



Effects of Nitrogen Application Rates and Irrigation Regimes on Root Growth and Nitrogen-Use Efficiency of Maize under Alternate Partial Root-Zone Irrigation

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Abstract

Root growth and its adaptation are quite important for efficient use of water and nutrients. The present study investigated the effects of alternate partial root-zone irrigation (APRI) coupled with nitrogen application on root growth and nitrogen-use efficiency (NUE) of maize (*Zea mays* L.). Treatments (conducted at Wuwei City, northwest China) included APRI with controlled irrigation at 45%, 65%, and 80% of field capacity (FC) (W1, W2, and W3, respectively) coupled with nitrogen application rate of 100, 200, and 300 kg N ha⁻¹ (N1, N2, and N3, respectively). The study found a significant interaction effect of irrigation regimes and nitrogen application rates on maize root growth and NUE. Compared with N2, N3 did not increase the length, surface area, weight, and volume of roots at the filling and maturity stages under W2, while it did under W3, which suggests that increasing nitrogen application rates did not compensate for the adverse effect of drought on root growth. In addition, NUE positively correlated with these root morphological parameters but negatively with the root-to-shoot ratio at the filling and maturity stages. The W2N2 treatment with moderate soil moisture and relatively high soil nitrate-nitrogen promoted total root growth and deeper roots and optimized vertical root distribution, with a low root-to-shoot ratio, resulting in the greatest NUE. These results suggest that moderately controlled irrigation (W2) combined with a reasonable nitrogen rate (N2) improves root growth and optimizes root distribution, resulting in a high NUE in maize under alternate partial root-zone irrigation.

Keywords Deficit irrigation · Root growth and distribution · Root-shoot ratio · Nitrogen utilization · *Zea mays* L

1 Introduction

Maize (*Zea mays* L.) is an important cereal crop used as human food, animal feed, and pharmaceutical and industrial raw material. It plays an important role in agricultural and industrial production (Abd El-Waheda and Ali 2013). The maize planting area in China has exceeded 35.45 Mha (ranked first globally), with an annual production of 2.18 Pg, which accounts for 22.0% of the world's total production

(FAO STAT 2020). However, the high-frequency and prolonged water shortage associated with climate change has reduced crop growth and food production in majority of the agricultural regions, including the maize production area in the Hexi Corridor of northwest China (Yu et al. 2020), which is one of the main producing areas of spring maize in China. Thus, increasing maize yield in this region is important to maintain national food security (Guo et al. 2022).

Nitrogen is one of the essential nutrients required for maintaining plant growth and development (Kant 2018; Tian et al. 2019). The application of nitrogen fertilizer improves maize yield, but excessive or unscientific use is common in intensive agricultural production (Xing et al. 2021; Guo et al. 2022). The excessive or unscientific use leads to several environmental issues such as ammonia (NH₃) volatilization, water pollution, and soil acidification (Ju et al. 2009) and reduces crop production (Li et al. 2020; Zou et al. 2020). Water scarcity is another major factor challenging maize production, especially in arid

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and semi-arid regions (Ran et al. 2017; Kang et al. 2021). Moreover, freshwater consumption is growing due to climate changes and urbanization, aggravating water shortage (Sarker et al. 2020). Therefore, it is important to explore practical ways to maintain maize yield, with relatively low nitrogen fertilizer and irrigation water inputs.

Water-saving irrigation technologies (e.g., deficit irrigation) show promise in improving crop water productivity (CWP) and for fighting water scarcity (Jha et al. 2017; Sarker et al. 2020). Alternate partial root-zone irrigation (APRI) is an improved method of deficit irrigation, which induces alternate soil dry and wet cycles in the root zone (Sarker et al. 2020). Consequently, APRI induces abscisic acid (ABA)-based root-to-shoot chemical signaling to regulate growth and water use, increasing CWP (Du et al. 2015; Zhang et al. 2019). Therefore, APRI is considered a water-saving irrigation technique and has been widely applied in water-deficit areas (Sepaskhah and Ahaadi 2010; Qi et al. 2020a, 2020b; Kang et al. 2021). However, Kirda et al. (2005) demonstrated that APRI cannot improve maize yield and enhance CWP compared with conventional deficit irrigation, possibly due to unscientific irrigation regime (Sadras 2009). Moreover, management decisions concerning nitrogen application help to improve grain yield and water- and nitrogen-use efficiencies (Li et al. 2009; Wang et al. 2017a). Therefore, the supply levels of irrigation water and chemical fertilizer should be coordinated to achieve high yield and resource-use efficiency under APRI for sustainable agricultural production.

Root growth is closely related to shoot growth and yield (Wang et al. 2014; Xu et al. 2019). Both water and nitrogen management regulates root morphology, which influences the nutrient absorption and water utilization capacity of plants (Xu et al. 2018; Wang et al. 2018). Length, weight, diameter, surface area, and volume are the major root morphological traits that influence the functionality of the root system (Ju et al. 2015). Moderate deficit irrigation improved wheat's root length density (RLD) (Li et al. 2010). Although drought inhibits the root length and dry weight, it may result in a greater proportion of roots in the deep soil layers (60–100 cm) to enhance the absorption of water and nutrients, favoring stable grain yields (Wang et al. 2014). However, excessive soil water adversely affects maize root growth, declining grain yield (Qi and Pan 2022). Similarly, a moderate rate of nitrogen fertilization as well as reduced and postponed basal application of nitrogen fertilizer could improve crop root growth and deeper roots (Peng et al. 2012; Tian et al. 2019). Conversely, high-nitrogen conditions did not improve root morphological traits (Rasmussen et al. 2015) and even inhibit root growth (Qi et al. 2019). Therefore, supply levels of irrigation water and nitrogen fertilizer should be carefully considered to improve root growth

and crop yield under water-saving irrigation techniques, such as APRI.

