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 insufficient 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.
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 seedlings 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 solution was replaced every three days and adjusted to pH of 5.0 using KOH or HCl every treatment was enclosed into the gas exchange chamber between 10 and 11.5 h for gas exchange measurements. Upon emergence, uniformly germinated seedlings were transplanted into solution culture containers in a growth chamber.

植物材料和方法

植物材料与生长条件

将小麦(Triticum aestivum L.)品种，小燕6号（耐旱品种）和新农1043（耐旱品种）的种子进行灭菌处理，然后在25°C的恒温条件下，用湿纱布浸泡48 h，直至种子萌发。萌发后的幼苗被移植到溶液培养容器中。

溶液培养容器为玻璃材质，长60 cm，宽10 cm，深30 cm，容积为2 L。容器底部有一根管道用于排出使用过的溶液。

植物生长环境条件（Heraeus Votsch，德国）为：植物光合量子通量密度为130 μmol m⁻² s⁻¹；日/夜温度：25°C/15°C；中午相对湿度：65%；12 h光周期。

溶液被自动控制程序自动控制。溶液每三日更换一次，并调整到pH为5.0，用KOH或HCl。

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 was lower than 10 mmol·L⁻¹. When nitrogen concentration was over 3.75 mmol·L⁻¹, leaf nitrogen content increased more rapidly than 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.

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.

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).

Leaf Gas Exchange and N Content Measurements

The gas exchange measurements were taken when seedlings had four leaves. A portable infrared CO₂ analyzer (Li-6400, Li-Cor, USA) was used to measure photosynthetic rate (Pn), transpiration rate (Tr), leaf conductance (gs), and intercellular CO₂ 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.

叶氮含量

叶氮含量随着氮素浓度的增加而增加，且在两个品种中为相对快速增加。当氮素浓度超过10 mmol·L⁻¹时，叶氮含量增加的速度比氮素浓度增加的速度更快。

叶气交换

叶气交换的响应与氮素浓度的增加呈对称型。Pn在低浓度（<10 mmol·L⁻¹）时先增加再减少，而在高浓度时（>12.5 mmol·L⁻¹）则减少得更快。

根测量

每个处理的根的鲜重、干重、长度和直径在不同层次中被测量。根样品被染色，然后通过扫描器分析根的周长（P）和表面积（A）。随后，P和A被用于计算根的长度（L）和直径（d），使用CIAT-root系统分析软件。

统计分析

标准误差、方差、回归和相关系数，以及回归系数的显著性差异，通过标准方法在DAPS统计软件（Feng和Tang，1997）中计算。

叶气交换和N含量测量

叶气交换测量在幼苗有四片叶子时进行。便携式红外CO₂分析仪（Li-6400，Li-Cor，美国）用于测量光合速率（Pn）、蒸腾速率（Tr）、叶导度（gs）和细胞间的CO₂浓度（Ci）。根的周长（P）和表面积（A）的计算使用了CIAT-root系统分析软件。
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.
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·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.
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 root 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 (Li, 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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Literature Cited


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有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。