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RESEARCH

Nitrogen application improved peanut yield and nitrogen use efficiency by optimizing root morphology and distribution under drought stress

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ABSTRACT

Drought stress and nutrient deficiency are two main factors that restrict the growth and yield of peanut (*Arachis hypogaea* L.) in arid and semi-arid regions. However, the effects of N fertilizer on root growth and pod yield of peanut under different water conditions are unclear. The growth, root morphology, and pod yield of peanut were studied under different water and N combinations. Two soil water treatments were tested: Well-watered (WW, 80%-85% field capacity) and drought stress conditions (DS, 55%-60% field capacity). Three N treatments were tested: no N application (NN), moderate N (MN, 90 kg ha^{-1}), and high N (HN, 180 kg ha^{-1}). Results showed that pod yield of peanut was limited by drought and N deficiency. Compared with NN, peanut shoot DM and pod yield were improved by MN under DS, with an average increase range of pod yield of 16.2% in the 2 yr. The annual average root length density (RLD) in the deeper soil layer (40-100 cm) was 5.5% higher under DS-MN than DS-NN treatment. The N use efficiency (NUE) was 12.3% higher under WW than DS treatment, and the NUE of MN was significantly higher than that of HN under different water treatments. Root lengths in 40-60 and 60-80 cm soil layers were also positively correlated with pod yield (r = 0.66** and 0.47**, respectively) and NUE (r = 0.60* and 0.85**, respectively). In this study, root growth in deeper soil was improved by MN application under DS, thus increasing yield and NUE of DS conditions.

Key words: Drought stress, nitrogen use efficiency, peanut, root architecture, water-nitrogen interaction.

INTRODUCTION

Peanut (*Arachis hypogaea* L.) is one of the most important oil crop and food legumes in the world, and is grown in many arid and semi-arid regions. Soil water deficit and nutrient deficiency are two main factors that restrict peanut growth, development, and yield in arid and semi-arid areas. Nitrogen is a macroelement for crop growth and it is often deficient in dryland soil (Lindquist et al., 2010). The duration and severity of drought is becoming more severe in many regions of the world (Mackay, 2008). The increase in arid land areas is posing a serious threat to crop production (Daryanto et al., 2015).

Drought can occur at any growth stage and it has a serious impact on plant growth, development, metabolism, economic yield, and seed quality (de Lima Pereira et al., 2016; Ye et al., 2018). The reduction in yield caused by drought stress varies greatly depending on drought time, intensity, and duration (Hamidou et al., 2012). Recent studies have shown that morphological characteristics such as leaf rolling, root morphology, root/shoot ratio (R:S), and internode length are associated with drought tolerance (Desclaux et al., 2000; Fry et al., 2018). The quantity, shape, distribution and physiological status of plant root system directly affects its capacity for uptake and utilization of water and nutrients. Many studies have shown that root size, root length distribution (RLD), root distribution in deep soil, and root surface area are related to drought resistance in peanut (Junjittakarn et al., 2014; Ding et al., 2017; Thangthong et al., 2018). In addition to the effect of water on plant growth and development, N availability also affects plant root development and water uptake (Kong et al., 2017; Song et al., 2019). Generally, N application can promote root growth and improve root activity under drought conditions (Xu et al., 2018). The ability to absorb water and N can be improved by root development, thus enhancing the resistance of plants to abiotic stress (Abid et al., 2016). However, N may play different roles under different soil moisture conditions. Clay et al. (2001) showed that N application had positive and negative effects on wheat growth under sufficient water and severe drought conditions, respectively, but had nonsignificant effect under mild drought conditions.

The sensitivity of peanut to water availability differs according to growth stage. The response of flowering and pod filling stages to water stress is more sensitive than that of early vegetative and late mature stages (Zhang et al., 2013). Over 60% of root growth occurs during flowering stage, and drought stress significantly reduces root growth (Koolachart et al., 2013). Much research has investigated the effect of water and N availability on peanut plant growth, physiological characteristics, and yield formation (Basal and Szabó, 2020; Xia et al., 2021), but it is unclear how the interaction between water and N management affects peanut root growth and morphology. The relationships between root traits and pod yield and NUE also remain unclear. In this study, peanut plants were grown in soil column experiments and drought stress was applied at the flowering stage. The objectives of this study were to evaluate the impact of water and N management regimes on root morphological traits, pod yield, and NUE and determine the relationship between root traits, pod yield, and NUE.