Excessive use of irrigation water and nitrogen fertilizer is a major concern in China (Ran et al. 2017; Zou et al. 2020). For example, the amount of nitrogen fertilizer used by farmers of the Hexi Corridor of northwest China has increased to 360–400 kg N ha⁻¹ per year for maize cultivation, which is 180–200% higher than the recommended nitrogen rate during the maize growing season (Yang and Su 2009). Thus, supplying chemical fertilizers and irrigation water in an efficient way is necessary for high resource-use efficiency in this region. Moreover, understanding the interaction between irrigation water and nitrogen fertilizer levels, their effects on root morphological traits, and their correlation with grain yield and nitrogen-use efficiency (NUE) is essential for sustainable agricultural production (Xu et al. 2018, 2019). Several studies have analyzed the combined effects of nitrogen fertilizer and irrigation water on shoot growth, yield, and water- and nitrogen-utilization efficiencies under conventional deficit irrigation (Ran et al. 2016, 2017; Zou et al. 2020; Li et al. 2020; Xing et al. 2021). We have also analyzed the effects of different supply levels of irrigation water and nitrogen fertilizer on shoot growth, grain yield, and CWP of maize under APRI (Qi et al. 2020b). However, the effects of APRI coupled with nitrogen fertilizer rates on root growth, its relationship with NUE, and the possible causes underlying this effect remain largely unknown.

Therefore, the objectives of this study were to (1) evaluate the performances of irrigation regimes and nitrogen application rates on maize root growth and distribution in the 0–100-cm soil layer and root-to-shoot ratio and NUE under APRI, and to elucidate the possible mechanisms and (2) analyze the relationships between the abovementioned root morphological traits and NUE. We hypothesized that coordinating irrigation water and nitrogen fertilizer supply levels may lead to reasonable soil water and nitrogen availability, improve root growth, and optimize root distribution, resulting in a high NUE in maize under APRI.

2 Materials and Methods

2.1 Experimental Site and Crop Management

A 2-year (2014 and 2015) field experiment was conducted on maize at the Wuwei Experimental Station for Efficient Use of Crop Water, Ministry of Agriculture and Rural Affairs, China (latitude 37°52'20"N, longitude 102°50'50"E; altitude 1581 m). The site belongs to a continental temperate climate zone, with a mean annual precipitation of 164.4 mm and annual evapotranspiration of 2000 mm. The field soil was light sandy loam, with an organic matter content of 15.90 g kg⁻¹, total nitrogen (N) of 0.85 g kg⁻¹, available N

of 40.43 mg kg⁻¹, total phosphorus of 0.93 g kg⁻¹, available phosphorus of 6.22 mg kg⁻¹, and available potassium of 236.24 mg kg⁻¹ at 0–40 cm depth. At the 0–100-cm depth, the soil bulk density was 1.45 g cm⁻³, and the field capacity (FC) was 0.30 cm³ cm⁻³ (Ran et al. 2016). The weather conditions of the experimental site are shown in Table 1.

The furrows and ridges were established in the experimental site, as reported by Qi et al. (2017). The ridges in the west–east direction were built 20 cm and 35 cm wide at the top and the bottom, respectively. As the phosphorus source, triple superphosphate (46% P₂O₅) was applied at a rate of 60 kg P ha⁻¹ before planting according to local farmers' practices. Maize (*Zea mays* L.) cultivar “Funong No.588” was planted in the ridges at a density of 73,000 plants ha⁻¹ on 16 April 2014 and 20 April 2015, and the crop was harvested on 19 September 2014 and 20 September 2015.

2.2 Experimental Design

The experiment adopted a randomized complete block design (water × nitrogen) with three replicates per treatment. Three controlled irrigation treatments at 45%, 65%, and 80% of FC, referred to as severe (W1) water deficit, moderate (W2) water deficit, and well-watered (W3), were adopted for maize production under alternate partial root-zone irrigation (APRI). Meanwhile, N fertilizer at 100, 200, and 300 kg N ha⁻¹ rates referred to as low N level (N1), moderate N level (N2), and high N level (N3), was adopted. According to Yang and Su (2009), 200 kg N ha⁻¹ is the recommended N rate for maize production in this region. Thus, the study was conducted using a total of nine treatments (W1N1, W1N2, W1N3, W2N1, W2N2, W2N3, W3N1, W3N2, and W3N3 (CK)). The size of each plot was 24–32 m² (4 m × 8 m in 2014 or 4 m × 6 m in 2015), with seven ridges and eight furrows. Nitrogen in the form of urea was applied before sowing and at the 12-collar stage (V12), and tasseling stage (VT); 40%, 30%, and 30% of the total N were applied at sowing, V12, and VT, respectively (15 April, 11 July, and 1 August in 2014; 19 April, 12 July, and 2 August in 2015).

The lower limit of FC was used as the threshold of irrigation. The eight furrows of each plot were divided into group A (odd furrows) and group B (even furrows). Meanwhile, 1.25-m long measuring tubes used to determine soil moisture content were placed at the bottom of two adjacent central furrows (furrows 4 and 5) in each plot (Fig. S1). The initial (sowing date) soil mass water content at 0–40 cm depth was 17.4% in 2014 and 16.8% in 2015, which met the water requirement of the germinating maize seeds. For W3, the first irrigation was applied to the odd furrows when the soil water content of furrow 5 reached the controlled lower limit, 13 and 12 days after the sowing (DAS) of seeds in 2014 and 2015, respectively; this resulted in relatively high soil water content in the odd furrows. Then, the even furrows (relatively low soil water content) were irrigated when the soil water content of furrow 4 reached the controlled lower limit (7 to 9 days after the last irrigation dates), resulting in relatively high soil water content in the even furrows. The odd furrows were irrigated again as mentioned before; thus, the furrows were irrigated alternately throughout the maize-grown season. The other (W1 and W2) plots were alternately irrigated, similar to the W3 plots (excluding the initial irrigation time and irrigation frequency) through both the growing seasons. The irrigation amount used during each irrigation event (mm) was calculated using the following equation (Qi et al. 2020b):

$$I = K \times S \times h(F_c - q) \quad (1)$$

where S is the area of the plot (m²); K is 0.5, which is the correction factor of S (since only one-half of furrows in each plot were irrigated in each event); h is the thickness of the wetted soil layer (m), 0.60 m deep from emergence (VE) to the six-collar stage (V6) and 1.00 m deep from V6 to the physiological maturity (R6); F_c is the field capacity (0.30 cm cm⁻³); and q is the controlled irrigation limit (cm cm⁻³).

A flexible irrigation system was installed to irrigate each plot separately, and the amount of irrigation water

Table 1 Precipitation, sunshine hours, and mean temperature during the growing season of maize in 2014 and 2015 at the experimental site

	April	May	June	July	August	September
Precipitation (mm per month)						
2014	20	17	12	46	75	5
2015	13	15	13	41	51	11
Sunshine (h per month)						
2014	213	226	279	312	259	235
2015	217	230	284	320	255	231
Mean temperature (°C)						
2014	7.6	14.2	17.2	22.2	22.3	21.6
2015	7.5	14.4	17.5	22.4	22.4	21.4

Temperatures are the monthly averages

was measured using a water meter. The number of irrigation events and the amount of total irrigation water used for the different treatments in the two growing seasons are presented in Table S1.

