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Formation and morphological characteristics of special root hairs on nodal roots of wheat (Triticum aestivum L.)

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Formation and characterization of special root hairs on wheat nodal roots were studied under conditions of the field experiments. The results showed that special root hairs formed around the basal portion of a nodal root in the arable layer of soil after jointing stage, and that distribution of special root hairs on a nodal root could be divided into concentrated, moderate, and sparse segment. Occurring density, length and diameter of the special root hair on the concentrated segments were greater or more than those on either the moderate or the sparse segments. Difference both in length and density between different root segments was extremely negative significant (P<0.01). Occurring density, length and diameter of the special root hair decreased with advance in growing period. All of the results from this study indicated that the special root hairs are real root hairs and functional.

Key words: Triticum aestivum L., nodal root, special root hair, formation, characterization.

INTRODUCTION

Root hairs are specialized root epidermal cells playing an important role in increasing surface area for absorption of water and nutrients, and contributing to the adhesion of the growing root to the rhizosphere (Feng et al., 2001; Bibikova and Gilroy, 2003). To date, lots of research activities have been conducted in diverse aspects of root hairs: (1) morphogenesis or initiation (Cho and Cosgrove, 2002; Kim et al., 2007), (2) formation and development (Grierson et al., 2001; Michael, 2001; van Bruaene et al., 2004), (3) morphology (Czarnota et al., 2003; Suzuki et al., 2003) and (ultra-)structure (Gestel et al., 2003; Ovečka et al., 2005; Yu et al., 2005), (4) exudate secretion (Czarnota et al., 2003; Yang et al., 2004), (5) uptake of water and nutrients (Ma et al., 2001a; Gahooonia and Nielsen, 2004; Kristoffersen et al., 2005), (6) genetic and molecular basis(Schiefelbein, 2000; Wang et al., 2004; Zhu et al., 2005; Kwasniewski and Szarejko, 2006), (7) interaction with external and internal factors such as hormones (Simone et al., 2000; Dolan, 2001; Rahman et al., 2002), and (8) regulation and control (Brauer et al., 1997; Ketelaar et al., 2002; Zhang et al., 2003; Müller and Schmidt, 2004). In particular, a surge in research activity in the areas mentioned above has appeared in the past decade in the model plant Arabidopsis thaliana (Ma et al., 2001b; Desbrosses et al., 2003; van Bruaene et al., 2004) because of its wide range of genetic resources available.

In wheat (Triticum aestivum L.), it is well known that root hairs generally develop both on seminal and nodal roots (Esau, 1977; Ma, 1999). The typical density of root hairs on a root was of several hundred hairs per square millimeter, and the total length of all the root hairs of a typical wheat plant could reach more than 10 km (Li, 1979). However, literatures on wheat root hairs are insufficient and fragmentary (Xing et al., 1998; He et al., 2006). The forerunners have mainly studied root hair formation (Gahooonia et al., 1997), morphology and structure (Gassmann and Schroeder, 1994; Gahooonia et al., 1997; Ma, 1999), molecular genetics (Shan et al., 2005), root hair-nutrient relations (Bole, 1977; Gahooonia et al., 1997), and manipulation of root hair growth (Xing et al., 1998; Kalaptur et al., 2004). Moreover, the knowledge
about wheat root hair is largely based on solution-cultured experimental materials from the laboratory, but data concerning the kinetics of formation and morphology of root hairs in situ during the growing period in the actual wheat production (Ma, 1999) and their importance to the plant (Baluska, 2000) are still lacking. What drew the authors’ attention the most in this current study was those hairy structures on the basal portion of a wheat nodal root. These structures lasting for a long time in middle and late growing period and stuck fast with lots of soil particles were defined as special root hairs (He et al., 2006). However, special root hairs have not been well understood yet, and little is known in areas of formation, morphology, structure, the mechanism responsible for physiological functions, and so on. Therefore, the main objective of this study was to investigate formation and morphological characteristics of special root hairs in the actual production practice under one nitrogen treatment(120 kg/ha) so as to provide new insights into regulation of special root hair development and improvement of physiological vigor of the root system in order to realize high-yield and good-quality cultivation.