MATERIALS AND METHODS

Experimental design

The experiments were conducted over 2 yr (May-September 2014 and repeated May-September 2015) at Shandong Peanut Research Institute, Qingdao (36°48′47″ N, 120°30′17″ E), China. Plants of peanut (*Arachis hypogaea* L.) 'Huayu 25' were grown in PVC (polyvinyl chloride) columns (40 cm in diameter, 110 cm in height), which were protected from rainfall by a mobile shelter. 'Huayu 25' was drought resistant genotype with 100 kernel weight of 98 g and the kernel to pod rate was 73.5%. The experiment was laid out in a randomized complete block design with two water regimes and three N levels. The two water treatments were: Well-watered (WW) treatment at 80%-85% field capacity (FC) and drought stress (DS) treatment at 55%-60% FC (Tojo Soler et al., 2013; Ding et al., 2017). The N was applied at three levels: No N (NN), moderate N (MN, 90 kg ha^{-1}), and high N (HN, 180 kg ha^{-1}). Each treatment had 12 peanut plants in six columns, in which three columns for root observation and another three columns for pod yield determination. The soil type was sandy soil which is suitable for peanut growth. Soil volumetric water content was 17.6% and 18.1% at field capacity in years 2014 and 2015, respectively. The soil nutrient status is shown in Table 1. The soil was screened by air drying and sieving before filling into PVC columns. Each column was filled with 110 kg sandy soil. In addition to N supply, 71 kg ha^{-1} P_2O_5 and 156 kg ha^{-1} K_2O were applied. The N was applied as urea. Phosphorus and K were applied as calcium superphosphate and potassium sulfate, respectively. All fertilizers were applied and mixed into the 0-20 cm soil layer in powdered forms prior to planting. ^{15}N isotopic dilution technique is an effective way to investigate N uptake form fertilizer (Wang et al., 2016). As to determine the fertilizer N uptake by peanut, the urea labeled with ^{15}N (Urea-$^{15}N_2$, abundance of 10.19%, Shanghai Chemical Research Institute, Shanghai, China) were used in 2015.

The experiment was conducted with 80%-85% FC from sowing to seedling emergence. Four seeds were sown in each PVC column, and two peanut plants were retained in each column at 10 d after sowing (DAS) in both years. Columns were randomly separated into two experimental groups: WW and DS treatments at the beginning of the flowering growth stage (R1, 35 DAS) (Boote, 1982). The soil moisture for DS treatment was allowed to gradually decline until it reached 60% FC in 0-60 cm soil layers at 45 DAS; the soil moisture was maintained at no more than 5% of desired level until 55 DAS, when re-watering was applied to the peanut at 80%-85% FC moisture level until harvest.

Table 1. Status of major nutrients, organic matter content, and pH of soil at the experimental site in 2014 (season 1) and 2015 (season 2).

Year	Organic matter	Total N	Available P	Available K	pH
	g kg^{-1}		mg kg^{-1}		
2014	15.8	1.7	45.2	128.3	6.5
2015	17.6	1.8	46.4	114.6	6.4

Soil moisture and water data collection

Soil water moisture in each column was measured at 5 d intervals at depths of 0-20, 20-40, 40-60, 60-80, and 80-100 cm using the TDR TRIME-tube system (IMKO GmbH, Ettlingen, Germany). Soil moisture was measured to calculate the sum of soil water content of each sample layer in each column as described by Zhang et al. (2017).

Root sampling

Root samples were collected after drought stress (at 55 DAS). After harvesting the shoot, the soil column was divided into five 20 cm layers. The root samples were separated from the soil layer and then washed with tap water. The cleaned roots were measured using a scanner. The WINRHIZO Pro2004a software (Regent Instruments, Quebec, Canada) was used to determine root length, root surface area, and root volume. The root length distribution (RLD) was calculated as the ratio of root length (cm) to soil volume (cm^3). The RLDs in upper (0-40 cm) and deeper (40-100 cm) layers (Songsri et al., 2008) were also calculated.

