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Review

Advances in root hairs in Gramineae and *Triticum aestivum*

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Relevant literatures in the past ten years showed that lots of research activities have been conducted in diverse aspects of root hairs, in particular, of the model plant, *Arabidopsis thaliana*. However, data on Gramineae root hairs are unsystematic. Much more research activities have been done theoretically than practically, and qualitatively than quantitatively. There are few studies relating active, quantitative and precise regulation and control of root hairs. With regards to wheat root hairs, literatures are insufficient. Particularly, data concerning the kinetics of formation, morphology and structure of root hairs *in situ* in the actual wheat production are still lacking. Future research need to be conducted before we could actively control development and improve physiological functions of wheat root hairs. Moreover, although careful observations found a hairy structure named 'special root hair' on the basal portion of a nodal root in wheat, little is known about its morphology, structure, among others.

Key words: Research prospects, root hair, Gramineae, *Triticum aestivum* L.

INTRODUCTION

Root hairs are specialized root epidermal cells playing important roles in increasing surface area for absorption and transportation of water and nutrients, and contributing to the adhesion of the growing root to the rhizosphere (Bibikova and Gilroy, 2003; Esau, 1977; Feng et al., 2001). To date, lots of research activities have been conducted in diverse aspects of root hairs: Morphogenesis or initiation (Bibikova and Gilroy, 2003; Cho and Cosgrove, 2002; Kim et al., 2007), formation and development (Bruaene et al., 2004; Galway et al., 1994; Michael, 2001; Müller and Schmidt, 2004), morphology (Czarnota et al., 2003) and (ultra-)structure (Czarnota et al., 2003; Kalaptur et al., 2004; Ove ka et al., 2005), exudate secretion (Czarnota et al., 2003; Yang et al., 2004), uptake of water and nutrients (Gahoonia et al., 1997; Kristoffersen et al., 2005; Ma et al., 2001a, 2001b), genetic and molecular basis (Grierson et al., 2001; Kwasniewski and Szarejko, 2006; Schiefelbein, 2000; Wang et al., 2004), interaction with environmental factors, such as hormones (Michael, 2001; Rahman et al., 2002; Simone et al., 2000), and control and regulation (Ketelaar et al., 2002; Michael, 2001; Müller and Schmidt, 2004; Zhang et al., 2003). In particular, a surge in research activity in the areas mentioned above has appeared in the past decade in the model plant, *Arabidopsis thaliana* (Bruaene et al., 2004; Galway et al., 1994; Ma et al., 2001b; Schiefelbein, 2000) because of its wide range of genetic resources available.

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ROOT HAIRS IN GRAMINEAE AND *Triticum aestivum*

Gramineae root hairs

Generally speaking, results obtained from other species can be used for reference when we study wheat (*T. aestivum* L.) root hairs. In *Arabidopsis* , foregoers have recently explored root hair initiation and gene expression (Cho and Cosgrove, 2002; Galway et al., 1994), root hair development and its genetic basis (Desbrosses et al., 2003; Grierson et al., 2001), morphology and its genetic control (Schiefelbein, 2000), *in vivo* dynamics of microtubules (Bruaene et al., 2004) and nucleus positioning (Ketelaar et al., 2002), the role of ethylene in root hair growth (Dolan, 2001), regulation of root hair development by light (Simone et al., 2000), phosphorus (Ma et al., 2001b), ethylene and auxin (Dolan, 2001; Rahman et al., 2002; Zhang et al., 2003), and other environmental factors (Müller et al., 2004).

Although literatures on *Arabidopsis* root hairs are relatively rich, those on Gramineae root hairs are with many gaps. In barley (*Hordeum vulgare* L.), more attention was focussed on molecular genetics of root hair formation (Kwasniewski and Szarejko, 2006) and development-phosphorus relationships (Gahoonia and Nielsen, 2004; Gahoonia et al., 1997; Kristoffersen et al., 2005). With regards to rice (*Oryza sativa* L.), root hair morphogenesis and its molecular genetics (Kim et al., 2007) and morphology and microstructures (Suzuki et al., 2003; Yu et al., 2005), and the role of root hairs in silicon uptake (Feng et al., 2001; Ma et al., 2001a) were investigated. As for maize (*Zea mays* L.), root hair microstructure (Brauer et al., 1997; Gestel et al., 2003), and development and its molecular genetics (Gestel et al., 2003; Zhu et al., 2005) were reported. In sorghum (*Sorghum bicolor* (L.) Moench), only a few studies were conducted on sorgoleone secretion (Czarnota et al., 2003; Yang et al., 2004) and manipulation of development (Yang et al., 2004).

