INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
19–0917/2020/24–2–201–206
DOI: 10.17957/IJAB/15.1425
http://www.fspublishers.org

*Full Length Article*

# Responses of Root Growth and Morphological Characteristics of Sweet Potato Plants to Varying Nitrogen Levels under Drought

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*Received 30 May 2019; Accepted 02 December 2019; Published 31 May 2020*

## Abstract

A split-root culture pot experiment, using discrete left and right compartments, was conducted in order to investigate the effects of three different nitrogen (N) combinations on fibrous root expansion and tuberous root differentiation under two levels of soil moisture in sweet potatoes. Under these two moisture conditions, sweet potato root biomass and root morphology were higher in the $N_{50}$ compartment than corresponding $N_0$ compartment in the $N_0/N_{50}$ treatment. Under normal moisture conditions, the root morphological traits in the $N_{150}$ compartment were higher than in the $N_0$ compartment; under drought stress, the $N_{150}$ compartment significantly decreased compared with the corresponding $N_0$ compartment. The $N_{50}$ and $N_{150}$ compartment root morphological characteristics showed no significant differences under normal moisture conditions. Under drought stress, however, in the $N_{150}$ compartment, root morphological characteristics decreased compared to in the $N_{50}$ compartment. The redundancy analysis (RDA) showed that $N_{50}$ was the ideal amount of N in both normal moisture and drought conditions while the excessive application of N ($N_{150}$) improved drought stress. The morphological properties of sweet potato roots were significantly affected by various soil moisture levels and local N availability, suggesting that the existence of suitable local N was necessary for root development under different water conditions. This information can be used to further optimize N fertilizer management strategies, allowing agricultural workers to increase crop yields, mitigate drought stress, and improve plant health by helping to ensure the availability of N under different soil moisture conditions.

**Keywords:** Sweet potato; Root Morphology; Soil moisture content; Nitrogen combination

## Introduction

Sweet potatoes are an essential food crop in many developing countries, and may hold potential for creating and maintaining food security in the future (Ma *et al.* 2012; Khan *et al.* 2016). The yield, stability, and improvement of sweet potatoes and other crops are essential for plant cultivators and breeders (Mukhopadhyay *et al.* 2011). Soil moisture content and N are the main limiting factors for the growth of sweet potato roots, and essential for growth (Marschner *et al.* 1996; Khan *et al.* 2016). Under drought conditions, sweet potato plants undergo changes in root morphology and physiological metabolism which help to adapt environmental stresses (Liu and Cheng 2011). The response mechanism of plant roots to N under different soil moisture conditions is a topic which has raised widespread concern among the agricultural, ecological, and environmental fields (Villordon *et al.* 2014).

The current understanding of the morphological characteristics of sweet potato roots is based on the explicit deployment of root axes to determine the spatial configuration of the root system, which exhibits great plasticity in response to external environmental conditions such as nutrient availability and soil moisture content (Lynch 1995; Bao *et al.* 2014). Recent studies have shown that the spatial and temporal fluctuations of N concentrations and morphology in soil environment, known as local N regimes, trigger a systemic signal that regulates plant root growth and development (Xu *et al.* 2012). It is apparent that localized N supply is critical for sweet potato root development (Lima *et al.* 2010); in ideal N conditions, the metabolic activity of the nitrogen-donating root system is increased, as is the distribution of the assimilate to the N-donating root system (Granato and Jr 1989).

Under drought conditions, the root morphology of sweet potatoes adapts in order to resist environmental stress (He and Dijkstra 2014). Sweet potatoes have been identified as a moderately drought tolerant crop; however, very sensitive to water deficit in the initial growth stage of storage roots (Mukhopadhyay *et al.* 2011; Villordon *et al.* 2012). Previous studies have shown that N can improve the drought resistance of crops, and regulating N levels may help reduce the impact of drought stress (Guo *et al.* 2003); it has also been acknowledged that root morphology is closely

**To cite this paper:** Zhang S, D Xiang, H Li, Q Liu (2020). Responses of root growth and morphological characteristics of sweet potato plants to varying nitrogen levels under drought. *Intl J Agric Biol* 24:201-206

related to the efficient absorption of water and nutrients (Wright and Wright 2004). The root system can activate complex regulatory networks to cope with fluctuations in the rhizosphere soil environment, thereby promoting the efficient uptake and utilization of water and nutrients (Xuan *et al.* 2017). A sound understanding of the possible relationship between the local N supply and the plant's ability to thrive in various moisture conditions is essential, as this knowledge can contribute to the development and testing of management practices that improve nutrient and water use efficiency and promote root development (Wang *et al.* 2013).