Shoot DM, root DM and pod yield

The shoot and root DM were obtained at 55 DAS. Fresh shoots and roots were oven-dried at 75 °C for at least 48 h; then, DM was determined. The shoot DM was the sum of stem DM and leaf DM. For each column, pod yield was obtained from plants at the final harvest. Pods were air-dried to approximately 8% moisture and pod dry weight was determined.

Plant N uptake and calculation

The samples (shoots, roots, and pods) of peanut were ground to a fine powder and then the total N content and ^{15}N enrichment in the plant were determined. The ^{15}N abundance was determined using an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Bremen, Germany) and the N concentration determined using an automatic Kjeldahl apparatus (K1100F, Haineng, Shandong, China). Calculation of N accumulation and N use efficiency (NUE) followed the methods of Wang et al. (2016):

$$\text{N accumulation} = \text{DM} \times \text{N concentration} \quad (1)$$

$$\text{Ndff (N derived from fertilizer)} = {}^{15}\text{N abundance of peanut}/{}^{15}\text{N abundance of labeled fertilizer} \times 100\% \quad (2)$$

$$^{15}\text{N fertilizer N accumulation} = \text{N accumulation} \times \text{Ndff} \quad (3)$$

$$\text{NUE} = {}^{15}\text{N accumulation amount of peanut}/{}^{15}\text{N amount of labeled fertilizer} \times 100\% \quad (4)$$

Statistical analysis

According to a randomized block design, the ANOVA was performed in SPSS 19.0 software (IBM, Armonk, New York, USA). Multiple comparisons were made using Duncan's multiple range test at a 5% probability level. Correlation was used to determine the relationship between root traits, pod yield, and NUE.

RESULTS

Dry biomass and R:S ratio

The effects of water and N on shoot DM and root DM were significant. The N application rate had a significant effect on R:S ratio. In addition, there were significant interactive effects between water and N application on shoot and root DM (Table 2). The DS treatment significantly decreased shoot and root DM of peanut compared with WW. The shoot DM first increased and then decreased with the increase of N application under DS treatment. The shoot DM of MN significantly increased by 13.3% (2014) and 10.7% (2015) compared to that of NN. The MN markedly decreased root DM and R:S ratio compared to NN.

Root morphological traits

Water and N had significant effects on root length and root surface area. Under different N application rates, root length, root surface area, and root volume of WW were significantly improved compared with that of DS treatment (Table 3). The root length, root surface area, and root volume were increased with increasing N application under WW treatment, while the peanut root morphological traits showed opposite trends under DS treatment. Under DS treatment, the morphological characters of roots significantly decreased with the increase of N application. On average over the 2 yr, root length, root surface area, and root volume were 2.4%, 3.2%, and 16.3% lower, respectively, for MN than NN under DS. The lower levels for HN were 9.7%, 8.2%, and 18.3%, respectively. There were significant interactions of water and N application on all root traits.

Spatial distribution of RLD

The RLD in the 0-20 cm soil layer was the largest among the five soil layers for both water treatments (Figure 1). Water had significant effects on RLD in each soil layer except for 80-100 cm. The RLD decreased with increased soil depth for WW treatment. Compared with NN, MN and HN increased the RLD in the five soil layers under WW treatment. The RLDs of MN and HN in the upper soil layer (0-40 cm) were improved by 8.2% and 11.7% (2014), and 12.2% and 20.6% (2015) compared to that of NN, respectively. Meanwhile, the RLD of MN and HN in the deeper soil layer (40-100 cm) was improved by 16.0% and 25.0% (2014), and 4.3% and 12.7% (2015) compared to that of NN, respectively. The RLD in the upper soil layer decreased with increased N application under DS treatment. The RLD of MN in 40-60 and 60-80 cm soil layers was 25.1% and 8.9% higher than that of NN in 2015, respectively. The RLD in 80-100 cm soil layer was 11.2% and 1.9% higher than that of NN in 2014 and 2015, respectively. Moreover, soil water conditions and N levels showed significant interactive effects on RLD in each soil layer.

Table 2. Effects of water level and N rate on shoot dry mass, root dry mass and root/shoot ratio of peanut in 2014 and 2015.