2.3 Sampling and Measurement

2.3.1 Soil Water Content

The volumetric soil moisture content at the central ridge of each plot (Fig. S1) was measured at an interval of 5 to 7 days using a portable soil moisture monitoring system (Diviner 2000, Sentek Pty. Ltd, Australia). The water content of the 0–100-cm soil profile was determined (10 cm as an interval) according to the method by Zhou et al. (2007).

2.3.2 Root Morphological Traits

The length, biomass, surface area, and volume of the roots were determined at the V6, silking (R1), and R6 stages, corresponding to 42, 89, and 151 DAS, respectively, in 2014, and 45, 91, and 151 DAS, respectively, in 2015. A hand-driven auger with an internal diameter of 10 cm and length of 1.25 m was used for sampling. Before sampling, the shoots of the plant were removed. Soil samples were collected from under the plant from five layers (0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, and 0.8–1.0 m) to a vertical depth of 1.0 m. All roots were washed and then arranged in a glass tray to scan; the root images were captured and analyzed with the WinRHIZO Root Analyzer Software (Regent Instruments Inc., Quebec, Canada) to measure length, surface area, and volume. Meanwhile, fresh roots were dried in an oven at 75 °C to consistent biomass. Root length density (RLD) (cm cm^{-3}) was calculated as the ratio of root length to the soil sampling volume.

2.3.3 Root-to-Shoot Ratio

Shoots were collected and split into different components, namely, leaf, stem, sheath, and ear, and the ear was further separated into the cob and kernel components at the R6 stage. All samples were then dried using a drier at 75 °C to a consistent weight for shoot biomass determination. Subsequently, the root-to-shoot ratio was calculated (Xu et al. 2018).

2.3.4 Crop Nitrogen Uptake

Three maize plants were sampled from each plot at the R6 stage (harvest) on 19 September 2014 and 20 September 2015 to analyze the N uptake. The aboveground plant parts were separated into grain and stover, dried at 70 °C to consistent biomass, weighed for biomass determination, and,

subsequently, ground (1 mm sieve) to determine the total N. The concentration of plant N was determined following the semi-micro Kjeldahl method. The total N uptake was determined from the products of dry matter in sum and grain and stover N concentrations (Wang et al. 2016).

2.3.5 Grain Yield and Nitrogen-Use Efficiency (NUE)

The maize plants in the two middle rows of each plot were harvested to determine the grain yield (adjusted to 15.5% moisture content). The NUE (kg kg^{-1}) was determined as the ratio of grain yield to available N (Pikul et al. 2005). The available N was determined as the sum of mineral N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) in the 0–100-cm soil profile at sowing and total N fertilization applied.

2.4 Statistical Analysis

Analysis of variance (ANOVA) was used to analyze the data on soil water content, soil $\text{NO}_3\text{-N}$, root length, root biomass, root surface area, root volume, root-to-shoot ratio, grain yield, and NUE following the GLM procedure of the Statistical Analysis System (SAS). Treatment means were analyzed by Duncan's multiple range test and considered statistically significant at $P_{0.05}$. Pearson correlation coefficient was calculated to analyze the relationships between grain yield, NUE, and root morphological traits.

3 Results

3.1 Soil Water Content

The water content of the 0–100-cm soil layer was comparable among the different N rates in each irrigation regime; therefore, the soil water content values of the three N treatments were pooled for further analysis. The average soil water content across the growing season decreased with soil depth deepening for all irrigation treatments (Fig. 1a, b). At the 0–70-cm depth, W3 resulted in the maximum soil water content, followed by W2 and W1. Below 70 cm, the average soil water content was comparable among the three irrigation treatments (Fig. 1a, b). Minor differences were detected in the soil water content between 2014 and 2015.

3.2 Root Morphology Traits

Root morphological traits including length, surface area, biomass, and volume in the 0–100-cm soil depth reached the maximum during the R1 stage in both the cropping seasons (Table 2). The root morphological parameters at the V6 stage decreased with the increase in N rates under each irrigation treatment, while these parameters,

Fig. 1 Soil water content in the 0–100-cm soil depths for different irrigation regimens in 2014 (a) and 2015 (b). Note: Data was the average of the measured soil water content with a same soil layer during the maize grown season. W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC)

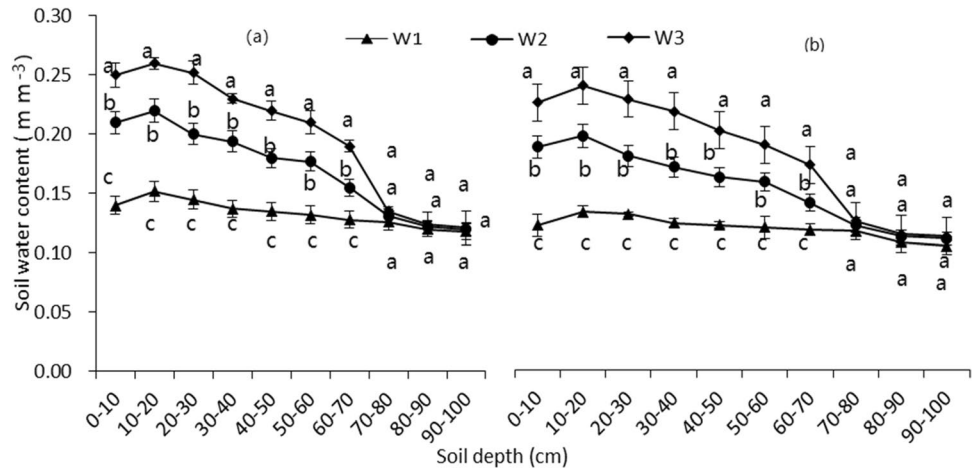


Table 2 Total root length (RL), root surface area (RSA), root weight (RW), and root volume (RV) in the 0–100-cm soil profile at the 6 collars (V6), silking (R1), and maturity (R6) stages of maize for different nitrogen application rates and irrigation regimens in 2014 and 2015

