1-fold, 10.6-fold, and 10.6-fold compared with pre-waterlogging values, indicating that root surface area responded more rapidly to delayed nitrogen application than root length.

Among nitrogen treatments, N1 had significantly higher root surface area than N3 and N4 before waterlogging. No significant differences existed among treatments during waterlogging. Seven days after relief, root surface area followed the order N4 > N2 > N3 > N1, with N4 being 29.5%, 20.7%, and 25.8% higher than N1, N2, and N3, respectively. Eighteen days after relief, N4 remained 10.7%, 4.4%, and 6.1% higher than N1, N2, and N3, respectively, showing faster recovery under N4 treatment. Compared with the control, waterlogging for 7 days reduced root surface area by 42.0%, 13.7%, 47.2%, and 67.9% in N1–N4 treatments, respectively. Seven days after relief, reductions were 34.8%, 27.8%, 27.4%, and 10.2%, respectively, and by 18 days after relief, reductions had narrowed to 3.8%, 4.7%, 5.6%, and 4.0%, respectively. These results demonstrate that post-waterlogging nitrogen application facilitated root surface area recovery, though values remained below control levels.

2.1.4 Root Diameter

Under control conditions, N1 root diameter was significantly higher than N2–N4 before jointing fertilizer application, while N4 and N3 were significantly higher than N1 after jointing fertilizer application. Seven days of waterlogging did not significantly affect root diameter compared with pre-waterlogging values. Eighteen days after waterlogging relief, no significant differences existed among nitrogen treatments, though root diameter increased by 0.7-fold, 0.8-fold, 0.7-fold, and 1.0-fold compared with pre-waterlogging values for N1–N4, respectively. The N4 treatment increased root diameter by 10.9%, 4.4%, and 10.9% compared with N1, N2, and N3, respectively, indicating that root diameter recovery was slower than that of root length and surface area.

2.2 Effects of Nitrogen Management on Leaf Area Index of Waterlogged Summer Maize

Seedling-stage waterlogging inhibited leaf growth, with waterlogged treatments showing significantly lower LAI than controls. At silking stage, waterlogged N1–N4 treatments decreased LAI by 15.3%, 13.5%, 13.3%, and 10.0% compared with controls in 2014, and by 22.5%, 20.2%, 17.0%, and 9.3% in 2015 [Figure 2: see original paper]. Waterlogging affected leaf growth, reducing green leaf area and limiting photosynthetic production.

Delayed nitrogen application increased LAI under waterlogging conditions. In 2014, N4 treatment showed significantly higher LAI than other nitrogen treatments under waterlogging. Waterlogged N3 and N4 increased LAI by 3.2% and 6.7% compared with N1, while control N3 and N4 increased by only 0.8% and 0.4% compared with N1. In 2015, waterlogged N3 and N4 increased LAI by 3.8% and 20.7% compared with N1, while control N4 increased by 3.1% compared with N1.

2.3 Effects of Nitrogen Management on Photosynthetic Characteristics of Waterlogged Summer Maize

Waterlogging significantly reduced net photosynthetic rate, stomatal conductance, and transpiration rate of ear leaves. At mid and late grain-filling stages, these parameters decreased by 16.1% and 28.9%, 25.0% and 12.1%, and 5.1% and 10.9% compared with controls, respectively. Intercellular CO concentration showed the opposite trend, increasing by 19.3% and 61.3% compared with controls. Analysis of both stages revealed that from mid to late grain-filling, waterlogged treatments showed greater declines in Pn, Gs, and Tr (38.9%, 31.1%, and 21.8%, respectively) than controls (27.9%, 41.2%, and 16.8%, respectively) , indicating accelerated photosynthetic decline under waterlogging.

No significant differences in Pn, Gs, or Tr existed among nitrogen treatments at mid grain-filling. However, at late grain-filling, N4 treatment showed significantly higher Pn, Gs, and Tr than N1 and N2. Under waterlogging, N4 increased Pn, Gs, and Tr by 63.3% and 55.3%, 43.2% and 7.0%, and 34.5% and 12.3% compared with N1 and N2, respectively, demonstrating that delayed nitrogen application improved photosynthetic performance of ear leaves during late grain-filling.

Discussion

The root system is the primary organ for water and nutrient absorption, and its morphology and spatial distribution directly affect nutrient uptake. Rational fertilization creates favorable rhizosphere conditions that ensure effective nutrient supply to maize roots. Nitrogen application promotes root growth, increases root hair density, and enhances root physiological functions. Applying nitrogen at the 10-leaf stage increases root weight and surface area distribution in the 0–20 cm soil layer, while nitrogen application at silking stage improves root distribution and activity in the 20–40 cm layer. This study showed that under normal water conditions, reducing basal nitrogen rate did not significantly affect root weight, length, or surface area during early growth, but all root morphological indices increased rapidly after jointing fertilizer application. Delaying nitrogen application to the big flare and silking stages synchronizes soil mineral nitrogen supply with crop uptake. The coupling effect of appropriate nitrogen rate and topdressing timing can simultaneously improve summer maize yield and quality while substantially reducing soil nitrate leaching.