		Shoot dry mass		Root dry mass		Root/shoot ratio	
Water level	N rate	2014	2015	2014	2015	2014	2015
		g plant^{-1}		g plant^{-1}			
WW	NN	10.73b	13.05c	1.79a	2.2a	0.17a	0.17b
	MN	11.60a	15.42a	1.56b	1.92bc	0.13c	0.12d
	HN	10.48b	13.96b	1.72a	2.06ab	0.16ab	0.15c
	Mean	10.94A	14.15A	1.69A	2.06A	0.16A	0.15A
DS	NN	8.06e	9.23e	1.45c	1.77c	0.18a	0.19a
	MN	9.13c	10.21d	1.31d	1.41d	0.14bc	0.14cd
	HN	8.71d	8.76e	1.39cd	1.28d	0.16ab	0.15c
	Mean	8.63B	9.40B	1.38B	1.48B	0.16A	0.16A
Water (W)		0.000**	0.000**	0.000**	0.000**	0.232^{ns}	0.015^{ns}
Nitrogen (N)		0.000**	0.000**	0.000**	0.010*	0.000**	0.000**
W×N		0.011*	0.047*	0.329^{ns}	0.000**	0.230^{ns}	0.077^{ns}

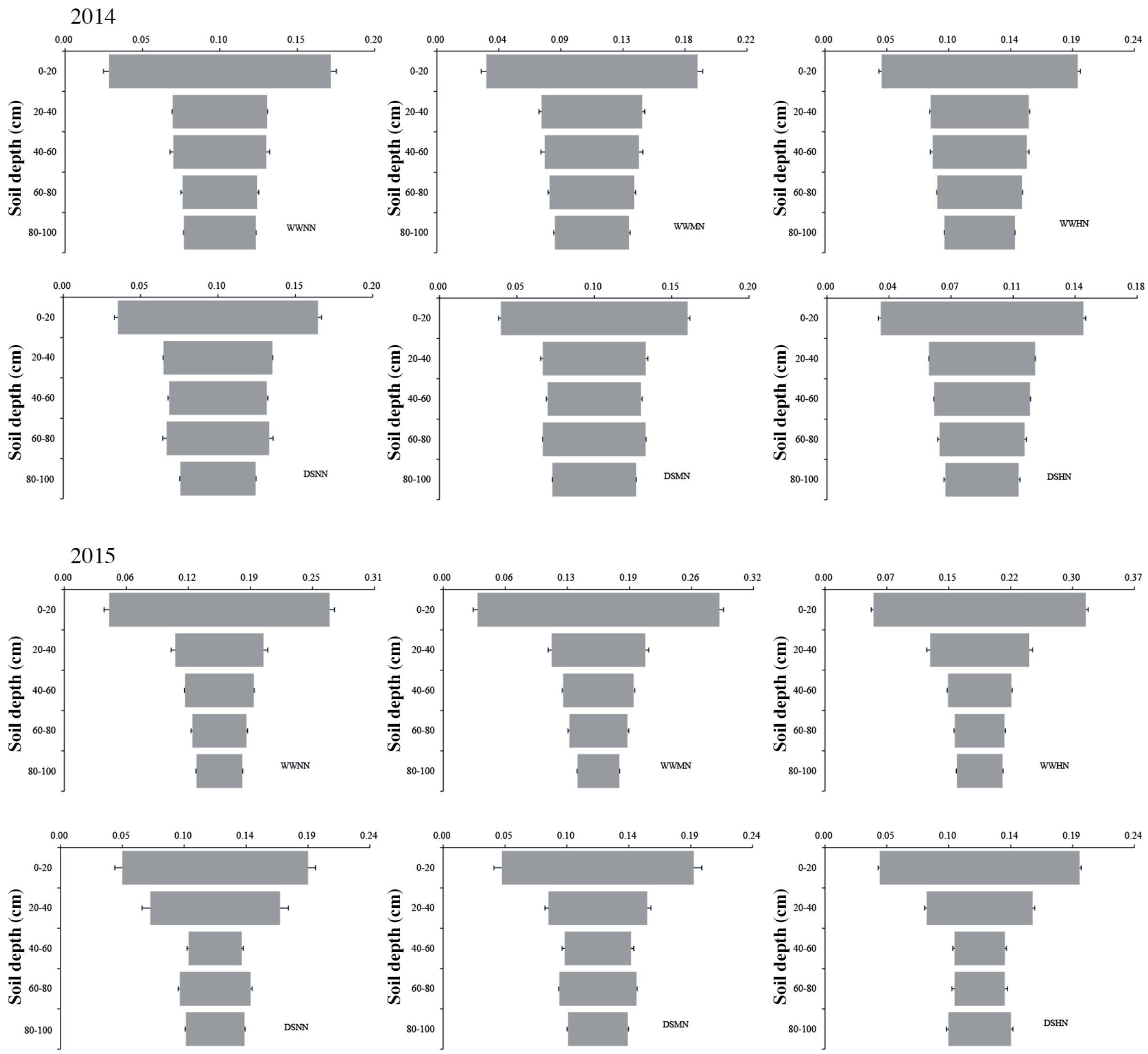
Mean values within a column followed by a different letter are significantly different at P < 0.05.
*, **Significant at P < 0.05 and P < 0.01 respectively. Ns: nonsignificant.
WW: Well-watered; DS: drought stress; NN: no N fertilizer; MN: moderate N 90 kg ha^{-1}; HN: high N 180 kg ha^{-1}.

