Structure and Function of the Root Cap

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Abstract: The root cap (RC) is a multilayered dome of spindle-shaped parenchyma cells that overlies the growing root tip. It is present in the roots of almost all crop species. This paper briefly reviews some topics on the structure and function of the RC in the major crop species such as maize and rice. Special attention is placed on its contribution to the root system formation, that is, the elongation and growth direction of axile roots. The cells produced in the RC meristem are pushed forward as new cells form beneath them, and eventually the cells on the periphery of the RC fall off. The life cycle of RC cells of maize has been studied extensively and ranges from one to seven days. Approximately 4,000 to 21,000 cells are present in a complete maize RC, and 1,400 to 3,200 sloughed cells can be found in the rhizosphere soil per day per root. These cells, called root border cells (RBCs), mix with RC mucilage and play important roles for the root growth in soil. The RBC-mucilage complex effectively reduces the resistance roots experience during penetration into field soil, about 30–40% of the resistance being reduced by the presence of RC alone. The RC is also a tissue integral to gravitropism, and is known to determine the direction of root growth. The size of amyloplasts and coumellae in RCs has a strong influence on determining the growth angle of axile roots. The function of the individual regions of the RC and how the RC tissues and cells are formed should be studied further to advance our understanding regarding the critical roles of the RC in crop root growth.

Key words: Exudation, Gravitropism, Growth direction, Mucilage, Root apical meristem, Root border cells, Root elongation rate, Root system.

The mass of roots associated with soil-grown crops is referred to as a root system. The crop root system is subjected not only to genetic variability but also to the phenotypic plasticity in response to various environmental signals (Weaver, 1926; Weaver and Bruner, 1927; O’Toole and Bland, 1987). Individual roots comprising a root system, however, have several common inherent characteristics relevant to growth and structures. In contrast to the leaves and stems, which are exogenously produced from a shoot apical meristem, roots develop endogenously either from stems (i.e., nodal roots) or from the axile root (i.e., lateral roots). Furthermore, while the stele of stems differs between plant species, the stele of roots is always actinostele regardless of the species. Unlike stems, the tips of all roots have a root cap (RC), which physically protects the root apical meristem as it penetrates the soil. RCs have many other important functions, most of which are closely related to their cellular structure. This paper provides a brief review of several topics related to the structure and functions of RCs of major crop species such as maize and rice. Special attention is placed on its contribution to the root system formation, that is, the elongation and growth direction of axile roots. Related review articles have been recently published elsewhere (Barlow, 2002; Hawes et al., 2002), and therefore, relevant information regarding the structure of the RC (Barlow, 2002) and function of root border cells (RBCs, Hawes et al., 2002) should also be acquired from these papers as a reference.

1. Formation and renewal of the RC

(1) Structure and formation of the RC

The RC is a dome of spindle-shaped parenchyma cells that covers the growing root tip. It is present on roots in all the major crop species, except for a few plant species such as aquatic, marshland, and parasitic species (Barlow, 2002). The structure of RCs varies across plant species. In rice and maize, for example, the central region of the RC consists of cells arranged in longitudinal files making up a columella (Moore and McClelen, 1983). In such plants, the RC can be divided into the initial cells, columella, and the lateral RC that surrounds the columella (Fig. 1). Taking into account its structure and the location of its cells, the lateral RC can be divided into three regions, namely, inner cells, outer cells, and root border cells (RBCs). RBCs are the sloughed RC cells that accumulate on the RC periphery. Most RBCs are single cells (Fig. 2)
and can be collected non-destructively without the use of special equipment. The collected cells are generally both genetically and physiologically intact. Their potential contribution to the understanding of cell biology and the interaction between plant roots and soil microorganisms has drawn much attention from scientists in many areas of plant and soil biology (Hawes et al., 1998, 2002).

(2) Root apical meristem and the RC

Like other root tissues, RCs are produced by a part of the root apical meristem. The RC can easily regenerate itself, even when surgically removed (Barlow, 1974; Barlow and Hines, 1982). While cells in the shoot apical meristem elongate only towards the base of lateral organs and stem tissues, cells in the proximal part of the root apical meristem produce cells in the direction of the root base, whereas those in the distal, or root-cap, meristem produce cells in the direction of the root apex. Nevertheless, cells in the root apical meristem are arranged in a simple and orderly fashion.

