

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

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Abstract

The Jianghuai region is affected by the Meiyu season, during which waterlogging stress readily occurs in the maize seedling stage, making it worthwhile to investigate how rational nitrogen fertilizer management can achieve stress alleviation. Using the summer maize variety 'Longping 206' as experimental material, this study examined the effects of different nitrogen fertilizer management strategies [all nitrogen applied as basal fertilizer (N1), 70% basal + 30% at jointing (N2), 50% basal + 50% at jointing (N3), and 30% basal + 50% at jointing + 20% at large trumpet stage (N4)] on root morphology and post-anthesis photosynthetic performance recovery in summer maize subjected to waterlogging at the seedling stage, in order to provide a theoretical basis for rational fertilization of waterlogged summer maize. The results showed that seven 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 effects of waterlogging on root morphological indices exhibited the following order: root length > root surface area > root diameter. Postponed nitrogen application had a significant compensatory effect on root growth after waterlogging; as the amount of postponed nitrogen increased, root weight, root length, and root surface area increased significantly. Eighteen days after waterlogging stress relief, root length in the N1-N4 treatments increased by 1.9-5.1 times compared to pre-waterlogging levels, root surface area increased by 6.3-10.3 times, and root diameter increased by 0.7-1.0 times; the compensatory growth effects of postponed nitrogen application on root morphological indices exhibited the following order: root surface area > root length > root diameter. Waterlogging reduced the canopy leaf area index by 9.3%-22.5%, while postponed nitrogen application increased the canopy leaf area index by 3.2%-20.7% compared to 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 net photosynthetic rate decreasing by 16.1% and 28.9% at the mid and late grain-filling stages, respectively; the decline in photosynthetic capacity in the late grain-filling stage was greater than that of the control, and non-stomatal limitation was the primary cause of the decrease in net photosynthetic rate under waterlogging stress. Under waterlogging stress, postponed nitrogen application treatments improved the photosynthetic performance of ear leaves, with photosynthetic capacity superior to that of earlier nitrogen application treatments. In regions prone to waterlogging damage during the seedling stage, appropriately reducing the basal fertilizer ratio and postponing nitrogen application to the jointing and large trumpet stages can produce favorable compensatory growth effects in waterlogged summer maize.

Full Text

Abstract

To study how reasonable nitrogen fertilizer management can mitigate damage from waterlogging stress, which frequently occurs during the rainy season in the Jianghuai region and affects summer maize at the seedling stage, field experiments were conducted using the summer maize cultivar 'Longping 206'. Four nitrogen application regimes were investigated: all nitrogen applied as basal fertilizer (N1), 70% basal + 30% at jointing stage (N2), 50% basal + 50% at jointing stage (N3), and 30% basal + 50% at jointing stage + 20% at big flare stage (N4). The effects of these regimes on root morphology recovery and post-anthesis photosynthetic performance of waterlogged summer maize were examined to provide a theoretical basis for rational fertilization of waterlogged summer maize. The results showed that 7 days of waterlogging at the seedling stage significantly inhibited root growth, with root weight, length, surface area, and diameter all decreasing significantly. The inhibitory effect followed the order: root length > root surface area > root diameter. Delayed nitrogen application had a significant compensatory effect on root growth after waterlogging, with root weight, length, and surface area increasing significantly as the proportion of delayed nitrogen increased. Eighteen days after waterlogging stress was relieved, root length in treatments N1-N4 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 compensatory effect of delayed nitrogen application on root morphology followed the order: root surface area > root length > root diameter. Waterlogging reduced leaf area index by 9.3%-22.5%, while delayed nitrogen application increased LAI by 3.2%-20.7% compared with all-basal application. Seven days of waterlogging at the seedling stage significantly reduced photosynthetic capacity of ear leaves during grain filling, with net photosynthetic rate decreasing by 16.1% and 28.9% at mid and late grain-filling stages, respectively. The decline in photosynthetic capacity was more pronounced at late grain-filling than in the control, with non-stomatal limitation being the main cause of reduced net photosyn-

thetic rate under waterlogging stress. Delayed nitrogen application improved photosynthetic performance of ear leaves under waterlogging stress, with better photosynthetic capacity than forward nitrogen application. In areas prone to waterlogging at the seedling stage, appropriately reducing the basal fertilizer ratio and delaying nitrogen application to the jointing and big flare stages can provide effective compensatory growth for waterlogged summer maize.

