Comparative Root Anatomy of Seminal and Nodal Root Axes of Summer Cereals with Special Reference to the Development of Hypodermis and Cortical Sclerenchyma

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Abstract: Seminal and nodal root axes play an important role as conducting pathways for transporting substances into and out of roots. The anatomical feature of the tissue at the basal portion of these axes in nine species of cereals was examined with emphasis on the hypodermis and the cortical sclerenchyma. In the seminal root axes, none of the species examined developed cortical sclerenchyma except rice. In contrast, all the species developed the cortical sclerenchyma in the nodal root axes. This phenomenon was regarded as a type of heterorhizy. The hypodermis consisted of more regularly arranged cells in the nodal root axes than in seminal root axes in all the species. The marked wall thickening of the hypodermal cells in the nodal root axes was observed in Japanese barnyard millet, pearl millet and foxtail millet but not in the other species. Some specimens of Japanese barnyard millet showed wall thickening also in the epidermis. The number of cortical sclerenchymatous layers varied with the species. The cortical disintegration was observed in the nodal root axes of all the species. However, in the seminal root axes, among the species examined, only finger millet, pearl millet, and foxtail millet did not show cortical disintegration. In these three species, the tissues external to endodermis tended to be deformed and sloughed off in the seminal root axes. Finger millet developed a thickened-wall cortical layer encircling the endodermis.

Key words: Cereal, Cortical disintegration, Cortical sclerenchyma, Heterorhizy, Hypodermis, Nodal root, Seminal root, Wall thickening.

Cereal root systems consist of seminal and nodal root axes and lateral roots produced on those axes. Lateral roots of different orders account for the major part of the surface area of the root system[10]. Seminal and nodal root axes from the framework of the root system[11], and thus determine the soil volume exploited by the root system. The axes also play an important role as conducting pathways for transporting substances into and out of the roots.

In relation to the growth stage of a plant, the seminal root is considered to be relatively important during the establishment of a young seedling, while the nodal root is important during later growth stages for collecting water and supplying it to the entire plant[12]. It is frequently observed that with progressing plant ages the epidermis is sloughed off from the root axis and the underlying...
hypodermis, or even the endodermis, become exposed to the soil. McCully and Canny pointed out, however, that there is a variation in respect to the loss of the epidermis depending on species, portion along the root axis, and the growth stage of the plant. One of the major significant roles of the outermost tissue, whether it is the hypodermis or the endodermis, is to protect the vascular system from the surrounding soil environment. It is, therefore, of special interest to examine what tissue is in contact with the soil and protects the inner parts of the root, especially those root portions near the soil surface where the temperature and moisture greatly fluctuate.

In this respect, we compared the anatomy of the tissues external to the endodermis of seminal and nodal root axes of nine species of summer cereals which differ in waterlogging and drought tolerances.

Materials and Methods

Nine species of summer cereals shown in Table 1 were grown for 35 days in root boxes (25×2×40 cm) under vinylhouse conditions. Another set of the same species were grown till heading in bigger root boxes (95×5×50 cm). The root boxes were filled with loamy sand soil at a bulk density of 1.30 g/cm³, to which a compound fertilizer was applied at the rate of 0.25 g (equivalent to N; 30 mg, P; 24 mg, K; 30 mg)/kg soil. Irrigation was done by submerging the root boxes in water for one hour once a week except for those with paddy rice which were kept under waterlogged condition throughout the experiment. Root sampling was done following the method of Kono et al. The sampled roots were fixed and preserved in FAA (Formalin 5: Acetic acid 5: 70% Ethanol 90).

Seminal roots were taken from the 35-day-old plants. To examine mature roots, nodal roots were taken from 2 to 3 nodes below the highest rooting node (Table 1) of the plants harvested at heading. For both seminal and nodal roots a 1-cm segment was taken from basal portions of 3 to 5 root axes. These segments were embedded in paraffin and transverse sections 40 μm thick stained with hematoxylin were made, and examined with light microscope.

Results

The emphasis of our observation in this study was in the tissues external to the endodermis of the seminal and nodal root axes. It seems that in previous works, the outermost layer of the cortex immediately underlying the epidermis and the underlying uni- or