MATERIALS AND METHODS

The experiment was conducted in the growing season of 2006 to 2007 in a sandy loamy soil on the farm of Henan Agricultural University, Zhengzhou, Henan, China (34° 48′ N, 113° 42′ E). In the arable layer of soil, content of organic matters, total nitrogen, alkali-hydrolyzed nitrogen, available phosphorus, and available potassium was 17.8 g/kg, 0.99 g/kg, 57.9 mg/kg, 44.4 mg/kg, and 204.8 mg/kg, respectively. Soil pH value was 7.9, soil bulk density was 1.1 g/cm³, soil porosity was 50%, field moisture capacity was 65%. The state-released cultivar, Yunong 949 (Guoshennmai 2005015), was used as the experimental materials.

Experimental design

A completely randomized design was employed with treatment levels of 120 kg /ha with replications. The experiment plot was 17.4 m² (5.8 x 3 m), with four replicates. Row spacing was 25 cm. A completely randomized design was used with three replications for each treatment levels of nitrogen 0, 120 and 240 kg /ha. The plot size was 5.8 x 3 m and the row spacing was 25 cm.

Root sampling and observation

The plant population was adjusted to 240 seedlings/m², equal to 4176 seedlings/plot. Fifteen representative wheat plants with expected root samples at each observational date were dug out from the arable soil of 25 to 30 cm thick at jointing stage(2007-03-14), at 7, 14, 21, 28, 35, 42, 49, 56, 63 and 72 days after jointing, and at late dough stage, respectively. A 40 to 50 cm interval for each row between 2 running sampling dates was preserved to avoid influence of the sampling gap on representativeness of plants at the consecutive sampling date.

Experimental design and research method

The earth attached root samples was pre-soak for 2 h to make it convenient to separate earth from the roots and to maintain vigorous root hairs. The root samples with several layers of wet gauze, was wrapped, put inside a plastic bag, and then transferred to the laboratory. The root samples were wash clean and the basal parts of nodal roots with special root hairs was randomly and attentively selected; 15 to 20 representatives was selected. The basal root parts were fix in Carnoy’s fixative for 30 min, and then transfer and preserve in 70% alcohol for later observation. By a common dissecting microscope (OLYMPUS CH20-BM), the forming site was carefully observed; occurring density, length and diameter of special root hairs on a nodal root (Figures 1 to 4).

Introduction of wheat variety

The wheat variety named Yunong 949 (Guoshennmai 2005015), varieties of sources: (Zhengtaiyu 92215/90m434) F1/90(232), selection by the Henan Agricultural University. It belongs to the weak springness, the mid-maturation. Plant height was about 80 cm. Suitable sowing period was October 10 to 25, the suitable plant population was 2.1 to 2.7×10⁶ seedlings/ha. Suitable for sowing in the central and north of Henan Province, in northern of Anhui Province and Jiangsu province, in central Shanxi Province, in Heze of Shandong Province which were the high-yield wheat production field.

Field management

The previous crop, slesbania (Sesbania cannabina Pers.), was plowed as ground manure at its full flowering stage. Half the amount of N fertilizer in different treatments was ground fertilized with 540 kg hm² calcium superphosphate and 187.5 kg/ha potassium chloride, and the other half of N fertilizer was top dressed at jointing stage. The sowing date was 2006-10-14. Seedlings were thinned and established at three leaf stage, and the plant population was adjusted to 2.4 × 10⁶ seedlings/ha. Other field managing practice of the experiment was just the same as in the common high-yield wheat production field. Monthly total precipitation respectively was 162, 50, 0, 59, 6, 0, 14, 64, 16 and 25 mm, and a total of 396 mm during the growing period (from 2006-09 to 2007-07). Irrigated 15, 30 and 30 m³ in 2007-11-25, 2008-03-05 and 2008-04-15 by spraying irrigation respectively.

Statistic and analytic methods

The data were analyzed by software SPSS 17.0.

RESULTS AND ANALYSES

Formation of special root hairs on a nodal root

Under growing conditions of the field experiment, the special root hair forming zone was limited to the adaxial or proximal portion (x̄ =10.2 cm, SD=0.59) of a nodal root after jointing stage. These special root hairs unevenly distributed on different segments of the basal root portion. By the number of root hairs formed, the basal nodal root portion could be divided into 3 segments from the proximal to distal end: the concentrated segment, the moderate segment, and the sparse segment. Length of these 3 segments was averagely 2.5 cm (SD=0.29), 2.7 cm (SD=0.53), and 5.0 cm (SD=0.28), respectively.
Concentrated root hairs were characteristic of the concentrated root segment. From jointing to anthesis or early grain formation, length of the concentrated segment was averagely 2.9 cm (SD=0.33). After anthesis or early grain formation, length of the segment decreased. At late dough stage, the length was even less than 2 cm ($\tau=1.9$ cm, SD=0.06), which was decreased by 58.9% compared with the maximum length over the observation time.