Year	Parameters	Stage	W1N1	W2N1	W3N1	W1N2	W2N2	W3N2	W1N3	W2N3	W3N3
2014	RL (cm)	V6	928 ± 55ab	913 ± 60ab	1002 ± 77a	800 ± 45b	790 ± 78b	811 ± 85b	526 ± 43d	678 ± 55c	621 ± 24c
		R1	5001 ± 101e	5478 ± 90d	4879 ± 87e	6236 ± 98c	7125 ± 87a	6587 ± 99b	4814 ± 54e	6230 ± 90c	6628 ± 89b
		R6	2765 ± 43e	3184 ± 24d	2312 ± 56f	3585 ± 40c	4507 ± 50a	4014 ± 65b	2210 ± 45f	3625 ± 26c	4124 ± 88b
	RSA (cm ²)	V6	345 ± 12a	355 ± 14a	370 ± 17a	289 ± 10b	280 ± 15b	282 ± 9b	210 ± 7d	245 ± 8c	250 ± 10c
		R1	1287 ± 46d	1430 ± 55c	1024 ± 34e	1684 ± 46b	2138 ± 87a	1903 ± 56b	1058 ± 55e	1761 ± 34b	1995 ± 43b
		R6	398 ± 13d	450 ± 14c	388 ± 15d	537 ± 21b	628 ± 32a	545 ± 41b	361 ± 22d	557 ± 19b	600 ± 24a
	RW (g)	V6	4.0 ± 0.3a	4.0 ± 0.3a	4.2 ± 0.4a	3.2 ± 0.2b	3.2 ± 0.4b	3.2 ± 0.2b	2.2 ± 0.1e	2.7 ± 0.2d	2.8 ± 0.1d
		R1	10.2 ± 0.5d	13.0 ± 0.6c	8.8 ± 0.5e	14.3 ± 0.6b	16.2 ± 0.7a	14.4 ± 0.5b	8.3 ± 0.4e	14.1 ± 0.3c	15.8 ± 0.6ab
		R6	6.9 ± 0.4d	9.1 ± 0.3bc	5.6 ± 0.3e	9.4 ± 0.4bc	11.2 ± 0.5a	9.9 ± 0.1b	5.1 ± 0.1e	8.5 ± 0.2c	10.1 ± 0.3b
RV (cm ³)	V6	25.7 ± 1.0a	26.1 ± 1.4a	26.7 ± 1.0a	22.1 ± 1.1b	25.2 ± 0.9a	23.1 ± 0.8b	19.0 ± 0.9d	20.7 ± 0.5c	20.2 ± 0.6c	
	R1	58.2 ± 1.7d	63.4 ± 1.7c	55.1 ± 1.2e	63.3 ± 1.6c	71.2 ± 2.0a	66.9 ± 0.9b	55.5 ± 1.0e	63.2 ± 1.3c	65.9 ± 1.3b	
	R6	37.1 ± 1.1c	40.1 ± 0.8b	33.1 ± 1.0d	38.3 ± 0.9b	45.3 ± 1.1a	41.3 ± 1.4b	32.9 ± 1.2d	40.5 ± 1.4b	44.2 ± 1.3ab	
2015	RL (cm)	V6	910 ± 54a	923 ± 47a	965 ± 61a	820 ± 23b	800 ± 20b	814 ± 34b	550 ± 18d	658 ± 14c	642 ± 16c
		R1	4678 ± 124e	5178 ± 87d	4170 ± 68e	6236 ± 99b	6721 ± 73a	6182 ± 87b	4013 ± 45e	5730 ± 55c	6228 ± 112b
		R6	2561 ± 78e	3304 ± 46d	2017 ± 35f	3585 ± 54c	4200 ± 90a	3815 ± 50b	2010 ± 47f	3420 ± 65c	3887 ± 85b
	RSA (cm ²)	V6	385 ± 19a	390 ± 16a	400 ± 16a	310 ± 18b	321 ± 20b	323 ± 10b	244 ± 8d	275 ± 11c	280 ± 14c
		R1	1007 ± 43d	1230 ± 37c	884 ± 21e	1680 ± 28b	1930 ± 32a	1687 ± 23b	858 ± 22e	1661 ± 69b	1792 ± 53ab
		R6	334 ± 13d	421 ± 11c	289 ± 10e	487 ± 18b	575 ± 21a	490 ± 15b	275 ± 9e	477 ± 11b	555 ± 25ab
	RW (g)	V6	4.1 ± 0.2a	4.2 ± 0.4a	4.3 ± 0.3a	3.3 ± 0.4b	3.3 ± 0.2b	3.3 ± 0.2b	2.4 ± 0.1e	2.8 ± 1d	2.9 ± 0.2d
		R1	10.1 ± 0.4d	12.2 ± 0.5c	9.5 ± 0.4de	14.3 ± 0.6b	15.1 ± 0.6a	14.1 ± 0.4b	8.8 ± 0.3e	12.6 ± 0.5c	14.8 ± 0.7a
		R6	5.8 ± 0.3d	7.1 ± 0.3c	4.2 ± 0.2e	9.4 ± 0.3bc	10.4 ± 0.5a	8.5 ± 0.3b	6.0 ± 0.2d	7.3 ± 0.2c	9.5 ± 0.4ab
RV (cm ³)	V6	26.7 ± 0.8a	27.1 ± 1.1a	27.3 ± 0.9a	23.1 ± 0.8b	26.2 ± 1.0a	24.0 ± 0.9b	20.0 ± 0.7d	21.3 ± 0.6c	21.4 ± 0.8c	
	R1	57.2 ± 1.5d	63.1 ± 2.2b	53.0 ± 1.5e	61.3 ± 1.4c	67.2 ± 2.4a	64.2 ± 2.0b	52.3 ± 1.4e	61.1 ± 1.7c	65.3 ± 1.8ab	
	R6	36.1 ± 1.4d	38.2 ± 1.7b	32.0 ± 1.0e	38.2 ± 1.3b	42.1 ± 1.7a	40.4 ± 1.9b	31.6 ± 1.5e	38.5 ± 2.0c	41.1 ± 1.1b	

Note: W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC), respectively. N1, N2, and N3 represent 100, 200, and 300 kg N ha⁻¹, respectively. Values (means ± standard error, n=3) followed by different letters within each row and same year are significantly different at the probability level of 0.05

except for root volume, were comparable among the different irrigation treatments under N1 and N2. However, these parameters were significantly lower in W1 than the other irrigation treatments under N3. These observations

collectively suggest that high N supply inhibits early root growth of maize under 45% FC (Table 2).