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

Introduction

Maize (*Zea mays*) is a major grain crop with high yield potential in the Jianghuai region of Anhui Province. However, maize production in this area is frequently subjected to waterlogging stress during the seedling stage due to the plum rain season. Continuous rainfall or flooding during the seedling stage creates soil waterlogging conditions that affect normal plant growth and development, making waterlogging stress an important abiotic factor limiting high and stable maize yields. Waterlogging at the seedling stage keeps roots in a low-oxygen state, reducing root activity, decreasing mineral element absorption, and substantially reducing dry matter accumulation. Previous research has shown that soil waterlogging causes leaf stomatal closure, reduces transpiration rate, and decreases photosynthetic rate. With prolonged waterlogging, chlorophyll content and photosynthetic enzyme activities decline, PSII photochemical efficiency decreases, and leaves senesce prematurely.

Nitrogen is a key nutrient that plays an important role in maize organ development, with significant yield increases following nitrogen application. Previous studies have found that rational fertilization accounts for 28%-30% of maize yield increase factors. Since soil nitrogen and applied nitrogen 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 induce lateral root elongation and increase plant nitrogen absorption. Studies also show that after water and nitrogen dual stress, local nitrogen resupply can restore nitrogen absorption rate in both temporal and spatial dimensions, indicating that rational nitrogen supply promotes better root growth. Root growth, metabolism, and vitality changes directly affect aboveground growth and development. While waterlogging reduces plant photosynthetic performance, rational nitrogen management can improve crop photosynthetic characteristics. Higher nitrogen levels can maintain photosynthetic rate and total nitrogen content in low-nitrogen-sensitive varieties after anthesis. Insufficient nitrogen supply reduces leaf chlorophyll content and accelerates leaf death, while nitrogen supplementation under deficiency conditions can improve leaf photosynthetic performance and stomatal limitation, increase PSII actual photochemical quantum yield, and alleviate photoinhibition and photodamage caused by waterlogging. Delayed nitrogen application can also mitigate the impact of seedling waterlogging on summer maize yield. However, previous root

research has focused mainly on drought stress, while studies on root characteristic changes in summer maize under seedling waterlogging stress and the effects of delayed nitrogen application on root and photosynthetic characteristics of waterlogged maize remain insufficient. Therefore, this study conducted field experiments to investigate the effects of different nitrogen management regimes 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 of waterlogged summer maize.

1.1 Experimental Site Conditions

The experiment was conducted during 2014-2015 at the Gangji Base of Anhui Academy of Agricultural Sciences in Hefei (31°57' 27.7 N, 117°11' 51.81 E). The test soil was clayey yellow-cinnamon soil. The 0-20 cm soil layer contained organic matter 21.6 g · kg⁻¹, hydrolyzable nitrogen 118.4 mg · kg⁻¹, available potassium 269.6 mg · kg⁻¹, and available phosphorus 25.4 mg · kg⁻¹. From June to September 2014, the average temperature was 23.5°C and rainfall was 734 mm; in 2015, the average temperature was 25.7°C and precipitation was 794 mm.

1.2 Experimental Design

The summer maize cultivar 'Longping 206' was used with a planting density of 75,000 plants · hm⁻². A waterlogging treatment for 7 days at the 4-5 leaf stage was imposed, maintaining a 1-2 cm water layer on the field surface without precipitation during the waterlogging period. Non-waterlogged treatment served as the control. Both waterlogging and control treatments included four nitrogen application regimes: all nitrogen as basal fertilizer (N1), 70% basal + 30% at jointing stage (N2), 50% basal + 50% at jointing stage (N3), and 30% basal + 50% at jointing stage + 20% at big flare stage (N4). Jointing fertilizer was broadcast-applied 2 days after waterlogging stress relief, and big flare fertilizer was applied at the big flare stage (applied in furrows and covered with soil). Total nitrogen application was 240 kg · hm⁻² as urea. All plots received P O 112.5 kg · hm⁻² and K O 112.5 kg · hm⁻² before planting, which were broadcast on the surface and incorporated by plowing.