<table>
<thead>
<tr>
<th>Species</th>
<th>Cultivar</th>
<th>Final rooting node of main stem*</th>
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</thead>
<tbody>
<tr>
<td>Paddy rice</td>
<td>Oryza sativa L.</td>
<td>Nipponbare</td>
</tr>
<tr>
<td>Upland rice</td>
<td>Oryza sativa L.</td>
<td>Norin 11</td>
</tr>
<tr>
<td>Finger millet</td>
<td>Eleusine coracana (Gaertn.)</td>
<td>Akiyama</td>
</tr>
<tr>
<td>Job's tears</td>
<td>Coix lacryma-jobi L.</td>
<td>yoto, local</td>
</tr>
<tr>
<td>Japanese barnyard millet</td>
<td>Echinoclos usitis</td>
<td>Hidaakabie</td>
</tr>
<tr>
<td>Common millet</td>
<td>Panicum milaceum L.</td>
<td>Shinano 1</td>
</tr>
<tr>
<td>Pearl millet</td>
<td>Pennisetum typhoidium Rich.</td>
<td>Miyazaki, local</td>
</tr>
<tr>
<td>Sorghum</td>
<td>Sorghum bicolor Moench.</td>
<td>Kokkyaku 2</td>
</tr>
<tr>
<td>Foxtail millet</td>
<td>Setaria italica Beauv.</td>
<td>Yachiymochi</td>
</tr>
<tr>
<td>Maize</td>
<td>Zea mays L.</td>
<td>Golden cross bantam</td>
</tr>
</tbody>
</table>

* At heading stage.
Fig. 1. Cross sections showing the outer region of seminal (odd numbers) and nodal (even numbers) root axes in basal part of summer cereals. 1, 2; paddy rice, 3, 4; upland rice. 5, 6; finger millet. 7, 8; Job's tears. 9, 10; Japanese barnyard millet. 11, 12; common millet. 13, 14; pearl millet. 15, 16; sorghum. 17, 18; foxtail millet 19, 20; maize.
Key to abbreviations: C; cortical lacunae, E; epidermis S; cortical sclerenchyma, *; hypodermis. Thick arrow in no. 5 indicates wall thickening of a cortical cell layer encircling the endodermis. Magnification of each figure is 360 times.
Fig 1. (continued)
multiseriate cortical cell layers characterized by their obviously thickened cell wall have not been clearly distinguished. It is probably because workers have been more concerned with physiological characteristics such as lignification and suberization which are common to both tissues than morphological differences like cell wall thickening. Indeed, McCully\textsuperscript{11)\textsuperscript{11)} showed that the autofluorescence of the cell walls is identical to both tissues. However, we found that a uniseriate cell layer just beneath the epidermis was clearly different in the degree of cell wall thickening from the underlying layer(s) of cells with thickened wall. Additionally, this uniseriate layer was also observed to consist of uniformly arranged cells. To avoid confusion, therefore, in this report the former cell layer is termed hypodermis and the latter cortical sclerenchyma.

1. Seminal root

As shown in Fig. 1 (odd number), the tissues in contact with the soil at basal portions of the 35-day-old seminal root axis varied among species. In paddy rice (1), upland rice (3), Job’s tears (7), Japanese barnyard millet (9), common millet (11), foxtail millet (17), and maize (19), the hypodermis was the tissue which was in direct contact with the soil, while it was the epidermis in sorghum (15). In finger millet (5) and pearl millet (13), the tissues external to endodermis such as epidermis, hypodermis, and cortex were often deformed or appeared compressed, and thus the soil contacting tissue was hard to specify. In some specimens of pearl millet, however, the endodermis was clearly observed as the outermost layer of the root axis. McCully\textsuperscript{11)\textsuperscript{11)} reported that maize, oat, wheat, sorghum, and Sudan grass had decorticated seminal root axis at their flowering stage.

We observed the following three distinct interspecific differences in the structures of tissues external to endodermis in the seminal root axes of the nine species examined: First was the wall thickening of cortical cells underlying the hypodermal layers. In the case of rice (1, 3), the uniseriate cell layer just beneath the hypodermis, which is composed of small, regular-sized cells with a thickened wall is well known as cortical sclerenchyma\textsuperscript{7,16). Development of this tissue, however, was not clearly identified in the species examined in this study except for paddy rice (1) and upland rice (3).

The second interspecific difference was found in the development of cortical disintegration. In addition to paddy rice (1) and upland rice (3), which have been widely reported to develop this structure, Job’s tears (7), Japanese barnyard millet (9), common millet (11), sorghum (15), and maize (19) also developed cortical disintegration. In contrast, the development was not clearly observed in finger millet (5), pearl millet (13), and foxtail millet (17).

Third was the wall thickening of a cortical cell layer encircling the endodermis. Among the nine species only finger millet (5, thick arrow) developed this thickened-wall cell layer, which was also reported in maize\textsuperscript{3,11).