Under waterlogging stress, maize root growth differs from normal water conditions. Seedling-stage waterlogging inhibited root growth, significantly reducing root dry matter accumulation, length, surface area, and diameter. This likely occurred because waterlogging suppressed primary and secondary root growth, resulting in thicker, shorter roots with fewer branches and almost no root hairs, while some roots suffocated and died, leading to reduced root length and surface area. Root length decreased by 24.9–55.4%, surface area by 12.8–39.9%, and diameter by 2.7–5.3%, with the degree of inhibition following the order: root length > root surface area > root diameter, consistent with previous research. After waterlogging relief, nitrogen topdressing improved soil fertility and promoted root growth, with stronger recovery capacity than basal-only application. The compensatory effect of delayed nitrogen on post-waterlogging root morphology followed the order: root surface area > root length > root diameter. Nitrogen supply significantly affects maize root growth, morphology, distribution, physiology, and exudation. Nitrogen increases summer maize yield primarily by enhancing root fresh weight, total root fresh and dry weight, and nitrogen content in middle and lower soil layers. While low nitrogen supply during early growth does not inhibit root growth, excessive nitrogen can be inhibitory. Therefore, relatively reducing the basal nitrogen proportion does not suppress plant growth, while shifting nitrogen application to jointing and big flare stages ensures adequate late-season nitrogen supply and provides excellent compensatory effects for root recovery after waterlogging. In regions with excessive rainfall during maize seedling stage, large amounts of nitrogen can leach into deep soil layers as NO -N. Since summer maize grows slowly in early stages, excessive early nitrogen application can cause severe nitrogen leaching and late-season deficiency, making delayed nitrogen strategies essential for synchronizing nitrogen supply with crop demand.

Postponed nitrogen application significantly improved leaf photosynthetic performance during middle and late growth stages. As the organ responsible for water and nutrient absorption and phytohormone synthesis, root growth and metabolic activity directly affect aboveground development and "light system" construction for yield formation. Waterlogging causes lower leaf yellowing and abscission, suppresses leaf area expansion and new leaf emergence, and produces narrow, thin leaves, reducing population LAI. Delayed nitrogen application increases mineral nitrogen content in soil during middle and late growth stages, enhancing cytokinin synthesis in roots and transport to leaves. This increases LAI in ear and above-ear layers to compensate for LAI reduction in lower layers, with compensation effects exceeding waterlogging-induced losses, resulting in higher population LAI under delayed nitrogen than under early nitrogen application.

Photosynthesis forms the basis for dry matter and yield formation. Some studies suggest stomatal limitation is the main factor reducing photosynthetic rate after 7 days of waterlogging, while non-stomatal limitation dominates after 14 days. This study found that 7 days of seedling-stage waterlogging reduced ear leaf Pn during grain-filling, with faster decline in late growth stages. Compared with controls, waterlogging reduced Pn and Gs but increased Ci, indicating that Pn reduction during grain-filling was not primarily caused by stomatal conductance but rather by reduced mesophyll cell carboxylation capacity. Waterlogging stress inhibited plant growth, reduced root activity, accelerated leaf senescence, decreased chlorophyll content and leaf area, and suppressed photosynthesis, ultimately causing yield losses exceeding 20%. Nitrogen deficiency is a primary factor limiting crop yield, affecting Rubisco and PEPC enzyme activities and reducing late-grain-filling Pn. Reducing basal nitrogen proportion and delaying application to jointing and big flare stages can increase LAI in ear and above-ear layers to compensate for lower-layer LAI reduction, extend leaf photosynthetic functional duration, improve light interception capacity, enhance population photosynthetic performance during grain-filling, and increase photosynthetic capacity compared with early nitrogen application.

In conclusion, seedling-stage waterlogging inhibited root growth, but post-stress nitrogen topdressing provided significant compensatory effects on root recovery. Waterlogging significantly reduced ear leaf photosynthetic capacity during grain-filling, with accelerated decline in late stages, and non-stomatal limitation was the primary cause of Pn reduction. In regions prone to seedling-stage waterlogging, adaptive nitrogen management strategies combining basal and topdressing applications with increased late-season nitrogen proportions can provide effective compensatory growth for waterlogged summer maize.

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