Table 3. Effects of water level and N rate on root length, root surface area and root volume of peanut in 2014 and 2015.

		Root length		Root surface area		Root volume	
Water level	N rate	2014	2015	2014	2015	2014	2015
		cm plant^{-1}		cm plant^{-1}		cm^2 plant^{-1}	
WW	NN	9009.24d	11963.12c	935.70c	1286.97c	11.50b	15.41c
	MN	10051.39b	13086.90b	1079.67a	1381.46b	12.61ab	16.67b
	HN	10576.80a	14091.54a	1057.16a	1466.00a	13.32a	18.35a
	Mean	9897.15A	13047.18A	1024.17A	1378.14A	12.48A	16.81A
DS	NN	9477.33c	9693.96d	978.57b	975.56d	13.28a	12.48d
	MN	9128.56d	9580.63d	929.45c	960.94d	11.51b	10.07e
	HN	8200.80e	9124.51d	900.23c	894.12e	11.49b	9.60e
	Mean	8935.56B	9466.37B	936.08B	943.45B	12.09A	10.72B
ANOVA (P value)							
Water (W)		0.000**	0.000**	0.000**	0.000**	0.207^{ns}	0.000**
Nitrogen (N)		0.003*	0.010*	0.018*	0.030*	0.549^{ns}	0.004*
W×N		0.000**	0.000**	0.000**	0.000**	0.001**	0.000**

Mean values within a column followed by a different letter are significantly different at P < 0.05.
*, **Significant at P < 0.05 and P < 0.01 respectively. Ns: nonsignificant.
WW: Well-watered; DS: drought stress; NN: no N fertilizer; MN: moderate N 90 kg ha^{-1}; HN: high N 180 kg ha^{-1}.

Figure 1. Root length density (RLD) in different soil layers of peanut grown under different water level and N rate in 2014 and 2015.



WW: Well-watered treatment; DS: drought stress treatment; NN: no N fertilizer; MN: moderate N; HN: high N.

Pod yield

Water and N application had significant effects on pod yield. Compared with WW, the annual average yield was 13.1% lower under DS (Figure 2). The yield in NN was lowest of all N rates for both water levels. The yield of MN was significantly higher for both water levels in both years compared with that of NN. The yields of MN were 32.2% and 17.7% greater than that for NN under WW treatment in 2014 and 2015, respectively; and correspondingly 20.1% and 12.3% higher under DS treatment. The HN rate had nonsignificant effect on pod yield compared with NN under DS treatment, but improved yield by 21.8% and 10.8% under WW treatment in 2014 and 2015, respectively. ANOVA showed that water and N had significant effects on yield.