The objective of present study was to investigate the effect of variability in local N availability measured by the root development of sweet potatoes under different water conditions, examining the effects of drought and N availability on the morphological characteristics of roots. This information will provide further insight into the external environmental stimuli of plant roots, such as soil moisture variability and nutrient availability, which can promote or hinder root formation.

## Materials and Methods

### Biological materials and soil

The sweet potato genotype Yanshu 25, mainly grown in northern China, was used as an experimental plant. Soil was collected from the top 20 cm of the soil profile at Jiaozhou Experimental Station, Qingdao Agricultural University (36.3°N, 120.3°E) in Shandong Province. The sampled soil was air dried and passed through a 2.0 mm sieve. The tested soil had the following characteristics with total N 0.3 $mg{\cdot}kg^{-1}$, available P (Olsen-P) 6.64 $mg{\cdot}kg^{-1}$, available K ($NH_4OAc$-K) 32.4 $mg{\cdot}kg^{-1}$, organic C 10.1 $mg{\cdot}kg^{-1}$, and pH of 7.24. After drying at room temperature, the test substrate was prepared by mixing soil and river sand in a ratio of 1:1 (v/v). The nutrient solution was added once as a base fertilizer to ensure the normal growth of the test plants.

### Culture device and experimental design

A modified two-compartment culture system was constructed (Villordon *et al.* 2013). A 35 cm high PVC pipe with a diameter of 12 cm was cut vertically into two equal parts with the same height and width. The pipe was divided by a 3 mm thick acrylic strip, separating it into a left root compartment and a right root compartment. The acrylic strip was secured with PVC glue to minimize the lateral movement of water. A notch at the top end of the acrylic strip allowed a sweet potato cutting to be set such that the vine on either side of the basal leaf gap or node were directed toward separate compartments.

A completely randomized design with a 2×3 factorial arrangement of treatments was used. The factors were soil moisture contents and N combinations in left and right compartments. The experiment established two conditions: normal (75–80% of field capacity) and drought (45–50% of field capacity). Three different N combinations were also tested in the left and right compartments; 0 and 50 $mg{\cdot}kg^{-1}$; 0 and 150 $mg{\cdot}kg^{-1}$; 50 and 150 $mg{\cdot}kg^{-1}$. Therefore, the following six treatments were tested: $N_0/N_{50}$ under normal soil moisture; $N_0/N_{150}$ under normal soil moisture; $N_{50}/N_{150}$ under normal soil moisture; $N_0/N_{50}$ under drought condition; $N_0/N_{150}$ under drought condition and $N_{50}/N_{150}$ under drought condition. This process was repeated four times for each experiment. The pot study was carried out during the pre-growing season of sweet potato from March to May in a greenhouse at Qingdao Agricultural University, with 14 hours of light and 10 hours of darkness comprising each 24-h photoperiod, day/night temperatures of 25°C/16°C, and 60% relative humidity.

### Sampling and analysis

During the first two weeks of our experiment, normal moisture conditions were maintained and soil moisture was maintained at 75 ± 5 % of field capacity and drought (soil moisture maintained at 45 ± 5 % of field capacity) conditions for the next three weeks. The plants were harvested after a total growth period of five weeks.

At harvest, the roots were floated on a waterproof tray and scanned using a dedicated Epson v700 scanner. The image acquisition parameters and the analysis accuracy were both set to "High", using the WinRHIZO (Version 2009) software for image acquisition and analysis.

### Data analysis

Analysis of variance was carried out using the S.P.S.S. software, version 19.0. Duncan's multiple range or Fisher's LSD was used to show significant differences between treatment means at $P < 5\%$. Relationships between treatments were tested by Pearson's correlation analyses. The redundancy analysis (RDA) used the Canoco version 4.5 software package. Significance of the first and of all ordinations axes was calculated by the Monte Carlo permutation test.