The relationships between the so-called initials and the individual plant tissues to which they give rise differ across plant species. In some plants, both the epidermis and the RC share an initial, whereas in others, the RC has its own initials, which are independent of those of the epidermis (Williams, 1947). In plants in which the initials of the RC are independent of those of the epidermis, periclinal and anticlinal divisions can be observed in the region adjacent to the root body-RC junction. These cell divisions are associated with the formation of the RC, and mostly occur in the first layer of the cells adjacent to the RC junction (Harkes, 1973). Periclinal division, in particular, occurs frequently in the central region of the RC, and is believed to give rise to columella. The cells along the periphery of columella cells are sometimes referred to as the rhombic meristem (Kawata et al., 1977), whose mechanism has not been clarified to date.

(3) Root growth and the RC

In the center of the root apical meristem there is a group of cells called the quiescent center, which does not divide as fast as the cells of the rest of the meristem. The life cycle of the cell in this region is known to be very long (Clowes, 1965). The presence of a quiescent center was first suspected in 1954 by Clowes, who found that the arrangement of columella cells in the region adjacent to the root body-RC junction remained unchanged over a certain period of time. Later on, microautoradiography experiments (Clowes, 1956a,b, 1958) and the observation of cell division processes (Jensen and Kavaljian, 1958) further confirmed the presence of a quiescent center. However, during the course of growth, organization of root apical meristem may change from “closed type” to “open type”, a fact which indicates that the activity of quiescent center cells may change over time (Armstrong and Heimsch, 1976).

The structure of the RC itself does not change over the course of root growth except for the very early stages of root initiation. For example, in rice, the RC that is formed immediately after root initiation (i.e., the primary RC) is quite different from the RCs formed at a later growth stage. The columella that can be clearly identified within the RC during...
later stages of growth is still quite immature in the primary RC, which merely contains parallel layers of cells in its central region. However, the RC formed after the sloughing off of the primary RC has a clearly distinguishable columella in its central region, because periclinal division, which is associated with columella formation, becomes accelerated shortly after the root initiation. The diameter of axile roots is subject to variation, and the diameter of the root apex also changes over the course of growth. However, there is a close interrelation between the diameter of the rice root apex and the size of the individual regions of the RC (Kawata et al., 1977). Thus, the structure of the RC of the axile roots more or less remains the same throughout the lifespan of the plant, even though there may be variations in the size of the RC.

(4) Life cycle of the RC

The cells produced in the RC meristem are pushed forward as new cells form beneath them, and eventually, the cells on the periphery of the RC fall off. The life cycle of RC cells has been studied in detail using maize as a model plant species. There is a rapid increase in amyloplasts containing starch granules as the cells originating from initial cells in the root apical meristem begin to form columella (Kawata et al., 1979; Moore and McClelen, 1983). The cells that have reached the periphery of the lateral RC have a reduced number of amyloplasts and an increased number of other organelles. The volume of these cells is estimated to be 10 times that of young cells that have just begun to divide (Juniper and Clowes, 1965). In particular, a prominent increase in the number and size of the Golgi apparatus (a cell organelle closely associated with secretory function), which produces a large number of

secretary vesicles (Fig. 3), can be found in the lateral RC cells, especially in the roots grown in compacted soil (Iijima and Kono, 1992). Details regarding Golgi vesicles will be discussed later in this paper. Old and mature cells that fall off from the peripheral region of the RC mostly consist of vacuole.