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 intervals between plots. During waterlogging treatment, impermeable plastic sheets were buried 50 cm deep to prevent water flow between plots. Other cultivation management practices followed high-yield field protocols.

1.3 Measurement Methods

1.3.1 Root Morphology Characteristics Roots were sampled at 1 day before waterlogging, 3 and 7 days after waterlogging, and 7 and 18 days after

waterlogging stress relief. Sampling was performed by digging 40 cm deep at 40 cm from the plant center, with 4 plants per plot and 4 replications. After extraction, roots were washed with a gentle water stream, dead roots and debris were removed, and roots were rinsed with distilled water. Samples were 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 (cm²), and root diameter (mm) per unit volume.

1.3.2 Leaf Area Index Determination Leaf area index (LAI) was measured at the silking stage. One plant was randomly sampled per plot with 4 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 source intensity of 1,500 mol · m⁻² · s⁻¹, net photosynthetic rate [Pn, mol(CO₂) · m⁻² · s⁻¹], stomatal conductance (Gs, mmol · m⁻² · s⁻¹), intercellular CO₂ concentration (Ci, mol · mol⁻¹), and transpiration rate [Tr, mmol(H₂O) · m⁻² · s⁻¹] of ear leaves were measured from 9:00-11:30 on sunny days at mid and late grain-filling stages. Plants with consistent growth stage and direction were selected, with 2 plants per plot and 4 replications.

1.4 Data Processing and Statistical Analysis

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

Results

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

2.1.1 Root Weight Waterlogging at the seedling stage significantly inhibited maize root growth, with root weight in waterlogged treatments being significantly lower than in the control. During the waterlogging period, no significant differences in root weight were observed among N1-N4 treatments. However, after waterlogging stress was relieved and jointing fertilizer was applied, treatments N2-N4 showed significantly higher root weight than N1. Seven days after waterlogging stress relief, root weight in 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 In the control treatment, N1 and N2 showed significantly higher root length than N3 and N4 during the early growth stage. Sixteen days after jointing fertilizer application (18 days after waterlogging relief), N3 and N4 treatments showed significantly higher root length than N1. Seven days of

waterlogging at the seedling stage 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 levels; after 7 days, decreases were 55.4%, 55.4%, 24.9%, and 34.6%, respectively. Following waterlogging relief and jointing fertilizer application, root length recovery in N3 and N4 was superior to N1 and N2. Seven days after stress relief, root length in N3 and N4 exceeded pre-waterlogging levels; by 18 days after relief, all treatments N1-N4 had recovered, increasing by 1.9, 2.3, 4.4, and 5.1 times compared with pre-waterlogging levels, respectively. This indicates that applying jointing fertilizer after waterlogging stress facilitates rapid root length recovery.

Among different 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 stress 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 root length growth after waterlogging.

2.1.3 Root Surface Area Seven days of waterlogging at the seedling stage reduced root surface area, following the same trend as root length but with smaller reduction magnitude. The reduction increased with waterlogging duration. After 3 days of waterlogging, root surface area in N1-N4 treatments decreased by 9.2%, 10.0%, 11.8%, and 10.7% compared with pre-waterlogging levels; after 7 days, decreases were 35.6%, 39.9%, 12.8%, and 30.4%, respectively. Root surface area recovered after waterlogging relief and jointing fertilizer application, with faster recovery than root length. Eighteen days after waterlogging relief, root surface area increased by 6.3, 7.1, 10.6, and 10.6 times compared with pre-waterlogging levels, indicating that root surface area responded more rapidly to delayed nitrogen application than root length.

Among different nitrogen treatments, N1 showed significantly higher root surface area than N3 and N4 before waterlogging. As waterlogging duration extended, no significant differences existed among N1-N4 treatments. Seven days after stress 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 was 10.7%, 4.4%, and 6.1% higher than N1, N2, and N3, respectively, demonstrating faster recovery in N4. Compared with the control, after 7 days of waterlogging, root surface area in N1-N4 treatments decreased by 42.0%, 13.7%, 47.2%, and 67.9%, respectively. Seven days after waterlogging relief, N1-N4 treatments were 34.8%, 27.8%, 27.4%, and 10.2% lower than the control; by 18 days after relief, differences narrowed to 3.8%, 4.7%, 5.6%, and 4.0% lower, respectively. This shows that applying jointing fertilizer after stress relief promoted root surface area recovery, though values remained slightly below control levels.