## Results

Root biomass (RB) was significantly affected by N combinations in both compartments under both soil moisture contents ($P < 0.05$) (Fig. 1). Under both moisture conditions, the dry weight of RB in the $N_0/N_{50}$ treatment was higher in the $N_{50}$ compartment than in $N_0$ compartment, and the increase between left and right compartments ($N_0/N_{50}$) under normal conditions was twice that of drought conditions. However, the RB in the $N_0/N_{150}$ treatment showed the complete opposite effect under both water conditions: the RB in the $N_{150}$ compartment was significant higher than in the $N_0$ compartment under normal moisture conditions, while $N_{150}$

compartment decreased RB compared to the $N_0$ compartment under drought stress. The RB showed no significant differences between $N_{50}$ and $N_{150}$ compartments under normal moisture conditions. However, the plants in the $N_{150}$ compartment decreased RB by half compared to those in the $N_{50}$ compartment under drought stress.

The root length (RL), root surface area (RSA), and root tip numbers (RTN) of sweet potato roots determine nutrient and water absorption efficiency. Under normal moisture conditions, RL and RSA in the $N_{50}$ or $N_{150}$ compartment were all significantly higher than in the corresponding $N_0$ compartment (Table 1). Drought stress decreased the RL and RSA of all N combinations. The RL and RSA of the plants in the $N_0/N_{150}$ compartment showed the opposite trend under both moisture conditions. In the $N_{50}/N_{150}$ treatment, the RL and RSA showed no significant differences from each other, while under drought stress, the RL and RSA in the $N_{150}$ compartment showed a significant decrease compared to the $N_{50}$ compartment.

The root average diameter (RAD) and root volume (RV) were used to characterize root differentiation. The effects of different N concentrations in left and right compartments on root differentiation differed significantly under both soil moisture conditions (Fig. 2A and B). Under normal moisture conditions, RV in right compartments ($N_{50}$ or $N_{150}$) were significant higher than in left compartment ($N_0$). In the $N_{50}/N_{150}$ treatment, $N_{50}$ compartment increased RV compared to the $N_{150}$ compartment. Under drought stress, RV in the $N_{50}$ compartment was significantly higher than in other compartments ($N_0$ or $N_{150}$). However, root morphological characteristics in the compartment with $N_{150}$ showed reduced RV compared with the $N_0$ compartment.

Based on the classification criteria of (Noh *et al.* 2013) sweet potatoes, their roots can be divided into the following categories: fibrous, secondary, and tuberous roots. Under normal moisture, total fibrous and tuberous root volume in the $N_{150}$ compartment was significant higher than that in $N_0$ compartment (Table 2). Under drought stress, total fibrous and tuberous RV in the $N_0/N_{150}$ treatment showed the complete opposite trend. There were no differences in total fibrous RV between the $N_{50}$ compartment and $N_{150}$ compartments. Under drought stress, total fibrous RV in the $N_{150}$ compartment was significant lower than in other compartments ($N_0$ or $N_{50}$).

RDA analysis was performed to calculate the contribution of factors of local N supply and the correlation between various explanatory variables under different moisture conditions. The cosine of the angle between the explanatory variables in the RDA analysis graph indicated the correlation. Under normal moisture conditions, the explanatory variables were mostly concentrated between $N_{50}$ and $N_{150}$ treatments, indicating that appropriate level of N fertilizer can induce root development and promote root differentiation and enlargement (Fig. 4A). However, with the variation of the soil moisture, the explanatory variables also changed. Under drought conditions, the explanatory variables were mostly concentrated around the $N_{50}$ treatment, indicating it as most suitable amount. While $N_{50}$ seemed to alleviate drought stress, the excessive application of N ($N_{150}$) appeared to increase drought stress. RDA analysis showed a significant positive correlation between $N_{50}$ and root growth and differentiation, but there was a significant negative correlation with $N_0$ and $N_{150}$ treatments (Fig. 4B).

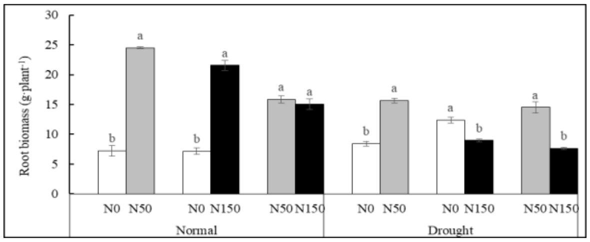

**Fig. 1:** Some statistical descriptive data of root biomass of sweet potato plants in two-compartment culture system. Paired t test was performed to determine if roots in each compartment varied in lateral root biomass