The total root length at the R1 and R6 stages increased up to N2 and then decreased with the increase in N rates

under W1 and W2, whereas it increased with the increase in N rates under W3 (Table 2). In this study, W2 resulted in the greatest root length under N1 and N2; however, W3 resulted in the greatest root length under N3. The W2N2 treatment resulted in the greatest root length, while the W3N1 and W1N3 treatments resulted in the smallest root length among the different treatments (Table 2). A similar pattern was observed for root surface area, root weight, and root volume at the R1 and R6 stages (Table 2). Only minor differences were detected in the root parameters between 2014 and 2015.

3.3 Root Vertical Distribution

The present study determined the RLD at the R1 stage to assess the root vertical distribution (Peng et al. 2012; Wang et al. 2018). The RLD declined with the increase in soil depth in maize plants under all treatments (Fig. 2a, b). The root system was mainly gathered in the topsoil; root length in the 0–40-cm soil layer accounted for 66.5–73.9% of the whole root system in the 0–100-cm depth (Table 3). The different irrigation regimes and N application rates of the study influenced maize root distribution (Fig. 2a, b). Here,

Fig. 2 Root length densities in the 0–100-cm soil depths at the silking (R1) of maize for different nitrogen application rates and irrigation regimes in 2014 (a) and 2015 (b). Note: Bars show mean ± standard error (n = 3); W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC), respectively. N1, N2, and N3 represent 100, 200, and 300 kg N ha⁻¹, respectively. Different letters within the same soil layer and year indicate significant difference (P < 0.05)

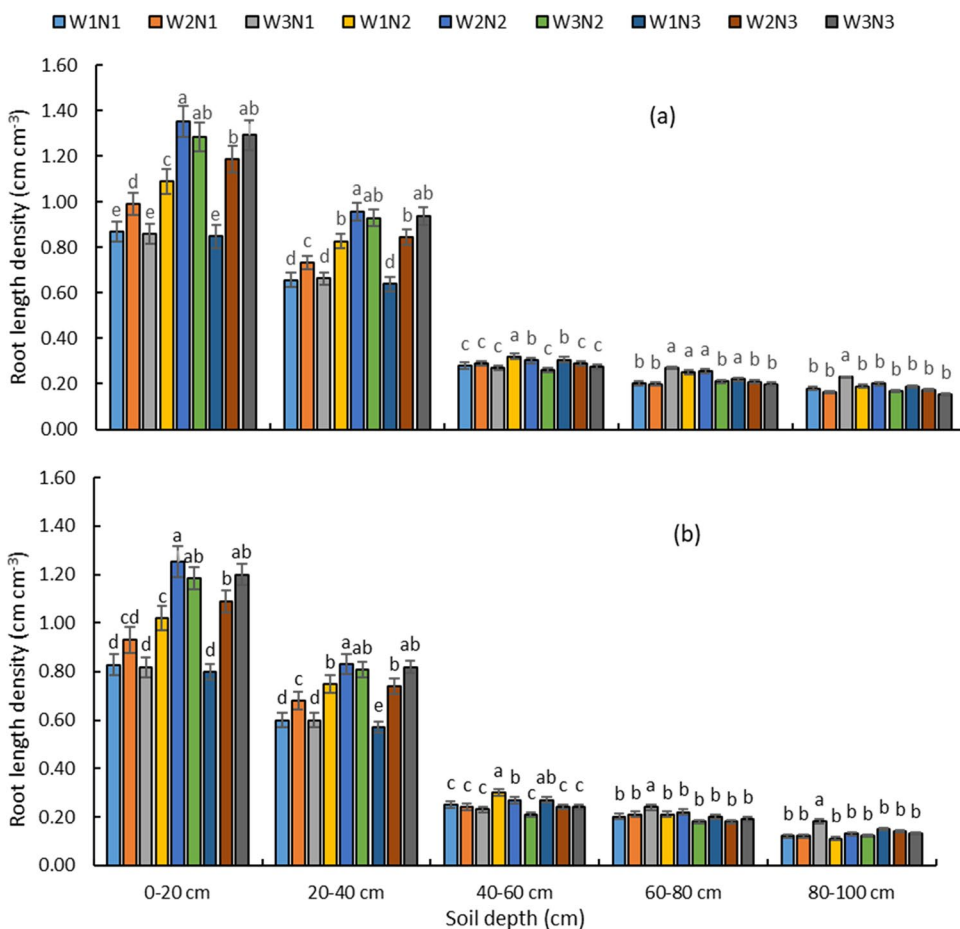


Table 3 The percentage of total root length in each soil depth to the sum of 0–100 cm soil depth (%) in maize for different nitrogen application rates and irrigation regimes

Soil depth	W1N1	W2N1	W3N1	W1N2	W2N2	W3N2	W1N3	W2N3	W3N3
0–20 cm	41.12	41.75	42.40	42.33	43.98	45.80	39.74	41.02	42.37
20–40 cm	25.33	26.87	25.41	28.65	27.61	28.09	30.29	30.14	30.33
40–60 cm	11.91	10.97	10.99	10.71	10.60	10.80	11.68	11.61	11.18
60–80 cm	11.29	10.34	11.28	9.27	9.89	8.26	9.75	9.92	9.11
80–100 cm	10.35	10.07	9.92	9.04	7.92	7.05	8.54	7.31	7.01

Note: W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC), respectively. N1, N2, and N3 represent 100, 200, and 300 kg N ha⁻¹, respectively. Total root length of each soil layer was averaged across the different positions (north, south, and under the plant) and 2 years for different treatments. Total root length of 0–100 cm depth was the sum of total root length of all soil layers

W2N2 produced the greatest RLD for the 0–40-cm soil layer, W1N2 for the 40–60-cm soil layer, and W3N1 for the 80–100-cm soil layer (Fig. 2a, b). Results obtained in 2014 and 2015 were similar.

Furthermore, the proportion of root length in the surface soil layer (0–20 cm) increased with the increase in controlled irrigation limits under a specific N rate (Table 3). Meanwhile, under a specific irrigation regime, the proportion of root length in the surface soil layer increased from N1 to N2 and then decreased from N2 to N3. Increasing levels of irrigation water and N fertilizer resulted in a lower percentage of root length in the deep soil layer (80–100 cm). W3N3 reduced the percentage of root length in the deep soil layer by 32.3% compared with W1N1.

