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Effect of nitrogen on root and shoot relations and gas exchange in winter wheat

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Abstract. The seedling growth of two drought-resistant wheat varieties was studied under solution culture in a plant growth chamber. The results showed that the shoot dry weight and leaf gas exchange parameters increased with the increase of nitrogen supply, but decreased when nitrogen supply reached a certain level. The optimum nitrogen concentrations for shoot dry weight and gas exchange were different among the varieties. The root growth was negatively correlated with the increase of nitrogen supply. The distribution of root length in different layers was similar for the two varieties. The root length was the longest at the layer of 5-15 cm, the shortest below 15 cm, and in between at the layer of 0-5 cm. The water use efficiency (WUE) decreased with increasing ratio of root to shoot (R/S), while leaf photosynthetic rate tended to increase initially and then decrease. The increase in R/S was unfavorable to increase WUE, and the appropriate R/S for leaf photosynthetic rate was about 0.5.

Keywords: Coordinate growth; Nitrogen nutrition; Root and shoot relation; Winter wheat.

Introduction

Drought stress and nitrogen deficiency are major constraints to winter wheat production and yield stability in most rainfed regions (McDonald and Davies, 1996). An efficient use of limited nitrogen resources and better growth under limited nitrogen supply are desirable traits for crops in drought environments. Nitrogen deficiency induces modifications of many morphological and physiological processes (Ciompi et al., 1996; Shangguan et al., 2000a). Leaf nitrogen is mostly used for synthesis of components of the photosynthetic apparatus, and about 75% of leaf nitrogen is allocated to the chloroplasts (Shangguan et al., 2000b).

The nutrient supply and demand of root and shoot are inter-dependent due to their different functions and local environment (Passioura, 1983; Siddique et al., 1990; Li et al., 2001). The ratio of root to shoot (R/S) is an index that reflects growth and dry matter accumulation between root and shoot (Lioert et al., 1999). The R/S is affected both by genetic (Passioura, 1983; O'Toole and Bland, 1987) and environmental factors, such as water status (Miao et al., 1998; Grant, 1998; Hebert et al., 2001), nutrient availability (Liang, 1996; Marsh and Pierzynski, 1998; Maranov et al., 1998), and soil texture (Vos et al., 1998). Root growth is closely related to physiological metabolism and dry matter accumulation in shoot (Siddique et al., 1990). An excessively low R/S indicates poor root growth, resulting in sufficient water and nutrients for shoot growth. An extremely high R/S may lead to root redundancy, which reduces shoot growth, yield, and water and nutrient use efficiencies (Zhang, 1995). Therefore, it is important to coordinate root and shoot relations and maximize dry matter accumulation and water and nutrient use efficiencies (Tomar et al., 1997; Kahn and Schroeder, 1999).

Nitrogen nutrition has significant effects on root and shoot relations (Feng and Liu, 1996; Lioert et al., 1999). Nitrogen deficiency increased root surface area, increased consumption of assimilates, reduced the amount of nitrogen transported to shoot, decreased shoot growth, and resulted in an increased R/S ratio. However, extra nitrogen nutrition caused an excessive shoot growth, reduced the assimilate availability for root, and reduced the R/S ratio (Passioura, 1983). Therefore, the amount of nitrogen nutrition applied to plants must be optimal for root and shoot relations. Previous studies have shown that effective use of nitrogen fertilizer increased leaf photosynthesis, promoted root development, and extended space for root to extract water and nutrients in soil (Li et al., 1999). However, related research is relatively scarce, and then the effect of nitrogen nutrition on root growth needs to be enhanced. Objectives of this study were to (1) investigate the responses of shoot and root growth, leaf exchange, and WUE to nitrogen nutrition and (2) determine the relationships between gas exchange, WUE and R/S.