The cells that have reached the lateral RC slough off from the RC surface into the soil. According to a previous study, a maximum of 3,000 to 7,000 cells may fall off per day from the RC of hydroponically grown maize (Clowes and Woolston, 1978). In case of soil-grown maize seedlings, 1,400 to 3,200 cells will be found in the rhizosphere soil (Iijima et al., 2000, 2004b). However, the number of cells that fall from the RC at any one time differs across plant species. In 1986, Hawes and Pueppke counted the number of cells sloughed off from the RC of various plants by shaking the root tip gently in the water and counting the number of cells that had been sloughed into the water. While only ten cells were liberated from the RC of tobacco plant, as many as 5,000 cells were removed from the RC of pine, showing a significant variation in the number of sloughed-off cells across species. Assuming that the size of the RC and the size of its cells remain unchanged over the developmental stages of the root, the number of the sloughed-off cells should be equivalent to the number of new cells produced by the RC meristem. Thus, if we can identify the number of cells comprising the RC, it will be possible to estimate the life cycle of RC cells, i.e., the length of time required for the new cells produced by the apical meristem to reach the lateral RC and slough off.

(5) Renewal of the RC

The life cycle of maize RC cells has been estimated
in several previous studies. Clowes (1961) conducted a microautoradiographic analysis of tritium-labelled thymidine uptake in cells in the S phase of the cell cycle, examined cells in the metaphase of the cell division cycle by using colchicine to inhibit spindle formation during cell division, and reported that the cell doubling time (the time required to double the cell population) of maize RC cells was approximately 12 hours. Similar methods were used in a study conducted by Barlow and Macdonald (1973), who estimated that the cell doubling time of the columella and that of the lateral RC is 14 hours and 22.5 hours, respectively. Clowes (1976) used a squash method to estimate the number of cells comprising the RC, and reported that the RC consists of 4,000 to 21,000 cells. These data suggest that the cells in the entire RC cells would be replaced by new cells within 1 to 1.5 days of RC formation (Clowes, 1971, 1976).

However, some researchers believe that the RC in maize has a longer life cycle. The surgically removed RC is known to regenerate itself within three or four days as a result of the increased activity of quiescent center cells in response to the removal of the RC (Barlow, 1974). According to a previous study that inhibited cell plate formation using caffeine to create cells with two nuclei and monitored the movement of these cells within the RC, it takes seven days for the cells to travel lengthwise along columella and two to three days to move widthwise across columella (Barlow, 1978). The results from these studies suggest that the life cycle of the RC should be two to seven days. Recently, Iijima et al. (2003a) examined the median longitudinal section of the RC (Fig. 4), and estimated the number of RC cells according to a morphometric method developed by Bengough et al. (2001). They reported that the RC grown in loose and compacted soil consists of 6,900 to 5,930 cells, with approximately 1,570 to 2,010 new cells being produced per day, respectively. These data suggest that replacement of all the RC cells by new ones would occur within 2.9 to 4.4 days of RC formation (Iijima et al., 2003a).

It is important to note that the shape of the sloughed-off RC cells may vary across plant species. For example, while the primary RC cells of paddy rice fall off in layers, the RC cells that are produced later in the growth stage of the rice plant tend to slough off one by one or in small patches (Kawata et al., 1979). However, the cells on the peripheral region of the RC usually fall off in layers, regardless of the growth stage of the axile roots. On the other hand, the RC cells of maize are known to fall off one by one (Morita and Iijima, 1999). Variation in the shape of the sloughed-off cells across plant species may be due to the difference in the RC cell structure. A cross section of the RC of various plants can be largely categorized into the following three types (Rost et al., 1996): a) cells arranged in concentric circles (Linum grandifolium), b) cells arranged in a spiral (Arabidopsis thaliana), and c) cells arranged in arcs (Gossypium hirsutum).

2. **Elongation of Roots and the RC**

The RC is located at the very tip of the root, in the front-line of root-soil contact, physically protecting the root apical meristem during root penetration into the soil. The RC aids root penetration not only when exposed to considerable mechanical impedance but also under ordinary growing conditions in the crop field. The friction created as the root grows between soil particles is reduced by sloughing off of RBCs and by secretion of mucilage.