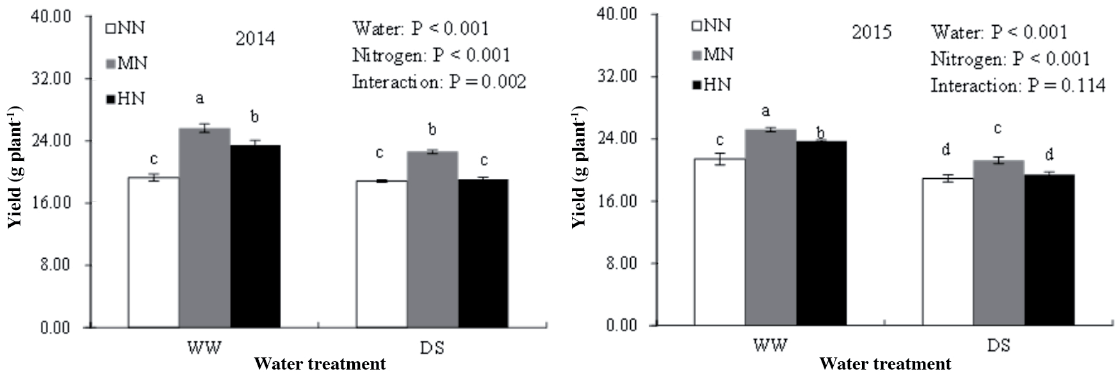
N accumulation and NUE in peanut

There were significant individual effects of water and N on N accumulation, fertilizer N uptake, and NUE, and the two factors also showed significant interactive effects on these characters (Table 4). Averaged across all three N rates, N accumulation in peanut was 17.0% greater in WW than DS treatment. Under both water treatments, peanut in MN rate accumulated significantly more N than the other N levels. The N uptake of the WW-MN treatment was highest but lowest in DS-NN among all water-N treatments. The N uptake followed the same sequences of MN > HN > NN under different water conditions, and there was nonsignificant difference between NN and HN under both water conditions. The absorption of ^{15}N fertilizer N significantly increased with increased N application. The percentage of ^{15}N fertilizer N was 21.2%-36.3% of total N uptake. On average, NUE was 12.3% higher under WW than DS treatment. The NUE in MN was significantly higher than that in HN treatment regardless of soil moisture conditions.

Correlation analysis of RLD with pod yield and NUE

The root distribution proportions in different soil layers were very important for pod yield and NUE. Except for the 20-40 cm soil layer, RLD was significantly positively correlated with pod yield (r = 0.434-0.655). The RLD in 20-40 cm soil layer decreased by N application under DS, while the yield increased, which may result in the insignificant correlation. The RLDs in 40-60 and 60-80 cm layers were significantly positively correlated with NUE (Figure 3). The relationship of RLD in different soil layers with yield and NUE showed that roots in deeper soil (40-100 cm) may contribute to yield maintenance and higher NUE.

Figure 2. The yield of peanut grown under different water level and N rate in 2014 and 2015.