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Materials and Methods

Plant Materials and Growth Conditions

The sterilized seeds of wheat (*Triticum aestivum* L.) varieties, *Xiaoyan No.6* (drought resistant) and *Xinong No. 1043* (drought resistant), were initially soaked in deionized water for 24 h, and then germinated in darkness at a constant temperature of 25°C on moist gauze for 48 h. Upon emergence, uniformly germinated seeds were seeded in sands. When the seedlings were about 2 cm tall, the healthy and uniform ones were transplanted into solution culture containers in a growth chamber.

The solution culture container was made of glass, 60 cm long, 10 cm wide, and 30 cm deep, with a volume of 2 L. There was a pipe to charge the used solution at the bottom of the container. The seedlings were transplanted into an aluminum frame wrapped with double nylon (120 items) net. The frame had screws to clutch on the edge of the container and were tied with a rubber band.

The environmental conditions in the plant growth chamber (Heraeus Votsch, Germany) were: a photosynthetic photon flux density of 130 μmol $m^{-2} s^{-1}$ over plants; day/night temperature: 25°C/15°C; midday relative humidity: 65%; and a 12-h photoperiod. The growing conditions were controlled automatically by a computer program. The solution was ventilated by electrical pump with a flow rate of 150 $ml·min^{-1}$ from 8:00 am to 10:00 am every day. The seedlings were initially grown in distilled water for 4 days after being transplanted. Thereafter, the nitrogen nutrient solution was added. The solution was replaced every three days and adjusted to pH of 5.0 using KOH or HCl every day.

Treatments

There were six nitrogen treatments in each variety: 0 $mmol·L^{-1}$ NO_3^-, 3.75 $mmol·L^{-1}$ NO_3^-, 7.50 $mmol·L^{-1}$ NO_3^-, 11.25 $mmol·L^{-1}$ NO_3^-, 15.00 $mmol·L^{-1}$ NO_3^-, and 18.75 $mmol·L^{-1}$ NO_3^- with six replications. All other ions in the solution were constant, except for SO_4^{2-} and Cl^-, which were used in equal portions to maintain charge balance. The basic nutrient solution was Hoagland solution. The compounds of the nutrient solutions were $Ca(NO_3)_2·4H_2O$: 0.5 $mol·L^{-1}$, KNO_3 : 0.5 $mol·L^{-1}$, NH_4N0_3 : 0.5 $mol·L^{-1}$, $MgSO_4·7H_2O$: 0.2 $mol·L^{-1}$, KH_2PO_4 : 0. 2 $mol·L^{-1}$, KCl : 0.5 $mol·L^{-1}$, $CaCl_2$: 0.5 $mol·L^{-1}$, Fe-EDTA, and mineral elements (A-Z solution).

Leaf Gas Exchange and N Content Measurements

The gas exchange measurements were taken when seedlings had four leaves. A portable infrared CO_2 analyzer (Li-6400, Li-Cor, USA) was used to measure photosynthetic rate (*Pn*), transpiration rate (*Tr*), leaf conductance (*gs*), and intercellular CO_2 concentration (*Ci*). The youngest fully expanded leaf of three plants of each treatment was enclosed into the gas exchange chamber between 10 and 11.5 h for gas exchange measurements. Plant water use efficiency was determined as the ratio of *Pn* to *Tr*.

Root Measurement

Fresh weight, dry weight, length, and diameter of root in each treatment were measured in different layers. The root samples were dyed. The image of roots was scanned by a numerical scanner to analyze the root perimeter (P) and surface area (A). Then P and A were used to calculate the root length (L) and diameter (d), using CIAT-root system analysis software (CID Inc., USA).

The shoot and root samples were oven-dried at 90°C for 30 min, then at 70°C for at least 48 h, and the dry matter weight was determined.

Leaf Nitrogen Content

For determining leaf nitrogen concentration, 200 mg of powdered material was analyzed with a modified Kjeidahl analysis using concentrated sulphuric and salicylic acid and Na_2SO_4, K_2SO_4 and Se in a ratio of 62:1:1 (w/w) as a catalyst (Page et al., 1982). The N-concentration of the digests was determined on a Skalar continuous flow analyser.