2.1.4 Root Diameter In the control treatment, N1 showed significantly higher root diameter than N2-N4 before jointing fertilizer application [Figure 1: see original paper]. After jointing fertilizer application, N4 and N3 showed significantly higher root diameter than N1. Seven days of waterlogging did not significantly affect root diameter compared with pre-waterlogging levels. Eighteen days after waterlogging relief, no significant differences existed among nitrogen treatments, but root diameter increased by 0.7, 0.8, 0.7, and 1.0 times compared with pre-waterlogging levels, with N4 being 10.9%, 4.4%, and 10.9% higher than N1, N2, and N3, respectively. This indicates that root diameter recovery was slower than root length and surface area after waterlogging stress.

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

Waterlogging at the seedling stage inhibited leaf growth, with LAI in waterlogged treatments being significantly lower than in the control. In 2014, LAI in waterlogged N1-N4 treatments decreased by 15.3%, 13.5%, 13.3%, and 10.0% compared with the control; in 2015, decreases were 22.5%, 20.2%, 17.0%, and 9.3%, respectively [Figure 2: see original paper]. Waterlogging affected leaf growth, reducing green leaf area and limiting photosynthetic production.

In 2014 under waterlogging conditions, N4 treatment showed significantly higher LAI than other nitrogen treatments, demonstrating that delayed nitrogen application increased LAI at the silking stage. In 2014, waterlogged N3 and N4 increased LAI by 3.2% and 6.7% compared with N1, while control N3 and N4 increased by 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 Regime on Photosynthetic Characteristics of Waterlogged Summer Maize

Waterlogging treatment significantly reduced net photosynthetic rate, stomatal conductance, and transpiration rate of ear leaves. At mid and late grain-filling stages, net photosynthetic rate, stomatal conductance, and transpiration rate decreased by 16.1% and 28.9%, 25.0% and 12.1%, and 5.1% and 10.9% compared with the control, respectively. Intercellular CO₂ concentration showed the opposite trend, increasing by 19.3% and 61.3% compared with the control. Analysis of photosynthetic parameters at mid and late grain-filling stages showed that under waterlogging treatment, net photosynthetic rate, stomatal conductance, and transpiration rate at late grain-filling decreased by 38.9%, 31.1%, and 21.8% compared with mid grain-filling, while the control decreased by 27.9%, 41.2%, and 16.8%, respectively. The decline in net photosynthetic rate and transpiration rate was greater under waterlogging than in the control.

At mid grain-filling, no significant differences existed among nitrogen treatments in net photosynthetic rate, stomatal conductance, or transpiration rate of ear

leaves. At late grain-filling, N4 treatment showed significantly higher net photosynthetic rate, stomatal conductance, and transpiration rate than N1 and N2. Under waterlogging treatment, N4 increased net photosynthetic rate, stomatal conductance, and transpiration rate by 63.3% and 55.3%, 43.2% and 7.0%, and 34.5% and 12.3% compared with N1 and N2, respectively, indicating that delayed nitrogen application improved net photosynthetic rate, stomatal conductance, and transpiration rate of ear leaves at late grain-filling.

Discussion

The root system is the primary organ for water and nutrient absorption, and its morphology and spatial distribution affect nutrient uptake. Rational fertilization can create a favorable rhizosphere soil environment and ensure effective nutrient supply to the maize rhizosphere. 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 increases root distribution and activity in the 20-40 cm soil layer. This study showed that under normal water supply, reducing basal nitrogen application did not significantly affect root weight, length, or surface area at the seedling stage, but all root morphology indices increased rapidly after jointing fertilizer application. Delaying nitrogen application to the big flare and silking stages can better synchronize inorganic nitrogen supply in the tillage layer with crop uptake. The coupling effect of appropriate nitrogen application rate and topdressing timing can simultaneously improve summer maize yield and quality while substantially reducing soil nitrate nitrogen leaching.