3.4 Root-to-Shoot Ratio

In maize, the root-to-shoot ratio decreased gradually with growth and reached the lowest level at the R6 stage (Fig. 3a, b). Only the N rates significantly influenced the root-to-shoot ratio at the V6 stage; the root-to-shoot ratio declined with the increase in N rates under each irrigation treatment. In addition, the different irrigation and N treatments significantly affected the root-to-shoot ratio at the R1 and R6 stages. Under a specific irrigation regime, the root-to-shoot ratio decreased with N rates. Under a specific N rate, W1 resulted in a root-to-shoot ratio greater than the other irrigation treatments (Fig. 3a, b). Among the different treatments, W1N1 resulted in the greatest root-to-shoot ratio at the three growth stages (Fig. 3a, b), which indicates that the maize shoots are more sensitive to water and nitrogen stresses than the roots. However, compared with N1, N3 decreased the root-to-shoot ratio more (15.6–20.4%) under W1 rather than under W3. The trends observed in 2014 and 2015 were similar (Fig. 3a, b).

3.5 Nitrogen-Use Efficiency (NUE)

Under a specific irrigation regime, the NUE increased up to N2 and then decreased with the increase in N supply rates (Table 4). Specifically, NUE increased up to W2 and then decreased with the increase in controlled irrigation limits under N1 and N2. The greatest NUE was observed under W2N2, and the smallest under W1N3. The trends observed in 2014 and 2015 were similar.

3.6 Correlation of Root Morphology Traits with Grain Yield and Nitrogen-Use Efficiency

The study's analysis revealed a significant or extremely significant positive correlation of length, dry weight, surface area, and volume of roots at the R1 and R6 stages with grain yield ($r=0.754^*–0.913^*$) and a negative relationship with

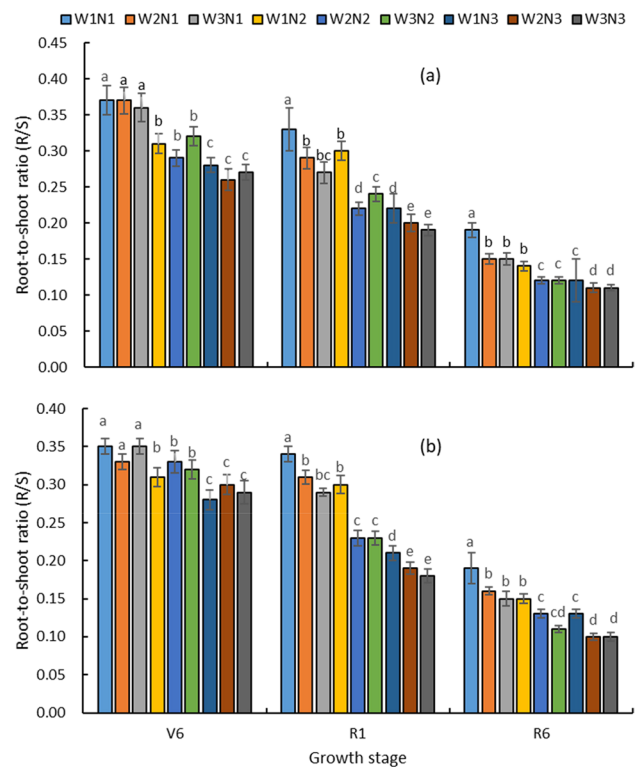


Fig. 3 Root-to-shoot ratio (R/S) of maize at the 6 collars (V6), silking (R1), and maturity (R6) stages of maize for different nitrogen application rates and irrigation regimes in 2014 (a) and 2015 (b). Note: Bars show mean \pm standard error ($n=3$); W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC), respectively. N1, N2, and N3 represent 100, 200, and 300 kg N ha⁻¹, respectively. Different letters within the same stage and year indicate significant difference ($P < 0.05$)

the root-to-shoot ratio from the V6 to R6 stage. A remarkable positive correlation was observed among length, dry weight, surface area, and volume of root at the R1 and R6 stages and NUE ($r=0.728^*–0.781^*$). Moreover, a significant or highly significant negative correlation was observed between the root-to-shoot ratio at the later growth stages and NUE (Table 5).

4 Discussion

Does APRI technology improve plant root growth and resource use efficiency? Earlier studies have shown that APRI enhances root morphology traits and NUE (Kirda et al. 2005; Hu et al. 2009; Wang et al. 2017a, 2017b; Qi et al. 2020a). The enhanced root growth was attributed to the alternate wet and dry cycles, which resulted in compensatory root growth in the re-watered compartment after exposure to soil drying (Du et al. 2015; Qi et al. 2019). In the present study, W2 resulted in a lower soil water content and relatively higher root morphological values and NUE.

Table 4 Grain yield and nitrogen use efficiency (NUE) of maize for different nitrogen application rates and irrigation regimes in 2014 and 2015

Treatment	2014		2015	
	Grain yield (kg ha ⁻¹)	NUE (kg ka ⁻¹)	Grain yield (kg ha ⁻¹)	NUE (kg ka ⁻¹)
W1N1	2888 ± 123e	14.7 ± 0.8c	2960 ± 157e	14.1 ± 0.5c
W2N1	4579 ± 212c	19.0 ± 1.1b	4524 ± 248c	18.7 ± 1.0b
W3N1	4445 ± 176c	15.5 ± 0.7c	4554 ± 222c	15.8 ± 0.9c
W1N2	3837 ± 112d	20.6 ± 1.7b	4112 ± 169d	21.3 ± 1.1b
W2N2	5801 ± 224b	25.2 ± 1.5a	5949 ± 290b	25.8 ± 1.1a
W3N2	5615 ± 199b	21.6 ± 1.0b	5583 ± 287b	21.2 ± 0.8b
W1N3	4439 ± 136d	10.2 ± 0.5d	4320 ± 187d	10.6 ± 0.3d
W2N3	6178 ± 210b	15.8 ± 1.2c	6250 ± 323b	15.1 ± 0.9c
W3N3	6814 ± 200a	16.3 ± 1.1c	6969 ± 275a	16.2 ± 1.1c

Note: W1, W2, and W3 represent 45%, 65%, and 80% of field capacity (FC), respectively. N1, N2, and N3 represent 100, 200, and 300 kg N ha⁻¹, respectively. Values (means ± standard error, $n=3$) followed by different letters within each column and same year are significantly different at the probability level of 0.05

Table 5 Correlation coefficients of maize yield and nitrogen use efficiency (NUE) with root characteristics at the 6 collars (V6), silking (R1), and maturity (R6) stages