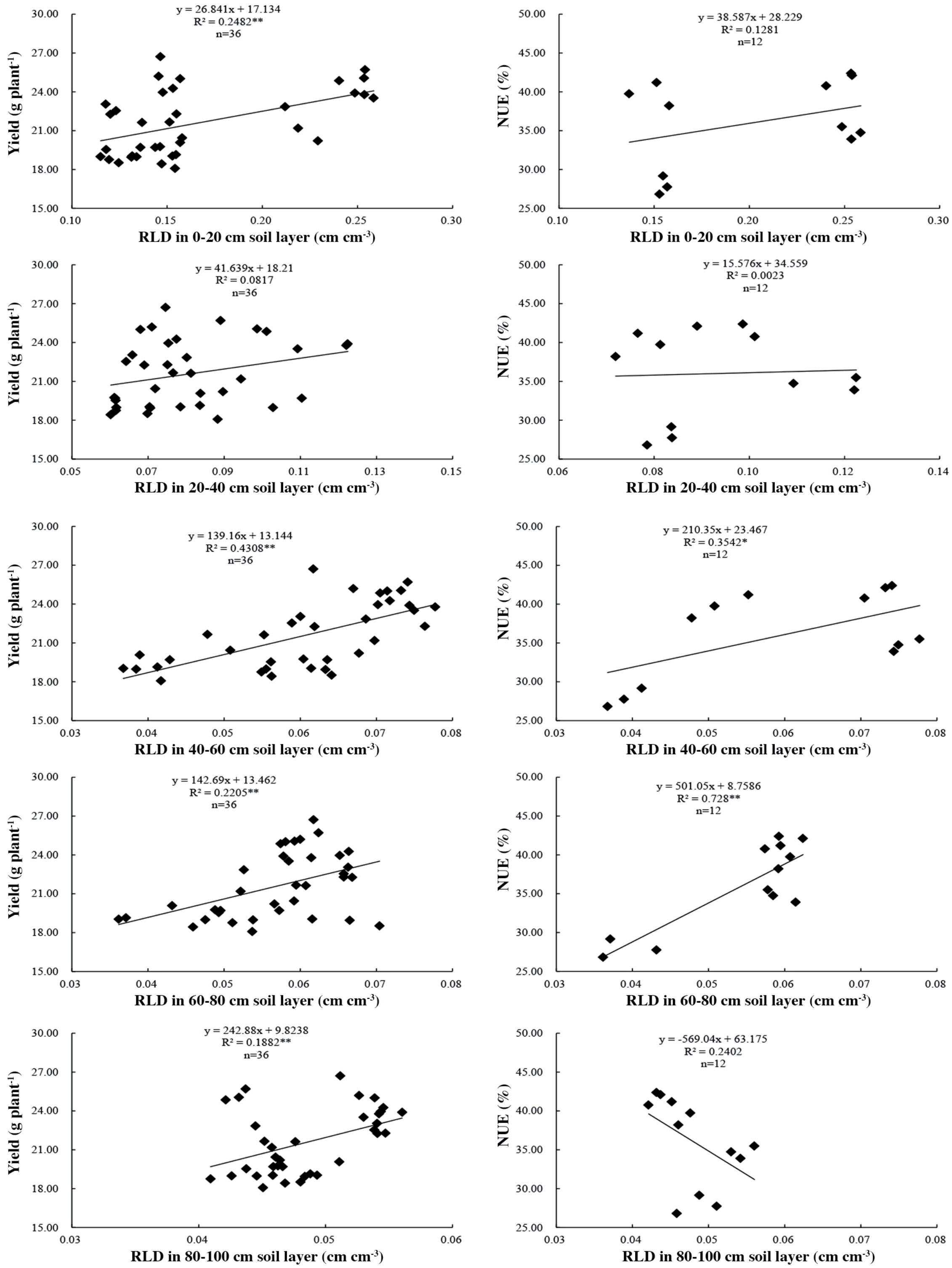
Error bars represent ± SE of the mean. The SE was calculated across three replicates.
Different letters indicate significant difference at P < 0.05.
WW: Well-watered treatment; DS: drought stress treatment; NN: no N fertilizer; MN: moderate N; HN: high N.

Table 4. The effects of water level and N rate on N accumulation, $\delta^{15}N$ fertilizer N accumulation and N use efficiency (NUE) of peanut in 2015.

Water level	N rate	N accumulation	$\delta^{15}N$ Fertilizer N accumulation	NUE
		mg plant^{-1}	mg plant^{-1}	%
WW	NN	1068.43b	-	-
	MN	1113.44a	236.19c	41.74a
	HN	1095.23ab	392.68a	34.70b
	Mean	1092.36A	314.43A	38.22A
DS	NN	863.41c	-	-
	MN	1067.62b	224.64c	39.70a
	HN	869.59c	315.66b	27.90c
	Mean	933.54B	270.15B	33.80B
ANOVA (P value)				
Water (W)		0.000**	0.000**	0.000**
N rate (N)		0.000**	0.000**	0.000**
W×N		0.000**	0.002*	0.000**

Mean values within a column followed by a different letter are significantly different at P < 0.05.
*, **Significant at P < 0.05 and P < 0.01 respectively.
WW: Well-watered; DS: drought stress; NN: no N fertilizer; MN: moderate N 90 kg ha^{-1}; HN: high N 180 kg ha^{-1}.

Figure 3. Relationships between root length density (RLD) in different soil layers with yield and N fertilizer use efficiency (NUE) of peanut grown under different water levels and N rate.



*, **Significance of the regression line at $P < 0.05$ and $P < 0.01$, respectively.