Statistical Analysis

Standard error, variance, regression and correlation coefficients, and significant differences among regression coefficients were calculated by standard methods with the DAPS - statistical package (Feng and Tang, 1997).

Results

Leaf Nitrogen Content

The leaf nitrogen content increased as nitrogen concentration increased in solution for both varieties (Table 1). The leaf nitrogen content increased more rapidly when the nitrogen concentration increased from 0 to 3.75 $mmol·L^{-1}$. When nitrogen concentration was over 3.75 $mmol·L^{-1}$, leaf nitrogen content increased slowly as nitrogen concentration increased.

Leaf Gas Exchange

The response of leaf photosynthetic rate (*Pn*) to nitrogen concentration was parabolic. The *Pn* increased first and then decreased as nitrogen concentration increased (Figure 1A). Comparing the two varieties, the *Pn* of *Xiaoyan No. 6* was higher than that of *Xinong No.1043* when the nitrogen concentration was lower than 10 $mmol·L^{-1}$. However, the *Pn* of *Xiaoyan No. 6* was lower than that of *Xinong No. 1043* when nitrogen concentration was over 12.5 $mmol·L^{-1}$ because the *Pn* of *Xiaoyan No. 6* decreased more rapidly than that of *Xinong No. 1043*.

The response of leaf transpiration (*Tr*) to nitrogen concentration was similar to *Pn* (Figure 1B). For both varieties, the *Tr* reached the maximum at nitrogen concentration of 7.5 $mmol·L^{-1}$, and then decreased as nitrogen concentration increased. The *Tr* of *Xiaoyan No. 6* was higher than that of *Xinong No. 1043* except at nitrogen concentration of 18.75 $mmol·L^{-1}$. Compared to *Pn, Tr* was more sensitive to nitrogen treatment.

Table 1. Mean values for leaf nitrogen content, root length, and root area of wheat under different nitrogen treatments.

Nitrogen treatments (mmol/L)	Leaf nitrogen content (%)		Root length (m/per plant)		Root area (cm^2/per plant)	
	Xinong No. 1043	*Xiaoyan No. 6*	*Xinong No. 1043*	*Xiaoyan No. 6*	*Xinong No. 1043*	*Xiaoyan No. 6*
0	2.20c	2.28c	14.93a	15.09a	137.00a	138.20a
3.75	4.54b	4.72b	14.99a	15.61a	101.88b	96.83b
7.50	4.93b	4.84b	15.08a	13.62b	95.52b	101.10b
11.25	5.44ab	5.18b	14.57b	10.89c	75.82c	86.24b
15.00	5.95a	5.29b	12.66c	11.44cb	56.67d	54.92c
18.75	6.10a	6.02a	10.97c	12.43b	52.44d	50.66c

Mean values within columns followed by the same letter (a-c) are not significantly different according to LSD (P<0.05).