Regression analysis showed that length of the concentrated segment after jointing stage ($y$) was significantly negatively correlated to days after jointing ($x$):
Figure 3. Morphology of special root hairs on the sparse segments of wheat nodal roots.

Regression analysis showed that length of the moderate segment after jointing stage ($y$) was significantly negatively correlated to days after jointing ($x$):

$$y = -0.0302x + 3.7258, r = -0.810^{**} (P<0.01).$$

On the contrary, length of the sparse root segment increased after jointing. At late dough stage, the average length reached to the maximum over the observation time, 7.2 cm (SD=0.61), which was 2.4 folds longer than the

$$y = -0.0233x + 3.3394, r = -0.870^{**} (P<0.01).$$

Similar to those of the concentrated segment, dynamics of length of the moderate root segment decreased as advance in growing period. Rather different from the variation in length of the concentrated segment, length of the moderate segment decreased by a greater extent after mid-grain-filling stage. At late dough stage, length of the moderate segment decreased by 72.9% compared with the maximum length over the observation time.
minimum, 3.0 cm (SD=0.51). Successive observations also showed that death and shedding of special root hairs first occurred on the distal end of the sparse segment. Dynamics of length of the sparse segment over the growing period indicated that special root hairs aged and ceased functions, if any, faster and faster as advance in growing period. Regression analysis showed that length of the sparse segment after jointing stage (y) was extremely significantly correlated to days after jointing (x): 

\[ y = 0.0574x + 3.0258, \quad r=0.980 \quad (P<0.01). \]

**Occurring density of special root hairs**

Occurring density of special root hairs on different basal segments of a nodal root varied from 40 to 138 hairs/mm² (\( \bar{x} =90 \) hairs/mm², SD=7.9) from jointing to grain formation, however, after grain formation the density significantly decreased (Figure 5). At late dough stage, the density was averagely as low as 49 hairs/mm² (SD=4.55). As showed in Figure 5, either in the concentrated, the moderate, or the sparse segment of a nodal root, dynamics of occurring density of special root hairs from growing stage to stage were similar, while at a certain growing stage difference in the density among the different nodal root segments was extremely significant (P<0.001). Average occurring density of special root hairs on the concentrated, the moderate, and the sparse segment was 128 hairs/mm² (SD=8.0), 100 hairs/mm² (SD=6.4), and 45 hairs/mm² (SD=8.6), respectively, from jointing to grain formation. After grain formation, the corresponding occurring density on the 3 root segments was 79 hairs/mm² (SD=3.9), 63 hairs/mm² (SD=4.3), and 23 hairs/mm² (SD=2.9), respectively.

Regression analysis further showed that negative correlations between occurring density of special root hairs (y) and days after jointing (x) were either significant or extremely significant. The regression equation and correlation coefficient value for the concentrated, the moderate, and the sparse segment were as follows:

\[ y = -0.5714x+139.24 \quad (r=-0.650) \quad (P<0.05), \]
\[ y = -0.5325x+111.82 \quad (r=-0.720^{**}) \quad (P<0.01), \]
\[ y = -0.3463x+52.727 \quad (r=-0.750^{**}) \quad (P<0.01), \]

**Length of special root hairs**

A moderate variation was observed in length of special root hairs on different root segments from jointing to grain formation. The root hair length on the concentrated, the moderate, and the sparse segment was averagely 0.96 mm (SD=0.04), 0.48 mm (SD=0.03), and 0.18 mm (SD=0.01), respectively. After grain formation, root hair length decreased. At late dough stage root hair length for the concentrated, the moderate, and the sparse segment decreased to 0.69 mm (SD=0.04), 0.37 mm (SD=0.03), and 0.15 mm (SD=0.01), respectively (Figure 6). As indicated Figure 6, length of special root hairs on the concentrated segment was longer than that on the moderate segment, and in turn, the later was than that on the sparse segment. Differences in length of special root hairs on the 3 segments were significant (P<0.001). Comparatively, dynamics in length of special root hairs on the sparse segment from jointing to mid-grain filling stage were moderate, but the hair length at around late dough stage was significantly reduced. With respect to the concentrated and the moderate root segment, the hair length decreased significantly after grain filling stage. Regression analysis showed that negative correlations between length of special root hairs (y) and days after jointing (x) were inconsistent for the concentrated, the moderate, and the sparse segment. The regression equation and correlation coefficient value for the

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**Figure 5.** Occurring density of special root hairs of wheat nodal roots. Scale bar = 1 mm.