DISCUSSION

Water and N are the major environmental factors that limit crop growth and production (Gonzalez-Dugo et al., 2011). Appropriate water and N application can have a coupling effect to achieve high and stable yield and high efficiency of water and fertilizer (Wang et al., 2013; Yin et al., 2014). Under drought or N deficiency, plants increase the distribution of photosynthetic product in roots to promote root growth, thus increasing the relative root dry weight and R:S ratio (Gheysari et al., 2009; Benjamin et al., 2014). In this study, water and N significantly affected the growth of peanut plants, shoot DM, root DM, and R:S ratio, and showed a significant interactive effect on DM accumulation and distribution (Table 2). The annual average shoot DM of MN significantly increased by 12.0% compared to that of NN. Compared with WW treatment, the R:S ratio of DS was higher under NN and MN treatments, while DS had no effect on R:S ratio under HN treatment. This may be the result of a limitation in DM translocation from shoot to root of HN under continuous soil drought. Similar to results of Wang et al. (2019), the R:S ratio under N application was lower than that of NN, and the reduction of MN was greater than that of HN under both water conditions. Therefore, N application had a positive effect on ameliorating the distribution of DM in root systems, so as to cope with drought stress.

The crop root architecture has strong plasticity. The changes in soil environment, water and fertilizer resources significantly influence plant root architecture. Nitrogen deficiency can increase root vertical expansion, promote root growth in deeper soil, while high N can inhibit root vertical expansion and promote root lateral growth (Yu et al., 2014; Ye et al., 2018). The results showed that water and N had an important role in regulating the root morphology and spatial distribution of peanut (Table 3; Figure 1). The root length, root surface area and root volume of peanut significantly decreased under the combination of drought stress and N deficiency (Table 3). Previous studies have shown that deeper root distribution is conducive to the acquisition and utilization of water and nutrients in deep soil (Mi et al., 2010; Jongrungklang et al., 2012; Junjittakarn et al., 2014). Compared with NN, N application significantly increased the root morphological traits under WW treatment. The root distribution in the deep soil decreased significantly, resulting in a large number of root surface aggregation. This was consistent with previous studies in maize (Wang et al., 2019). Under DS treatment, the distribution ratio of the root system in the deep soil layer greatly increased. On average, the RLDs of MN in 60-80 and 80-100 cm soil layers were 4.5% and 8.5% greater than that of NN level, respectively (Figure 1), indicating that root development and vertical expansion were optimized by MN under drought stress. Thus, appropriate N application promoted root growth in the deeper soil layers.

Appropriate fertilization under soil drought stress is beneficial to drought resistance of crops and increase the yield under drought stress. A significant interaction of N and water was observed for soybean and corn yield (Humbert et al., 2013; Basal and Szabó, 2020). In this study, the pod yield of NN in 2014 was 9.9% lower than that in 2015 under WW. This may be that the average temperature and light duration during peanut growth in 2014 were less than those in 2015, which inhibited peanut growth. The pod yield of N application treatments under WW were basically equal in 2 yr, which indicating that N application could alleviate some effects of environmental stress and improve peanut pod yield under WW condition. Under DS, high N application rate is not recommended. Compared with low N rate, flower and pod numbers per plant and seed yield were decreased at a high N rate under drought stress (Basal and Szabó, 2020). The MN application increased pod yield under different water treatments, and on average the promotion effect of MN was 14.2% greater than for HN treatment under DS condition (Figure 2). The water and N treatments had significant effects on N uptake and NUE of spring barley. And NUE and N uptake decreased after drought stress (Hoseinlou et al., 2013). In this study, drought also decreased the N uptake and NUE of peanut. We also observed that pod yield and NUE showed significant positive correlations with RLD in deep soil layers (40-60 and 60-80 cm) (Figure 3). Thus, appropriate application of N fertilizer could optimize root morphology and distribution, alleviate the stress of drought on peanut growth, and so improve the peanut yield and NUE.

CONCLUSIONS

Compared with well-watered (WW) treatment, drought stress conditions (DS) decreased root length, root surface area, and yield. Peanut root morphology was significantly affected by water conditions. The root length, root surface area, and root volume increased with increasing N application under WW treatment, while peanut root morphological traits showed opposite trends in DS treatment. The moderate N (MN) application under DS caused lower R:S ratio and greater root length density (RLD) in the deeper soil layer, which could coordinate the development of underground and aboveground parts to facilitate peanut yield. The MN significantly improved annual average pod yield by 16.2% compared to no N application (NN) under DS treatment. The pod yield and N use efficiency (NUE) were positively correlated with root length in 40-60 and 60-80 cm soil layers. Thus, the effect of drought stress on peanut growth can be alleviated by increasing moderately N fertilizer application to increase the yield and NUE.

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