Root characteristics	Correlation coefficients between yield			Correlation coefficients between NUE		
	V6	R1	R6	V6	R1	R6
Root length	-0.621	0.822*	0.765*	0.489	0.728*	0.735*
Root dry weight	-0.576	0.875**	0.913**	0.353	0.735*	0.727*
Root surface area	-0.775*	0.812*	0.776*	0.454	0.747*	0.781*
Root volume	-0.673	0.828*	0.754*	0.534	0.776*	0.757*
Root-shoot ratio	-0.725*	-0.924**	-0.886**	-0.465	-0.768*	-0.834**

Note: The data were presented on average between the 2 years because they behaved the same. * and ** indicate significant differences at the 0.05 and 0.01 levels, respectively

Generally, moderate water deficit improves root water conductivity and efficiency by increasing root xylem number and stimulating lateral root growth and root surface area (Prince et al. 2017). Meanwhile, alternate wetting and moderate soil drying improve soil aeration, increasing the soil nitrogen availability, photosynthesis, antioxidant defense system, osmoregulation (Qi et al. 2021), and, subsequently, nitrogen accumulation (Wang et al. 2017b). The alternate soil wetting and drying cycles also promote pre-stored carbon remobilization from leaves to grains during maturity (Yang and Zhang 2010), leading to a high harvest index (Table S2) and improving NUE (Xu et al. 2019). Several studies have proven that the improvement of harvest index is an important contributor to high crop yield and resource-use efficiency in cereal crops (Yang and Zhang 2010; Wang et al. 2016). However, W1 inhibited root growth and NUE, probably because the severe water stress disturbed the carbon–nitrogen balance, induced root cell death, damaged leaf tissue, and reduced photosynthesis (Buckley et al. 2017; Kang et al. 2021). Similar results were found in maize under conventional deficit irrigation (Ran et al. 2016; Li et al. 2020). Meanwhile, Wang et al. (2014) showed that low soil nitrogen availability reduces root growth, consistent with the decreased root morphological parameters at the later growth

stages under N1. Low nitrogen supply inhibited plant ability to transport the assimilates to sinks (Yang et al. 2012), reducing the harvest index and partially accounting for low NUE. Moreover, high nitrogen supply limited root growth and extension in the deeper soil layer and increased water and nitrogen depletion, resulting in leaf rolling and lower NUE under water deficit conditions (Wang et al. 2018), possibly accounting for the inhibited root morphological parameters under the W1N3 and W2N3. These results suggest that too low irrigation limit (W1) and nitrogen application rate (N1), as well as unmatched supply of water and nitrogen (W1N3), have detrimental effects on root growth, resulting in low NUE under APRI; therefore, such strategies should be avoided in maize production.

Optimal supply of irrigation water and nitrogen fertilizer improves root growth, while an excessive or low supply inhibits root growth, subsequently affecting shoot growth and grain yield (Wang et al. 2014; Xu et al. 2018; Qi et al. 2019). In the present study, nitrogen application rates influenced root morphological traits varied with irrigation regimes, suggesting that a significant interaction effect of irrigation water and nitrogen fertilizer on the root growth of maize under APRI. For example, N3 further weakened the root growth under W1 rather than N1. Generally, too

low water disturbs the perception of roots, leading to root cell death (Kang et al. 2021). Studies have shown that water deficit reduces mass flow and inhibits nutrient release rate (Hu et al. 2009; Li et al. 2009), which reduces nitrogen utilization (Wang et al. 2017b) and inhibits root growth (Wang et al. 2014). Here, W1N3 resulted in the highest soil $\text{NO}_3\text{-N}$ content in the 0–40-cm soil layer (Fig. S2a,b), inhibiting root growth and extension in deep soil (Wang et al. 2018) due to prolonged dehydration of cell tissues (Sattelmacher et al., 1993). Moreover, under W1N3, the leaf area index was inhibited (Qi et al. 2020b), accounting for the reduced transfer of photoassimilates from aboveground parts to the root system (Xu et al. 2019). However, W3N3 resulted in the most excellent root values. Under optimal supply, plants extract sufficient water and nitrogen (Li et al. 2009), improving shoot (Zou et al. 2020; Qi et al. 2020b) and root (Wang et al. 2014) growth. In support, Ogawa et al. found (2005) that the supplemental nitrogen ameliorated the photosynthetic rate of maize by promoting photosynthetic enzyme activity, inhibiting abscisic acid production, and stimulating gibberellic acid and cytokinin synthesis under well-watered conditions. These observations together indicate that the nitrogen application rates should be upregulated with highly controlled irrigation limits (W3) to improve the root growth of maize under APRI.

In addition to the root morphology, the spatial distribution of the root system in the soil profile significantly affects the absorption of soil water and nutrients, thereby influencing crop productivity and resource-use efficiency (Xu et al. 2021). The architecture and distribution pattern of the root system has high plasticity and is regulated by changes in soil water, nutrients, and various other factors (Wang et al. 2014; Ju et al. 2015). In the present study, W1N1 led to the smallest RLD in the 0–40-cm soil layer due to the lowest supply of water and nitrogen (Kang et al. 2021), but with the highest proportion of root length in the 60–100-cm soil layer. This observation could be related to water deficit and/or nitrogen deficiency that reduce lateral root growth, enhancing the longitudinal growth to explore and utilize soil water and nutrients from the deeper soil layers (Wang et al. 2014). On the contrary, W3N3 led to relatively high RLD and a high proportion of root length in the 0–40-cm soil layer. In wheat, 75% of FC irrigation constantly retained high soil water content in the 0–60-cm soil layer, with the root system mainly distributed in the top 20 cm (Zhang et al. 2009). Here, W3 resulted in the greatest soil moisture content in the 0–40-cm soil layer, which contributed to root gathering. In contrast, a high supply of nitrogen fertilizer inhibits root extension to deep soil and improves root gathering around the rhizosphere soil (Trachsel et al. 2013; Mu et al. 2015). However, high root concentration in the surface makes water and nutrient uptake harder in plants under drought or nutrient deficiency (Mu et al. 2015; Zhang et al. 2009). Thus,

more roots in the deep soil layer favor water and nutrient uptake on a broader scale, improving resource-use efficiency as well as plant drought resistance (Mi et al. 2010; Wang et al. 2014). In addition, the maize root system is generally gathered in the topsoil layer (0–40 cm), which indicates that appropriate soil water and nitrogen availability in the top layer rather than in the deep layer (60–100 cm) helps maintain an extensive root system (Qi and Hu 2017). Thus, it is important to coordinate root growth and distribution by regulating irrigation water and nitrogen supply to improve resource-use efficiency and crop yield (Wang et al. 2014; Xu et al. 2018). Interestingly, W2N2 coordinated the percentage of total root length in each soil depth due to relatively optimal soil water and $\text{NO}_3\text{-N}$ content (Fig. S2a,b). Generally, the moderate soil water content in the 60–70-cm soil layer improves the root system in the deep soil (Jha et al. 2017; Wang et al. 2019). Moreover, W2N2 resulted in a greater RLD in the 60–100-cm soil layer due to the synergistic supply of irrigation water and nitrogen fertilizer (Qi et al. 2020b). In support, Xu et al. (2018) reported that alternate soil watering and moderate drying interact with reasonable nitrogen rate and enhance rice root growth in the deeper soil layers. Therefore, we argue that moderately controlled irrigation limit (W2) combined with a reasonable nitrogen rate (N2) stimulated the growth of deep roots and optimized the vertical distribution of the root system in maize under APRI.