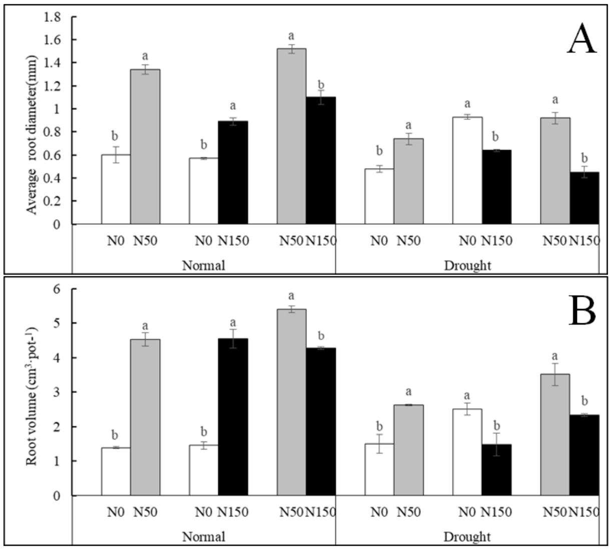

**Fig. 2:** Adventitious root average diameter and root of the total volume in sweet potato as influenced in two-compartment culture system under two moisture conditions

## Discussion

The spatial fluctuations of N concentrations (local N supply) are critical for sweet potato root signal transduction, growth and development (Zhang and Forde 1998; Lima *et al.* 2010; Xu *et al.* 2012). The root phenotype is based on the response of the root system to the local supply of nutrients, or the competitive response to local changes in nutrients (Zhang *et al.* 2007). In the present study, different N supplies in each compartment could significantly affect the root development of sweet potatoes; when the N concentrations on both sides were different, the plants in

**Table 1:** Effects of different nitrogen rates on root morphological characteristic of sweet potatoes under different moisture conditions

| Moisture treatment | Local nitrogen supply treatment combination | | Length of lateral root (cm·pot$^{-1}$) | | Root surface area (cm$^2$·pot$^{-1}$) | | Tips (numbers) | |
|---|---|---|---|---|---|---|---|---|
| Normal | $N_0$ | $N_{50}$ | 853.04 b | 2098.47 a | 123.13 b | 340.66 a | 1461.03b | 2475.33a |
| | $N_0$ | $N_{150}$ | 1094.65 b | 2465.38 a | 146.73b | 374.23a | 1861.11 b | 3400.66 a |
| | $N_{50}$ | $N_{150}$ | 2048.49 a | 2249.06 a | 345.57 a | 348.59 a | 3381.67 a | 2972.33 a |
| Drought | $N_0$ | $N_{50}$ | 1073.65b | 1559.37 a | 153.05b | 248.97a | 1850.55 a | 1747.66 a |
| | $N_0$ | $N_{150}$ | 1359.59a | 919.60 b | 177.09 a | 123.6b | 1916.44 a | 1438.33b |
| | $N_{50}$ | $N_{150}$ | 1603.26 a | 1222.16 b | 264.41 a | 159.38b | 2291.33 a | 1804.00 b |

**Table 2:** Effect of nitrogen supply roots on root diameter and distribution of sweet potato roots under different moisture conditions

| Moisture treatment | Local supply treatment | V ≤ 1.50 mm | 1.50 < V ≤ 3.00 mm | 3.00 < V ≤ 4.50 mm | V > 4.50 mm |
|---|---|---|---|---|---|
| Normal | $N_0$ | 0.98b | 0.48b | 0.48b | 0.54b |
| | $N_{50}$ | 3.32a | 1.11a | 0.65a | 4.04a |
| | $N_0$ | 1.23b | 0.39b | 0.44a | 0.67b |
| | $N_{150}$ | 3.68a | 1.27a | 0.40a | 1.04a |
| | $N_{50}$ | 2.78a | 1.27a | 0.50a | 3.40a |
| | $N_{150}$ | 2.96a | 1.06ab | 0.42a | 0.20b |
| Drought | $N_0$ | 1.39b | 0.32b | 0.25a | 0.85b |
| | $N_{50}$ | 2.38a | 1.04a | 0.40a | 1.81a |
| | $N_0$ | 1.89a | 0.72a | 0.74a | 1.34a |
| | $N_{150}$ | 1.06b | 0.63a | 0.54a | 0.65b |
| | $N_{50}$ | 2.69a | 1.45a | 0.73a | 1.83a |
| | $N_{150}$ | 1.48b | 0.46b | 0.42ab | 0.02b |

each compartment showed different levels of N competition. Our studies suggested a competitive advantage relative to the compartment with local N supply of ($N_{50}$), compared to the compartments with absent N or very high N, in terms of access to nutrients and soil moisture. Those were similar to earlier work (Kim *et al.* 2002; Villordon *et al.* 2012) which provided evidence that within a certain range of N application, the total volume of roots in the early stage of sweet potato development increased with the increase of N application rate; however, the total amount of root differentiation gradually decreased.