Under waterlogging stress, maize root growth differed from normal water supply conditions. Seedling waterlogging inhibited maize root growth, substantially reducing root dry matter accumulation and significantly decreasing root length, surface area, and diameter. This may be because waterlogging inhibited growth of primary and secondary roots, making roots thicker and shorter 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% and root surface area by 12.8%-39.9%, with the inhibitory effect following the order: root length > root surface area > root diameter, consistent with previous research. After waterlogging relief, topdressing nitrogen improved soil fertility and promoted root growth, with stronger recovery than all-basal application. The compensatory effect of delayed nitrogen on root morphology recovery followed the order: root surface area > root length > root diameter. Nitrogen supply significantly affects maize root growth, morphology, distribution, physiology, and exudation. Nitrogen application mainly increases summer maize yield by increasing fresh root weight, total fresh and dry weight in the surface soil layer, and nitrogen content in middle and lower root layers. Low nitrogen supply in early growth stages does not inhibit root growth, while higher nitrogen levels can be inhibitory. Therefore, relatively reducing the basal nitrogen ratio

does not inhibit plant growth, while delaying nitrogen application to the jointing and big flare stages ensures adequate late-season nitrogen supply and provides good compensatory effects on root recovery after waterlogging. In areas with excessive precipitation during the maize seedling stage, large amounts of nitrogen can leach into deep soil layers in NO_3^- -N form. Since summer maize grows slowly in early stages, excessive early nitrogen application can cause severe nitrogen leaching and insufficient nitrogen supply during later growth stages, making delayed nitrogen management strategies necessary to synchronize nitrogen supply with crop uptake.

Delayed nitrogen application significantly improved leaf photosynthetic performance during middle and late growth stages. As the organ for water and nutrient absorption and plant hormone synthesis, root growth, metabolism, and vitality changes directly affect aboveground growth and development and influence the establishment of the aboveground “photosynthetic system” and yield formation. Waterlogging causes lower leaves to yellow and abscise, inhibits leaf area expansion and new leaf emergence, and results in narrow, thin leaves. Waterlogging-induced death of lower leaves reduces canopy leaf area index. Delayed nitrogen application increases mineral nitrogen content in soil during middle and late growth stages, enhances cytokinin synthesis in roots and transport to leaves, and increases LAI in ear and upper canopy layers to compensate for LAI reduction in lower layers. This compensation effect exceeds the LAI reduction caused by waterlogging in lower layers, resulting in higher canopy LAI under delayed nitrogen application compared with forward nitrogen application under waterlogging stress.

Photosynthesis is the foundation for crop dry matter and yield formation. Some studies suggest that stomatal limitation is the main factor causing photosynthetic rate decline in maize under 7-day flooding, while non-stomatal limitation is the main factor under 14-day flooding. This study showed that 7 days of seedling waterlogging reduced net photosynthetic rate of ear leaves during grain filling, with faster decline during later growth stages. Compared with the control, waterlogging for 7 days reduced net photosynthetic rate and stomatal conductance during grain filling but increased intercellular CO_2 concentration, indicating that the decline in net photosynthetic rate was not mainly caused by stomatal conductance but rather by reduced mesophyll cell carboxylation capacity. Waterlogging stress inhibited plant growth, reduced root activity, caused leaf senescence, decreased chlorophyll content and leaf area, suppressed photosynthesis, reduced net photosynthetic rate, and ultimately caused yield losses exceeding 20%. Nitrogen also affects plant photosynthetic efficiency, and insufficient nitrogen supply is a primary factor limiting crop yield. Inadequate nitrogen supply affects Rubisco and PEPC enzyme activities, and reduced enzyme activity leads to decreased net photosynthetic rate during late grain filling. Reducing the basal nitrogen ratio and delaying nitrogen application to the jointing and big flare stages can increase LAI in ear and upper canopy layers to compensate for LAI reduction in lower layers, extend leaf photosynthetic functional duration, improve light interception capacity, enhance canopy photo-

synthetic performance during grain filling, and increase photosynthetic capacity compared with forward nitrogen application.

Waterlogging at the seedling stage inhibited root growth, but topdressing nitrogen after stress relief had significant compensatory effects on root growth. Waterlogging significantly reduced photosynthetic capacity of ear leaves during grain filling, decreasing net photosynthetic rate, with faster decline during late grain filling than in the control. Non-stomatal limitation was the main cause of reduced net photosynthetic rate under waterlogging stress. In areas prone to seedling 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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