Studies have shown the complementary and interaction effects of water and nitrogen on the root system of maize under conventional deficit irrigation (Li et al. 2009; Wang et al. 2018). Consistently, increasing application of nitrogen fertilizer rates cannot offset the detrimental effect of drought (W1 and W2) on root growth of maize under APRI. Xing et al. (2021) found that the increasing nitrogen dose aggravated the side effects of severe water deficit, decreasing biomass accumulation, carbon gain, and plant-level water-use efficiency. However, an earlier study illustrated that increasing the application rate of nitrogen fertilizers could balance the detrimental effects caused by conventional water deficit (Ran et al. 2016). These differences in effects among various studies may be due to the differences in tested crops, weather conditions, and irrigation methods (Li et al. 2009). Here, the root system experienced alternate soil drying and wetting under APRI, possibly aggravating the degree of water deficit caused by W1 and W2 compared with the conventional deficit irrigation (Sadras 2009). Indeed, the reason behind this is not apparent and demands further investigation.

Coordinating root and shoot growth is also vital for crop yield. High irrigation frequency and nitrogen application rates resulted in a lower root-to-shoot ratio in wheat under conventional uniform irrigation (Wang et al. 2014). In the present study, high controlled irrigation limit and nitrogen application rate promote the growth of shoots instead of roots, as evidenced by the smaller root-to-shoot ratios under

the W3N3. Roots are the major sink for assimilates, requiring twice as much photosynthesis to produce dry matter than shoots (Passioura 1983). This implies that crops with a lower root-to-shoot ratio can partition more carbohydrates to shoots (Xu et al. 2018; Ju et al. 2015) and enhance shoot growth. Consistent with this argument, W3N3 enhanced shoot biomass in maize (Table S2). However, although with a low root-to-shoot ratio, W1N3 had low shoot biomass and grain yield, probably due to the high nitrogen supply that significantly reduced plant growth rate, net photosynthetic rate, leaf area, and nitrogen uptake and accelerated leaf senescence under severe water deficit conditions (Qi et al. 2020b; Xing et al. 2021).

Dry weight, length, surface area, and activity of roots were found significantly and positively correlated with grain yield and NUE of maize under conventional uniform irrigation (Xu et al. 2018). Our study also found that root morphological parameters at the R1 and R6 stages are closely related to maize yield and NUE. This correlation could be related to the enhanced root growth at the later growth stages that improves leaf area index (Qi et al. 2020a), contributing to extended photosynthesis (Giunta et al. 2008), and thus establishing a solid foundation for high shoot biomass (Table S2). Meanwhile, the greater RLD and root biomass indicate a high supply requirement of nutrients and water for plant growth (Wang et al. 2016; Xu et al. 2018), improving the plant nitrogen status (Qi et al. 2020b), consistent with the enhanced nitrogen uptake in maize (Table S2). However, root morphological traits at the V6 stage negatively correlated with NUE, probably related to the enhanced root growth under low nitrogen supply. Under low soil nitrogen, plants respond in two different ways; roots grow towards fertilized soil, and the growth of lateral roots in the nitrogen-supplied area is enhanced (Mi et al. 2010). Meanwhile, a relatively higher proportion of assimilates is transferred to roots, improving root length and surface area to explore available nutrients for crop growth (Sattelmacher et al. 1993; Wang et al. 2014). Root growth is closely related to the assimilates obtained from aboveground parts (Ogawa et al. 2005). At the initial growth stage, vigorous root growth is achieved at the cost of less dry matter positioning to shoots (Tian et al. 2019). The reduced shoot growth leads to inadequate carbon supply for maintaining the growth of earlier developed nodal roots and elongation of later-developed nodal roots (Peng et al. 2012); this partially accounts for the reduced nitrogen accumulation under low nitrogen conditions (Table S2) and consequently a low NUE. Moreover, the root-to-shoot ratios were relatively low at the R1 and R6 stages under high NUE, consistent with Xu et al. (2018) findings in rice. These results suggest that more assimilates are supplied for shoot growth under an optimized combination of water and nitrogen, which was observed under W3N3 and W2N2 in the present study. In addition, compared to

W3N3, the treatment W2N2 results in the greatest root parameters and highest NUE and the second-greatest grain yield, with a reduction of irrigation water by 14.3–15.9% (Table S1) and nitrogen fertilizer by 33.3%. Thus, the study's findings suggest that moderate water deficit (W2) combined with a reasonable nitrogen rate (N2) maintains grain yield and improve NUE of maize under APRI by optimizing root growth and distribution.

5 Conclusions

Our study observed a significant interaction effect of irrigation water and nitrogen fertilizer on root growth and nitrogen-use efficiency under alternate partial root-zone irrigation. For maize, a high nitrogen application rate (300 kg N ha⁻¹) only improved root growth under well-watered conditions (80% of field capacity), suggesting that high nitrogen application rate is recommended under well-watered conditions. Moreover, nitrogen-use efficiency was closely related to root morphological parameters (length, dry weight, diameter, surface area, and volume) but negatively with the root-to-shoot ratio at the filling and maturity stages. Moderate water deficit (65% of field capacity) coupled with a reasonable nitrogen rate (200 kg N ha⁻¹) regulated the root-to-shoot ratio, enhanced root growth, and optimized root vertical distribution by regulating soil water and nitrogen availability; therefore, the plants achieved a high nitrogen-use efficiency. The study thus presents useful physiological evidences that support appropriate coupling of water and nitrogen supply (65% of field capacity interact with 200 kg N ha⁻¹) to improve the resource-use efficiency of maize under alternate partial root-zone irrigation.

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Declarations

Conflict of Interest The authors declare no competing interests.

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