**Figure 6.** Length of special root hairs of wheat nodal roots. Scale bar = 1 mm.
Diameter of special root hairs

Diameter of special root hairs on different nodal root segments varied a little. On the concentrated, the moderate, and the sparse segment, the root hair diameter was 7.2 μm (SD=0.65), 6.1 μm (SD=0.50), and 5.0 μm (SD=0.53), respectively, from jointing to earring (Figure 7). After earring, the diameter of the root hairs on those 3 corresponding root segments significantly decreased to 6.2 μm (SD=0.73), 4.8 μm (SD=0.66), and 3.2 μm (SD=0.52), respectively (Figure 7). Figure 7 also showed that the special root hairs on different segments of a nodal root significantly differed in diameter. After booting the order of diameter of special root hairs on the different root segments was consistently as the concentrated segment > the moderate segment > the sparse segment (P<0.001) only with an exception that an irregular change was observed during the period 7 to 21 days after jointing. Regression analysis showed that negative correlations between diameter of special root hairs (y) and days after jointing (x) were inconsistent for the concentrated, the moderate, and the sparse segment. The regression equation and correlation coefficient value $y = -0.0316x + 7.5909$ ($r = -0.370$) were not significant for the concentrated segment while for the moderate segment, the equation and correlation coefficient value $y = -0.0316x + 6.5909$ ($r = -0.690$) ($P<0.05$) were significant and for the sparse segment the equation and correlation coefficient value $y = -0.0512x + 5.9561$ ($r = -0.880$) ($P<0.01$) were extremely significant.

**DISCUSSION**

It has been well-known that a plant root hair is generally a long tubular outgrowth of an epidermal root cell (Esau, 1977; Kim et al., 2007) via polarized tip growth (Ridge and Emons, 2000; van Brunaen et al., 2004). It is also widely accepted that wheat root hairs forms on the mature zones both of seminal and nodal root tips. When cultured in the laboratory or grown under the field production conditions, root hairs on the aged root tissues gradually died and shed off (with a life span of 15 to 20 days) as the mature root zone advances downwards into the deep layers of soil and subsequently root hairs forming segments moved down into the soil.

Under the typical high-yield field conditions (sandy loam) in Zhengzhou of Henan Province, wheat plant was noted to root into a soil layer 1 m deep at jointing stage (Ma, 1999), indicating that the normal root hair occurring segments were about 1 m away from the plant base at that time. However, it is interesting that there are “hairy structures” universally formed on the 10 cm basal portion of a normal nodal root after jointing. One could hardly tell the visual difference between these hairy structures and those normal root hairs. If the hairy structures are live root hairs, one cannot explain why these root hairs did not shed off the aged portion of the nodal roots even as late as at middle and late growing stages.

The authors’ previous work defined these hairy structures as special root hairs, and reported an abundant production of special root hairs on nodal roots (He et al., 2006). Furthermore, other observations both from research activity and production practice show that special root hairs of this kind not only occur in wheat, but also in other gramineous species as barley (Hordeum vulgare L.). Preliminary results from this study seem to indicate that these special root hairs are somewhat as the normal root hairs.

Special root hairs seldom form on the root parts below the 10 cm basal portion (surely not including live root tips). They are unevenly limited to the special root hair forming portion and assume a gradual decreasing trend from the basal end downwards.

The facts that length of the concentrated and the moderate root segment decreased but length of the sparse segment increased and that occurring density of special root hairs decreased as advance in growing period suggested that: (1) special root hairs decreased in response to ageing nodal roots and strengthening lignification of roots; (2) mutual adaptation existed between development of special root hairs and aboveground parts of the plant, especially after grain formation roots were in decay as grains became the metabolic centers of nutrients. Additionally, such a varied distribution pattern of special root hairs may play a pronounced role in uptake of nutrients, if any, at middle
and late growing stages. However, it needs to verify further if the special root hairs play the same role as the normal root hairs. Given that the physiological roles the special root hairs play are just what the normal root hairs do, it appears that one cannot emphasize too much the physiological importance of special root hairs to absorb, transport and partition water and nutrients in the arable layer of soil. Thus, the hope is that this hypothesis will stimulate further investigations before the structure and physiological significance of special root hairs are fully understood.

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