(1) **Elongation of roots and RBCs**

Some of the RBCs are known to survive at least a few days in the rhizosphere soil after their release from RC (Vermeer and McCully, 1982). When cultured under appropriate conditions, the RBCs can stay alive for up to a month (Gochnauer et al., 1990). Furthermore,
when cultured in a medium containing a plant growth regulator, RBCs can be stimulated to undergo cell division (Hawes and Pueppke, 1986). RBCs are believed to play important biological roles for the growth of the root (Hawes et al., 1998). Furthermore, they are known to supply carbon to the soil reservoir, impacting the carbon cycle in a given ecosystem. However, little is known about the roles of RBCs in the rhizosphere soil because RBCs are glued to the soil particles by the mucilage secreted by the root, and detaching them from the soil particles can easily destroy the cell walls of RBCs. According to a recently developed method to quantify the RBCs in the clayey soil, recovery rates of 90 ± 1% were achieved using a combination of surfactants, sonication, and centrifugation (Iijima et al., 2004b).

Reduction of the friction between soil and the growing root is believed to be one of the most important biological roles of RBCs (Bengough and Mckenzie, 1997). In order to prove this hypothesis, Iijima et al. (2000) conducted a study using maize radicles grown in compacted soils. The number of maize RC cells sloughed into sand increased as a result of higher mechanical impedance, from 1930 to 3220 d−1 per radicle. This represented a 12-fold increase in the number of cells sloughed per mm root elongation. Furthermore, the proportion of the RC surface covered by RBCs was estimated to be 7% for the control and 103% for the compacted soil, respectively. These data suggest that RBCs act as a cushion between the root apical meristem and the soil during root penetration into the compacted soil (Fig. 5).

(2) Elongation of roots and the RC mucilage

Amount of mucilage secreted by the RC in maize has reported to be positively correlated with the root elongation rate, implying that fast-growing roots exude more mucilage (Iijima et al., 2003c). In fact mucilage has long been believed to play a major role in reducing the friction from root growth in soil. As mentioned earlier, the Golgi apparatus is especially active in the cells comprising the lateral RC. Both the size and number of cisternae that comprise the Golgi apparatus and secretory vesicles increase steadily as these cells become older. Secretory vesicles that have reached the periphery of the outermost cell walls bind and fuse with plasma membrane, which results in the release of mucilage (Fig. 3). As a result, the whole RC will be covered by the mucilaginous layer (Fig. 2). Although many researchers have assumed that the RC mucilage potentially help root penetration into the soil, this assumption has not yet been proven directly due to the difficulty involved in the quantitative assessment of the RC mucilage (Guinel and McCully, 1987). A quantitative evaluation of mucilage exudation activities reducing higher soil friction in compacted soil was conducted by the observation of the outermost RC cells (Iijima and Kono, 1992). The lateral RC cells of the maize grown in a compacted soil increased the number of Golgi apparatus and secretory vesicles. This indicated that the secretory activity of the outermost cells of the RC is more prominent in plants grown in compacted soil as compared with the plants grown in loose soil, presenting one piece of collateral evidence that the mucilage may act as a lubricant to aid root penetration into soil.

As discussed above, both RBCs and mucilage will reduce the mechanical impedance roots experience during penetration into compacted soil. The contribution of these two factors was quantified using a decapping technique in which the RC was removed without disturbance to root elongation. Root penetration resistance (actual pressure experienced by the root) of intact and decapped roots were 0.31 and 0.52 MPa, respectively, when the roots were grown in compacted soil (Iijima et al., 2003b). The contribution of RC to the reduction of mechanical impedance of roots during their penetration into soil was reported to be 40% in a sandy loam soil (Iijima et al., 2003b) and 30% in a loamy sand soil (Iijima et al., 2004a). In a series of studies, the contribution of RBCs and mucilage was quantified separately by using decapping and mucilage adding treatments (Iijima et al., 2004a). The contribution of mucilage and the presence of the RC without mucilage to the lubricating effect of the RC (percentage decrease in root penetration resistance) were 43% and 58%, respectively. The treatment of RC without mucilage can be regarded mainly as the effect of the RBCs’ function under the experimental conditions.
3. Roles of the RC mucilage