Advance in *T. aestivum* root hairs

In wheat, it is well known that root hairs generally develop both on seminal and nodal roots of wheat (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, the literature on wheat root hair is insufficient and fragmentary (He et al., 2000, 2006; Xing et al., 1998). The forerunners only primarily studied root hair formation (Gahoonia et al., 1997), morphology and structure (Gahoonia et al., 1997; Gassmann and Schroeder, 1994; Ma, 1999), and molecular genetics (He et al., 2007; Shan et al., 2005; Shi et al., 2006), root hair-nutrient relations (Bole, 1973; Gahoonia et al., 1997), and manipulation of root hair growth (Kalaptur et al., 2004; Xing et al., 1998).

He et al. (2006) noted the hairy structures on the basal portion of a nodal root. These structures, lasting for a long time in the middle and late growing period and stuck fast with lots of soil particles, have once been defined as 'special root hairs'. But the special root hairs is yet to be well understood, and little is known in areas of morphology, structure, the mechanism responsible for physiological functions, and so on.

PROSPECTS OF RESEARCH ON ROOT HAIRS IN GRAMINEAE AND *Triticum aestivum*

Gramineae root hairs

Comparatively speaking, more attention has been paid to studies in areas of initiation, morphology and genetic basis than in areas of physiological characteristics and functions. Much more research activities have been done theoretically than practically, and qualitatively than quantitatively. Of limited studies on regulating and controlling root hairs, there are few relating active, quantitative and precise regulation and control of root hairs. This is especially true for Gramineae root hairs. Particularly, data seem to be more deficient on root hairs in Gramineae. As for the different species in Gramineae, research progress did not keep pace with each other. For example, deepness and broadness of studies in millet, barley and sorghum followed either rice or maize. With regards to any species in Gramineae, current data are unsystematic and far away from the need of production practice.

T. aestivum root hairs

Normal root hairs in T. aestivum

Up to now, literatures on wheat root hairs are not with few gaps. Future research need to be conducted before we could actively regulate and control development and improve physiological functions of wheat root system by the academic achievements. Therefore, further related studies are needed to bridge the gaps in different aspects.

The knowledge about wheat root hair is largely based on solution-cultured experimental materials from the laboratory. A plant root hair is generally a long tubular outgrowth of an epidermal root cell (Esau, 1977; Kim et al., 2007; Li, 1979) via polarized tip growth (Bruaene et al., 2004) . However, under conditions of field production, extrusion of soil particles leads to kinks and swellings of root hairs. This conclusion is supported by the microscopic results from some field-based studies (Kim et al., 2007; Ma, 1999) . At present, data concerning the kinetics of formation, morphology and structure of root hairs *in situ* during the growing period in the actual wheat production (Ma, 1999) and their importance to the plant are still lacking.

Special root hairs in T. aestivum

It has widely been accepted that wheat root hairs are formed on the mature zones of both the 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 d) as the mature root zone advances downwards into the deep layers of soil and subsequently root hairs forming segments moved down into the soil. But there appears a special phenomenon about special root hairs.

Normally, wheat plant could root into a soil layer 1 m deep at the jointing stage under the conditions of the typical high-yield field (sandy loam) in Zhengzhou, Henan, China, indicating that the or normal root hairs occurring segments were about 1 m away from the plant base. However, it is interesting to note that special root hairs are universally formed on the 10 cm basal portion of a normal nodal root after jointing as showed by research and production practice (Zhang et al., 2009). One could barely tell the morphological difference between these hairy structures and those normal root hairs. If these structures are live root hairs, one cannot explain why root hairs did not shed off on the aged portion of the roots at the middle and late growing stages, and does not know how they form and what physiological functions they play.

Careful observations supported the fact that these hairy structures are with many soil particles adhesive to their surface. Previous work reported an abundant production of special root hairs on the nodal roots, and such special root hairs were observed to be different from normal root hairs in forming site and life span (He et al., 2006). In addition, other observations both from research activity and production practice shows that such special root hairs are not only formed in wheat, but in other species of Gramineae (He et al., 2006).

In the high-yield production practice, it was also found that the special root hairs are unevenly distributed on the root hair forming portion, assuming a gradual decreasing trend from the basal end downwards. The fact that length of the concentrated and the moderate root hair forming segments decreased while length of the sparse root hair forming segment increased and 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 including root hairs were in decay, as grains became the metabolic centers of nutrients (Zhang et al., 2009). 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.

It was observed that special root hairs are commonly protruded and branched and in the middle and late growing period, the root hair cell walls thickened (Zhang et al., 2009). As such, this might be some of the mechanisms of special root hairs that prevent the root hair cells from losing water and from defending environmental stresses, such as diseases and pests. Field observations also confirmed that special root hairs lived long, some of which even lasted a long period from jointing to late dough stage. Due to the length of the growing period, it is not clear if the special root hairs are living cells and if they play the same role as the normal root hairs. Given that the physiological roles the special root hairs played are just like those the normal root hairs do, it appears that one cannot emphasize too much on 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 physiological significance of special root hairs is fully understood.

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