2. Nodal root

Basal portions of nodal root axes shed epidermis with the hypodermis forming the root surface in paddy rice (2) and upland rice (4) as shown in Fig. 1 (even number). Foxtail millet (18) and pearl millet (14) were characterized by the partial loss of epidermis and the thickened wall of hypodermal cells. Conversely, almost complete epidermis remained intact in finger millet (6), Job’s tears (8), Japanese barnyard millet (10), common millet (12), sorghum (16), and maize (20). Many intact root hairs were also observed in finger millet (6) and sorghum (16). The thickened wall of epidermal cells found in Japanese barnyard millet (10) was also worth noting.

In contrast to the seminal root axis, all the species examined developed a uni- or multiseriate cell layer with a thickened wall immediately underlying the hypodermis in the nodal root axes. Nevertheless, the number of layers was different with species ; one or two layers were found for paddy rice (2), upland rice (4), and finger millet (6) ; four to six layers for Job’s tears (8), Japanese barnyard millet (10), pearl millet (14), and sorghum (16) ; approximately ten layers for common millet (12), foxtail millet (18), and maize (20). In addition, the degree of the thickening also differed, i.e., the cell walls were distinguishably more heavily thickened in Japanese barnyard millet (10), pearl millet (14), and foxtail millet (18), compared to those of the other species. Moreover, the staining property of the thickened cell wall of pearl millet (14) with hematoxylin was very distinguishable from that of the rest.
of the species examined. Further study is needed on the interspecific differences in the degree of thickening and the deposited substances in the cell wall in relation to the age and longevity of the nodal root to be examined.

Although the cortical disintegration in the nodal root axis was recognized in all the species, it was found that the cortex in the basal portions was less disintegrated than in the distal portions.

**Discussion**

The most interesting finding in this investigation was that in all the species examined, the development of the cortical sclerenchyma was not observed in the seminal axes but found in the nodal root axes, except for paddy rice and upland rice. This phenomenon is regarded as a type of heterorhizy and has not been reported elsewhere to the knowledge of the authors.

In general, structural differences are associated with functional differences. Significance of the cortical sclerenchyma has been well documented, such as filtration of excess soil solution, defense for plants against attack by microorganisms, check of oxygen leak from roots, and mechanical support for the structure of cortical aerenchyma. Clarkson and Robards, who studied the process of wall thickening in the endodermis, suggested that the cell layers with the thickened wall may function to prevent water leakage at the basal portions of root axes located near the soil surface, especially under high temperature and dry conditions. Despite the significance of the thickening of cell walls, the cereal species except for the rice plants did not develop the cortical sclerenchymatous tissues at the basal portion of their seminal root axes. Thus, it may imply that the surface of the seminal root axis of those species, usually grown under limited water conditions, greatly contribute to collecting water needed for the establishment of young seedlings. It was also reported in rice plants that the cortical sclerenchyma serves as a hindrance to the outward extension of lateral roots. This fact can be interpreted in a similar manner, i.e., despite all disadvantages of not having the cortical sclerenchyma, those species give priority to the development of lateral roots which are critically important for water collection.

In contrast, as mentioned earlier, the rice plants formed the cortical sclerenchymatous tissues in seminal axes that are important for the establishment of seedlings grown under anaerobic and reductive environments. As also mentioned earlier, the tissue may function as a mechanical support to cortical disintegration and the mechanism for preventing the reduced substances from entering into roots.

On the other hand, in nodal roots that support most parts of the plant’s life cycle after seedling establishment, it seems reasonable to assume that the roots vigorously develop cortical sclerenchyma as a protective mechanism against various stress factors.

It has been reported that the substances deposited on the wall of cells constituting the hypodermis, the endodermis and the most parts of the stele are suberin and/or lignin. These substances are hydrophobic and are hardly decomposed by microorganisms since they are secondary metabolites. Although we did not conduct any histochemical studies on these deposited substances, they are most probably suberin or lignin based from the studies of other workers.

Our present results are not yet enough to warrant discussion of the relationship between the development of the cortical sclerenchyma and the drought and waterlogging tolerance of the species examined. What makes the problem rather complicated is that, in our preliminary observation, the development of the cortical sclerenchyma was found to be substantially changeable depending on the portion along the root axis and the soil moisture environment under which the root is grown. As stated above, the cortical sclerenchyma together with the endodermis may form double layers for checking water loss from roots. In this aspect, therefore, we assume that careful examination of the effects of different environmental factors on cell wall thickening and the development of both tissues will provide us with some clues to reveal the significance of these tissues in relation to the waterlogging and drought tolerance of the plants.

Finally, it needs to be noted that the mature root tissues at the basal portion were so hard that it made the preparation of the specimen difficult. Under such conditions, both the tis-
sues of outer layer of the cortex and around the stele could not be observed in the same section. There is, therefore, a need for the improvement of the method, including using others such as frozen sectioning and resin embedding.

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References


* In Japanese with English summary.
** In Japanese.
*** Translated from Japanese by the present authors.