Mucilage secreted from the RC has several other important functions in addition to reducing mechanical impedance discussed above. Mucilage contains various substances such as carbohydrate, amino acid, organic acid and enzymes (Rovira, 1969; Eastman and Peterson, 1985). Polysaccharide components, which make up the largest proportion of the mucilage, are thought to be a major source of nutrients for soil microorganisms. For this reason, many microorganisms reside in root exudate-amended soil called rhizosphere. Some microorganisms break down substances which cannot be absorbed by the root and convert them into plant usable forms (Curl and Truelove, 1986). Furthermore, some of the substances secreted by the root can solubilize minerals within the soil for plant availability. The mucilage secreted from the tobacco root is known to promote solubilization of cadmium (Mench and Martin, 1991), and the pigeon pear root is known to solubilize iron phosphate (Ae et al., 1990). Carboxyl, which is similar to pectin in structure, may influence cation exchanges, indirectly contributing to nutrient absorption of the root. Acid phosphatase may aid the nutrient absorption by hydrolyzing organic phosphate esters into assimilable inorganic phosphate (Rougier, 1981). Furthermore, mucilage may contain allelopathic compounds that hinder plant growth and these may be discharged into the rhizosphere soil outside the root system.

The mucilage secreted from the RC acts as a glue to bind the soil particles together in clumps forming soil aggregate (Rougier, 1981). Together with the mucilage secreted by the root hair, RC mucilage is known to create a soil sheath that envelopes the root (Wullstein and Pratt, 1981; Buckley, 1982; Sako et al., 1999). Soil sheath is particularly prominent in plants grown in dry soil (Huang et al., 1993), and thus it is believed to prevent root desiccation. This assumption is supported by studies conducted to examine the physical properties of the RC mucilage (Read et al., 1999, 2003). According to these studies, the surface tension of the mucilage is reduced under dry soil conditions, giving moisture to the rhizosphere soil surrounding the root. There is also an increase in the viscosity and elasticity of the soil water along the periphery of the root, which acts to hold the soil in place. Thus, rhizosphere stabilization in soil is achieved, ensuring a constant and steady supply of water to the root zone. To sum up, RC mucilage not only helps prevent desiccation of the root system but also binds the root to the surrounding soil and contributes to the supply of nutrients and water to the root.

4. Root tropism and the RC

Besides all the above-mentioned functions, the RC is also an integral tissue of a plant’s tropisms such as gravitropism, hydrotropism (Takahashi, 1997), and thigmotropism (Ishikawa and Evans, 1992). Although plant gravitropism has been extensively studied in the past, there are still several phenomena relevant to gravitropic response that cannot be fully explained by conventional theories. Most of the previous studies regarding the effects of gravity on plant root growth are mainly focused on the following four topics (Juniper, 1976; Jackson and Barlow, 1981): 1) identification of possible gravity receptors; 2) identification of how gravistimulation sensed by the root is transduced into signals and the characteristics of the gravity signals in plants; 3) identification of the gravity transduction pathway and how the signal is transferred to the cells of the elongation zone; and 4) identification of the mechanisms involved in the root’s curvature response.

1) Perception, transduction and transmission of gravistimulation

Both in roots and stems, gravity perception is strongly believed to involve statoliths (statolith theory). Graviperceptive cells called statocytes are located in the columella of the RC. Amyloplasts in statocytes act as statoliths, which sediment in the direction of the gravity vector, triggering gravitropism. The statolith theory is supported by the following facts: 1) the root ceases to exhibit gravitropism when a certain portion of the RC is surgically removed; 2) the region of the RC where amyloplast are located coincides with the region of the RC that perceives gravity; and 3) gravitropism is lost when amyloplasts are chemically removed but is restored once the amyloplasts are regenerated (Juniper, 1976; Jackson and Barlow, 1981; Moore and Evans, 1986). Recently, Swarup et al. (2005) found that root gravitropism requires the lateral RC and epidermal cells for transport of (and hence for the response to) a mobile auxin signal.

Besides gravitropism, plant roots are also known to show a hydrotropic response. A tendency by plant roots to grow towards moisture has been known since the late 19th century. However, due to the difficulty in distinguishing between hydrotropism and gravitropism, there are few studies available on the mechanism of hydrotropism. In recent years, however, a positive hydrotropic response of the root was confirmed in a study that used a mutant pea plant that did not exhibit gravitropism (Takahashi, 1997). Just as with the root gravitropism, the region of the root that responds to hydrotropic stimulation is the RC (Takano et al., 1995).