The ability of plant roots to proliferate preferentially in nutrient-rich soil has been well documented in the literature (Zhang *et al.* 2007). N deficiency triggers a “foraging” response, wherein the roots continue to deepen as though they were seeking N deeper in the soil. Meanwhile, N saturation signals the roots to enrich in the soil surface (Okamoto *et al.* 2013; Tabata *et al.* 2014). Previous studies on wheat roots showed that the increase in water infiltration depth caused by high N application directly affected the growth and distribution of crop roots. When the N application rate is high, the roots of the crops are mainly distributed in the upper soil to absorb the surface moisture. When N levels are low, the crop roots expand to the lower layers of soil and increase the absorption of the deeper soil moisture (Wang *et al.* 2001). The present study results showed that the root morphology of plants with access to a suitable N supply shows uniform dispersal growth, while in the case of N deficiency or N excess, the root morphology shows a pronounced pattern of "long and thin" roots or "short and fat" roots, respectively, under normal water conditions (Fig. 3 A). Water and nutrients are not only the main stress factors affecting dryland agricultural production, but also a pair of factors which are complementary and interactive. Soil moisture affects the transformation and availability of nutrients in soil; in turn, these nutrients also affect the ability of plants to uptake water efficiently and can mitigate or exacerbate drought stress (Huang *et al.* 2002).

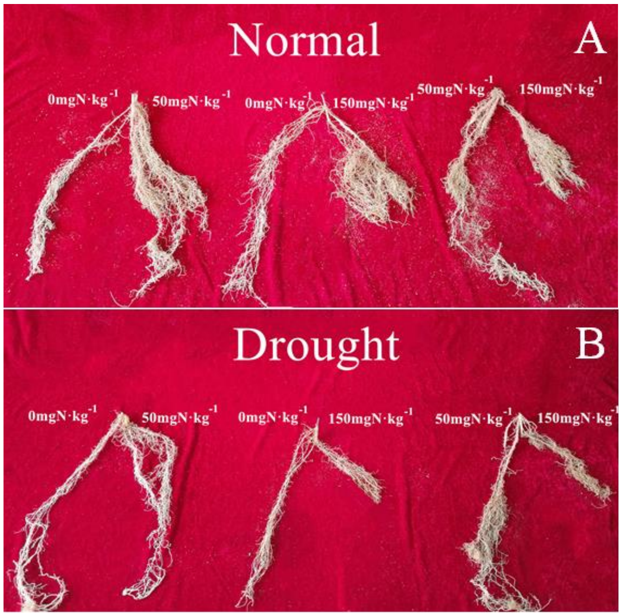

**Fig. 3:** Representative adventitious root samples under normal and drought conditions from two-compartment culture system. The adventitious roots that were still attached to the plant were placed on red cloth to facilitate image capture

Sweet potatos are more drought-tolerant than other crops, but their rooting, branching, and tuber stages are relatively sensitive to moisture conditions (Zhang *et al.* 1999). Adequate root growth after transplanting requires