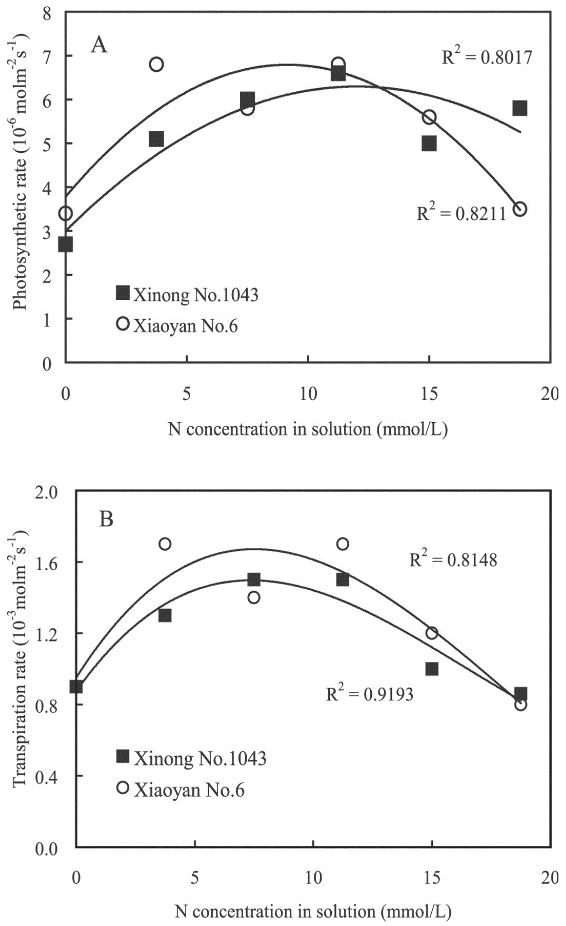

Figure 1. The photosynthetic rate (A) and transpiration rate (B) of wheat leaves under different nitrogen treatments condition.

Shoot and Root Dry Weight

The plant shoot dry weight increased with increasing nitrogen supply, reaching the maximum when the nitrogen concentration was 11.25 mmol·L^{-1}. Thereafter, shoot dry weight decreased as nitrogen supply increased. At most nitrogen concentrations, shoot dry weight of *Xiaoyan No. 6* was higher than that of *Xinong No. 1043* (Table 2).

The root dry weight decreased as nitrogen concentration increased for both varieties, indicating lower nitrogen concentration was more favorable to the accumulation of root growth than to shoot growth. There was no significant difference in root dry weight between the two varieties (Table 2).

The variation of root weight at different depths of *Xinong No. 1043* was similar to that of *Xiaoyan No. 6*, and the root growth of *Xinong No. 1043* was more sensitive to nitrogen than that of *Xiaoyan No. 6*. With the increase of nitrogen supply, the root dry weight below the 10 cm layer was reduced. For the root dry weight at 0-10 cm, root dry weight increased at 3.75 mmol·L^{-1}, then decreased as nitrogen supply increased when nitrogen concentration exceeded 3.75 mmol·L^{-1}.

Root Length, Surface Area and Root /Shoot (R/S) Ratio

For both varieties, total root length was significantly reduced at higher nitrogen concentrations (Table 1). For *Xinong No. 1043*, total root length decreased when nitrogen concentration was over 11.25 mmol·L^{-1}. For *Xiaoyan No. 6*, root length decreased when nitrogen concentration was over 7.5 mmol·L^{-1}. For both varieties, total root length was the highest at the 5-15 cm depth layer, shortest below 15 cm, and intermediate at 0-5 cm.

Table 2. Mean values for shoot dry weight, root dry weight, and root/shoot of wheat under different nitrogen treatments.

Nitrogen treatments (mmol/L)	Shoot dry weight		Root dry weight		Root/shoot	
	Xinong No. 1043	*Xiaoyan No. 6*	*Xinong No. 1043*	*Xiaoyan No. 6*	*Xinong No. 1043*	*Xiaoyan No. 6*
0	0.062c	0.061c	0.064a	0.062a	1.01a	0.99a
3.75	0.167b	0.191b	0.066a	0.064a	0.39b	0.33b
7.50	0.178ab	0.186b	0.059a	0.051b	0.33b	0.27b
11.25	0.205a	0.267a	0.040b	0.054b	0.22c	0.21bc
15.00	0.180ab	0.198b	0.035b	0.039c	0.22c	0.19c
18.75	0.169b	0.184b	0.031b	0.030c	0.18c	0.17c

Mean values within columns followed by the same letter (a-c) are not significantly different according to LSD (P<0.05).

For *Xinong No. 1043*, the average root diameter at 0-5 cm and below 20 cm was greater than that at 5-15 cm, especially at 10-15 cm in which the root diameter was the smallest. For *Xiaoyan No. 6*, the smallest root diameter was found between 5-15 cm. Based on the root length and diameter, the main uptake part of the root system in wheat seedlings was at the 5-15 cm depth since the root length was the highest and diameter was the smallest for this layer. For both varieties, the root surface area decreased as nitrogen concentration increased (Table 1).