The surgical removal of the RC inhibits the gravitropic response of the root but promotes root elongation. A growth inhibitor produced in the RC is thought to be moved from the cap through the apex to the root base, and is believed to affect the gravitropic response of roots. It is not yet scientifically clear exactly how the sedimentation of amyloplasts (statoliths) can affect the chemical signals that alter the amount
and concentration of the growth inhibitor. One theory suggests that gravity-induced sedimentation of amyloplasts acts as a valve that inhibits the passage of growth inhibitor through plasmodesmata (Juniper, 1976). Another theory holds that the endoplasmic reticulum (ER) which is distributed at the periphery of statocytes is pressed upon by amyloplast (Sievers and Volkmann, 1972; Volkmann and Sievers, 1975). Although amyloplasts in mutants that show little gravitropic response sediment in response to gravistimulation, the ER in these mutants do not show a polarized distribution pattern observed in the statocytes of the wild-type. In view of these facts, it can be assumed that amyloplasts and ER are key factors influencing the amount and concentration of growth inhibitors. However, some researchers do not agree with any of the above-mentioned theories (Ransom and Moore, 1983).

On the other hand, although many studies have been conducted in recent years regarding sensory systems in plants, there are still varying views regarding the gravity signal transduction pathway in roots. According to a previous study, the root bends even when the epidermis and outer cortex are surgically removed, indicating that growth inhibitors may pass through the endoderms, not through the epidermis or through the outer cortex (Björkman and Cleland, 1991). However, in similar experiments which removed both tissues in roots, the gravitropic response was observed when the RC mucilage was added to the surgically removed root tip portion. The result from this study indicates that the gravity signal transduction pathway may be transmitted by the presence of RC mucilage (Yang et al., 1990; Maison and Moore, 1991). Recently, involvement of the lateral RC to the gravitropism of root was proved. The root gravitropism of Arabidopsis requires auxin to be transported via the lateral RC to the elongating epidermal cells (Swarup et al., 2005).

(2) Root curvature and growth regulators

Downward growth (curvature) of the root is initiated in the elongation zone of the root. The upper side of the horizontally placed roots grows faster than the lower side, resulting in differential growth of the upper and lower sides of the roots. This mechanism causes the root to curve downward towards the center of gravity. In fact, several studies have proved that the cells on the upper side of the root become longer than those on the lower side. It is unknown, however, exactly whether this is due to the inhibition of growth on the lower side or to the promotion of growth in the upper side. Although the amount and concentration of the growth inhibitors transferred from the RC to the elongation zone have been reported to be higher in the lower part of the root, examples of promoted elongation in the upper side of roots and different distribution pattern of growth inhibitors along the root axis in upper and lower side have also been reported (Pilet and Nougarède, 1974; Barlow, 1983; Feldman, 1985).

Abscisic acid (ABA) can be a potential candidate to inhibit root elongation, and it is supposed to be transmitted from the RC to the elongation zone. However, some researchers argue that auxin plays a more important role in growth inhibition (Jackson and Barlow, 1981; Moore and Smith, 1984; Yuk-Kiu and Moore, 1985; Evans, 1991). Furthermore, there is evidence suggesting the involvement of calcium ion and calmodulin in auxin action (Feldman, 1985; Moore and Evans, 1986). An increase of ABA concentration in a drought stressed plant would cause the plant to close stomata in the leaves (Davies and Zhang, 1991). On the other hand, cytokinin produced in the root tip is transported to leaves and delays senescence in leaves. Cytokinin was detected in the bleeding sap of the rice plant, and a positive association was found between the cytokinin activities and senescence delay in leaves.