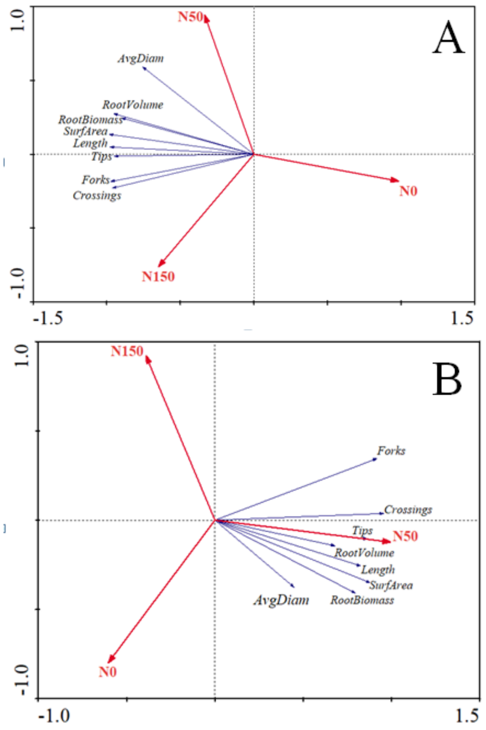

**Fig. 4:** Independent and interactive action of growth substrate moisture and nitrogen rate (N) on the properties of the root morphological characteristics in ordination diagrams from redundancy analysis (RDA). Under normal moisture conditions, the coordinate from the first ordination axes explained 66.5% of the variance. The significance (according to Monte Carlo permutation tests) of all canonical axes was $p = 0.024$, indicating that the presence of $N_{50}$ and $N_{150}$ had a significant influence on the sweet potato root morphological characteristics. Under drought conditions, the coordinate from the first ordination axes explained 45.5% of the variance. The significance (according to Monte Carlo permutation tests) of all canonical axes was $P$=0.044, indicating that the presence of $N_{50}$ had a significant influence on the sweet potato root morphological characteristics. $N_0$=without nitrogen supply; $N_{50}$=50mg·N kg$^{-1}$; $N_{150}$= 150 mg·N kg$^{-1}$

adequate water supply (Belehu and Hammes 2004). Drought stress will adversely affect adventitious root differentiation of sweet potatoes and hinder the formation of tuber roots, ultimately resulting in the reduction of the number of tuber roots (Villordon *et al.* 2012). The present study showed that the growth and differentiation of the corresponding root system of $N_0$ and $N_{50}$ were not significantly reduced under drought stress, while the root biomass in the $N_{150}$ compartment was significantly decreased (Fig. 3B). Our results were similar to previous researches on wheat (Liang and Chen 1996; Zhang and Zhang 2001), which provided evidence that under drought conditions, excessive application of N fertilizer would lead to a significant decrease in root volume and biomass. Li and Shao (2000) also reported that under water stress, excessive application of N fertilizer to wheat led a significant increase in the rate of root cell membrane damage, deterioration of the root water environment, decreased water retention capacity, and reduced drought resistance. Possible reasons were that excessive N application promotes the increase of root biomass in the surface layer of soil, which has little significance for actual drought resistance as it does not provide sufficient water storage capacity, and the lack of deep roots leaves plants unable to draw moisture from deeper levels of soil when there is little water accessible at the surface (Jackson *et al.* 2008). Nitrogen supply significantly increases root moisture content and enhances roots' ability to absorb and retain water (Passioura 1983). Appropriate amounts of N can increase the total root weight in deep soil, thereby enhancing the water absorption capacity of the roots, decreasing the cell membrane damage rate, and improving the ability to resist dehydration and maintain turgor pressure. Recent studies have shown that in order to reduce the effects of drought stress on N uptake after plant roots sense drought signals, plants activate specific signals to promote N uptake (He and Dijkstra 2014). In particular, drought stress caused mutations in certain proteins, which reduced plants' N absorption but enhanced drought resistance (Guo *et al.* 2003; Castaings *et al.* 2009; Marchive *et al.* 2013), indicates that plants can adjust their N-collecting activity under drought stress to maintain survival. Rational application of N fertilizer can meet plants' needs for soil nutrients, promote the growth and development of sweet potatoes, and increase biomass and yield. It can also improve the physiological functions of sweet potatoes, as well as reducing the adverse effects of drought stress. However, these outcomes are greatly affected by the amount of N fertilizer applied. With the increase of the amount of N fertilizer applied, the beneficial effects of N gradually weaken.

## Conclusion

The present study investigated the effects of three different N combinations on root morphological traits under two levels of moisture in sweet potatoes. Results of the present study demonstrated that variation in N rate and local availability profoundly affect root architecture development in sweet potatoes. The appropriate N application rate ($N_{50}$) can both promote the development of roots and induce roots to differentiate into storage roots in normal or drought condition. However, excessive application of N fertilizer ($N_{150}$) might aggravate drought stress, the amount of N fertilizer should be appropriately reduced under drought conditions. The results of this research can guide the revision or enhancement of current management practices.

## Acknowledgments

This research was funded by the China Agriculture

Research System (No. CARS-10-B10). We are grateful to Prof. Qing Chen for valuable comments on an earlier version of this manuscript. We are also thankful for the constructive comments received from anonymous reviewers and the editors.

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