The changes of R/S of the two varieties were similar under different nitrogen treatments. The R/S decreased gradually with the increase of nitrogen concentration, but it was increased when the nitrogen concentration exceeded 12.5 $mmol \cdot L^{-1}$ (Table 2). Comparing the two varieties, R/S of *Xinong No. 1043* was greater than that of *Xiaoyan No. 6*.

Discussion

The manipulation of crop physiological function to raise yield is always an important issue in agronomy, genetics, and ecology. The research on plant integrated response, root establishment, and rhythmical changes of shoot and root is still underway (McDonald and Davies, 1996; Li et al., 2001). In recent years, such research has focused on root and shoot interactions (Passioura, 1983; McDonald and Davies, 1996; Lioert et al., 1999; Hebert et al., 2001). Much has been conducted on root establishment, architecture and function, growth dynamics, metabolism, effects of genetics and the environment on root growth, and the relationship between root growth and yield (Passioura, 1983; O'Toole and Bland, 1987; Siddique et al., 1990; Li et al., 2001). Root growth appears related to genetic factors, soil conditions, temperature, and seed size (Lioert et al., 1999). The modern cultivars usually have a well-developed and deep root system to increase resistance to drought. However, in old cultivars, root growth is inhibited after the tillering stage, and the ultimate yield is reduced (Zhang and Shan, 1998). Cultivars with a greater R/S usually have a relatively greater water and nutrient uptake capacity, higher yield stability, and greater drought resistance (Passioura, 1983). The R/S of early maturity varieties is smaller than that of late maturity. The root density increased in soil profile under irrigation, while the root penetrating capacity increased under drought conditions (Tomar et al., 1997). Liang (1996) found that increasing nitrogen supply increased R/S due to increase of root dry weight and the number of seminal roots. In the present study, nitrogen deficiency significantly decreased nutrient uptake by roots and nutrient supply to shoots. Therefore, root growth has a significant effect on shoot growth. The experimental results also indicated that root growth was significantly correlated with seedling growth.

Both shoot dry weight and gas exchange parameters increased first and then decreased as nitrogen supply increased. However, the optimal nitrogen concentration for shoot dry weight and gas exchange parameters was different. Nitrogen concentration had a negative effect on root growth (Table 2). Maranov et al. (1998) found that increasing nitrogen increased root growth but decreased shoot growth when plants grew under severe water stress because the limited water extracted by roots was mainly consumed by the root system itself and only a small amount of water was transported to shoot. In this study, both roots and shoots were grown under well-watered conditions, and a small quantity of nitrogen nutrition could meet the demand of root growth. However the demand of shoot growth would be met only when the nitrogen concentration was relatively high due to the position of the shoot as compared to the root. In dryland farming areas, crop production is mainly dependent on the highly efficient use of limited water and its full extraction by roots. The results of our study showed both root and shoot growth was significantly correlated with WUE, and an increase in both root and shoot could increase WUE. Because of the high inter-dependence between root and shoot, the stronger the root system, the better the foundation for the robust shoot growth and more efficient water use (Feng and Liu, 1996). However, it was also found that WUE decreased with increasing R/S (Figure 2A) while the response of leaf photosynthetic rate to R/S exhibited a parabolic trend (Figure 2B), indicating that the increase of R/S was unfavorable to improving WUE The optimum R/S for photosynthetic rate was about 0.5.