(3) Growth direction, plagiogravitropism and the RC

The axile roots that compose the framework of cereal root system grow in various directions. Although the mechanism underlying the gravitropic response in roots has not yet been fully clarified, there are several reliable theories, as mentioned herein above, which help us understand the orthogravitropic response of axile roots. Another important aspect regarding the direction of root growth is plagiogravitropism, which is the root elongation deviating from the vertical direction. In upland rice, a clear relationship was found between the growth direction and structure of the RCs (Araki et al., 2002). The axile roots that elongated vertically formed wide columellae and large amyloplasts in the RC cells. In case of axile roots of maize, the size of amyloplasts in the collumella cells had a strong influence in determining the growth angle of each nodal roots (Ito et al., 2004). These results indicate the close relationship of growth direction of axile roots, which determine part of the root system configuration, and the RC structure. Lateral root elongation, however, has not been analyzed due to the difficulty of analyzing the RC in lateral roots. Although the mechanism of this phenomenon has not been fully studied so far, several existing theories explaining root tropism may help us understand the complex mechanism of plagiogravitropism. For example, as mentioned earlier with respect to the gravitropic mechanism of the seminal root, the amyloplast-ER relationship may be applied to the gravitropic response in lateral roots. Although ER is distributed at the periphery (apical side) of the statocytes in lateral roots as observed in axile roots, the amyloplast-ER relationship shows the dorsiventrality (Sievers and Schmitz, 1975). However,
it is not yet known how the relationship between amyloplast and ERs influence the elongation of lateral roots. Furthermore, some researchers are skeptical about whether amyloplast actually influence ER in any way with respect to plagiogravitropism (Ransom and Moore, 1983).

Some researchers claim that either the difference in the size of the RC or the difference in the columella-RC ratio between the axile and lateral roots may be the factors contributing to differential growth direction between the two. Previous studies have shown that the RC size and the columella-RC ratio of the axile root are greater than those of lateral roots (Ransom and Moore, 1983; Moore and Pasieniuk, 1984a, b). The findings of these studies suggest that the amount and concentration of growth inhibitors produced in the RC may be the factors causing the deviation of the lateral root elongation from the vertical direction. Pilet (1982) claimed that seminal roots of maize were subject to genetic variability, and reported that while a positive correlation was found between the RC size and the degree of gravitropic response, a negative correlation was found between the size of the ablated area in the RC by decapping treatment and the degree of gravitropic response.

5. Concluding Remarks: future challenges for RC research on root system formation

Root system architecture is modified by soil physical stresses such as higher mechanical impedance in the no-tillage field (Iijima et al., 2005, 2007), drought stress (Siopongco et al., 2005; Tsuji et al., 2005; Zegada-Lizarazu et al., 2006a,b, 2007), and so on (Iijima and Kato, 2007). Under such an environment, root penetration into the hard pan layer (Kubo et al., 2006) allows crop roots to grow into deeper soil layer, which often alleviates the crop yield reduction due to the physical stresses. The deep rooting is mainly determined by the direction of root growth (rooting angle) and root elongation rate. RC is closely related with these two factors. The RC is involved in the perception, transduction, and transportation of growth inhibitors and other physiological function of the RC should be identified.

In order to increase our knowledge on the above-mentioned three topics, it is necessary to clarify the function of the individual regions of the RC and understand how the RC tissues and cells are formed, which would be a fourth issue to be studied in future. Cylindrella is formed through the periclinal division of the initial cells located in the central region of the root tip. It is believed that, while the region of the root tip surrounding the apex of clyindrella is pushed outward in the direction of root growth, the cells in the base of the RC are pushed inward to the opposite direction as the root grows. This would naturally cause substantial mechanical stress on the cells comprising the lateral RC, possibly affecting the sloughing off of RC cells.

A gene that is expressed specifically in the maize RC has been isolated in recent years (Matsuyama et al., 1999). The mRNA of this zmGRP4 gene is never expressed in stems and leaves, only rarely expressed in the root body, and strongly expressed in the root tip, especially in the lateral RC. Signals have been detected by immunohistochemical analysis in the mucilage secreted by the RC. The root mucilage is also known to contain a zmGRP4 protein. The effective utilization of knowledge gained from this study has the potential to further enhance our understanding of the structure and function of the RC.

Acknowledgements

This work was funded by the grant-in-aid (B2-15380014) from the Japanese Ministry of Education, Culture, Sports, Science, and Technology.

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* in Japanese with English summary.
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