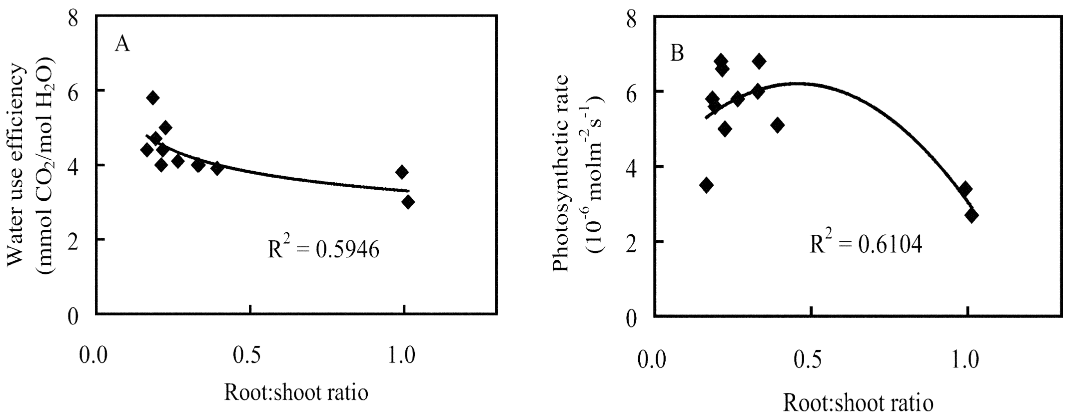

Figure 2. The relationship of R/S and WUE_I (A) and that of R/S and Pn (B) of wheat.

Wheat is one of the main crops planted extensively in semi-arid and semi-moist areas, and different cultivars have different adaptability to nitrogen and water. Wheat's adaptable mechanisms for drought at different nitrogen levels were probably different. Low nitrogen wheat adapted to drought through a drought resistant structure, high nitrogen wheat through osmotic adjustment (Xue and Chen, 1990). A close relationship also existed between wheat adaptability to water and features of root growth (Liang, 1996; Li et al., 2001). Non-drought resistant wheat cultivars' sub-roots mostly expanded shallowly, and the angle was big; however, drought resistant wheat cultivars expanded deeply, and the root angle was small, so different drought resistant cultivars have different root morphology (Duan et al., 1997). The drought resistant wheat cultivars had the character of root/shoot and a greater quantity of root at deep layers (Miao et al., 1998; Shangguan and Shao, 1999). The semi-arid area of the Loess Plateau had a deep soil profile, a loose soil structure, and a great storage capacity for soil water. The deep soil profiles not only allow plant roots to expand more deeply, they also reinforce the resistant ability of crops by using deeply storied water (Shangguan and Shao, 1999). A greater ratio of roots/shoots maintained the water balance in plants well. However, if the root system is deeply extended, the shallow storied water is limited, and then the significance of the great ratio of roots/shoots loses importance. Therefore, during agricultural production in a semi-arid area, choosing wheat cultivars of different resistance in different quantities of nitrogen fertilizer to benefit the root distribution and absorbing ability that can improve wheat photosynthetic response and productivity.

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氮素營養對冬小麥根莖關係和氣體交換的影響

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在植物生長箱通過溶液培養方式，對不同氮素條件下二種抗旱的小麥品種西農 1043 和小偃 6 號的幼苗根苗生長特性進行了研究，結果表明在不同氮素濃度下，氮肥用量的提高對地上部幹重和葉片氣體交換參數表現為增效效應，當用量增至一定程度時，地上部幹重和葉片氣體交換參數均呈下降趨勢，只是兩個小麥品種各自的適宜氮素用量存在差異。培養介質氮素濃度低時，有利於小麥根系幹重累積，培養介質氮素濃度高時，不利於根系幹重累積。西農 1043 和小偃 6 號根長分佈基本相似。西農 1043 和小偃 6 號不同深度根長分佈基本相似，根系長度為表現出如下趨勢：5-15 cm 層次根系最長，0-5 cm 層次次之，15 cm 以後層次根長最短。小麥根莖比的增加並不利於葉片水分利用效率的提高，而葉片光合作用最優的根莖比為 0.5 左右。

關鍵詞：冬小麥；氮素營養；根莖關係；協調生長。