Crop Ecology

Rooting Nodes of Deep Roots in Rice and Maize Grown in a Long Tube

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Abstract: Penetration of the roots deep into soil layer (deep roots) may alleviate growth inhibition under various soil stress conditions. In this study, the nodes from which deep roots had emerged were examined at the heading stage in rice and maize grown in a 2 m long tube. The effect of soil mechanical stress on the rooting nodes of deep roots was also examined. The roots that emerged in a relatively early growth stage, that is, the roots from coleoptilar, 1st and 2nd node in rice, and the seminal root and roots from the coleoptilar, 1st and 2nd nodes in maize, penetrated into the deep soil layer. The node which produced the highest number of deep roots was the 1st node in rice and the coleoptilar node in maize. Seminal root of rice and seminal adventitious roots of maize did not penetrate into the deep soil layer although they emerged at an early growth stage. In the rice root system, the nodal roots, emerged from the upper portion of the node, tended to penetrate deeper than the nodal roots emerged from the lower portion of the same node. Soil compaction did not affect these tendencies.

Key words: Axile root, Deep root, Maize, Rice, Rooting habit, Soil compaction.

Cereal crops have various nodal roots differing in depth of penetration into soil. Some nodal roots penetrate deep into the soil (deep root), and can absorb the water and nutrients accumulated in the deep soil layer. Crops developing a deep root system can alleviate growth inhibition by various soil stresses. For example, many investigators have suggested that it is necessary for crops to have a deep and profusely branched root system to avoid drought stress (Hurd, 1974; Taylor, 1980; Jordan and Miller, 1980). Lilley and Fukai (1994) demonstrated that rice plants with a high root length density in the deep soil layer take up more water from that layer than those with a low root length density under drought stress conditions, and they stated that severe stress could be avoided by the water from the deep roots. This was also observed in maize (Sharp and Davies, 1985). Deep rooting is supposed to be an important factor for plant-breeding programs to increase drought tolerance (Kramer, 1983; Fukai, 1995). In addition, absorption of mineral nutrients accumulated in the deep soil layer by deep roots may contribute to the circulation of minerals in the field. In spite of such importance, there have been few studies on the physiological and ecological characteristics of the deep root.

The crop root system consists of diverse roots with different characteristics. Axile roots forming a framework of a root system are mainly composed of seminal roots and nodal roots occurring from various nodes. The factors determining the depth of axile roots may be elucidated by comparison of the penetration depth of each axile root. Taylor and Terrell (1982) and Canadell et al. (1996) reviewed the rooting depth in various plants, but did not show which roots penetrated the deepest. Morita et al. (1992) observed that seminal roots were the longest in the root system of wheat under field conditions using the wall profile method. Pellerin and Pagès (1994) examined the root length and root elongation rates in maize under field conditions, classifying roots by the rooting node. However, the depth of each componential root was not examined. Actually, it is not easy to clarify quantitatively which roots penetrate into the deep soil layer under field conditions.

The objectives of this work are to specify the rooting nodes of deep roots in maize and rice, and to examine the effects of soil mechanical stress on the rooting nodes of deep roots.

Materials and Methods

Maize (Zea mays L., cv. Robust 30-71) and rice (Oryza sativa L., cv. IRAT 109) were grown in polyvinylchloride tubes. In the control, the tubes were 2 m long and 0.075 m in diameter. For the compacted soil treatment (compact), two 0.5 m long tubes were connected to make a 1 m long tube with the same diameter as the control. The tubes in both groups were cut vertically into two pieces and tied by metal rings. The tubes were filled with air-dried loamy sand at the soil bulk densities of 1.33 Mg m⁻³ for the control, and 1.50 Mg m⁻³ from 0.2 to 0.5 m depth for the compact. The bulk densities of the other layers in the compact were the same as that in the

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control. A powdered compound synthetic fertilizer (N : 12%, P<sub>2</sub>O<sub>5</sub> : 16%, K<sub>2</sub>O : 14%) was mixed into the soil at the rate of 0.4 g kg<sup>-1</sup> in both groups. Four replicate tubes were used for each species and treatment.

These tubes were placed in a 0.9 m deep concrete watertank under a vinylshade. The tubes were submerged up to 0.9 m from the bottom by filling the watertank with water for one day, and drained. They were simultaneously watered from the soil surface to make the whole soil columns wet enough before sowing. One day after the drainage, three pregerminated seeds of both species were sown in the tube at a 10 mm soil depth on July 10, 1996. The seedlings were thinned to one plant per tube 4 days after sowing (day 4).

All tubes were watered from the soil surface at 7-day intervals using an auto irrigator, and were allowed to drain. One tube with maize in the control was used for monitoring water regime in the soil column. The tube was perforated (22 mm in diameter) at 0.3 m intervals to monitor soil water contents. A nylon mesh pack filled with soil was inserted into the perforated hole, and after the water content of soil in the pack was equilibrated with that in the soil column, the water content of the former was measured. This method was employed to prevent the destruction of the soil structure. The soil water content was measured just before irrigation and one day after the irrigation at days 14–15, 28–29 and 35–36. A quarter strength Hoagland solution equivalent to 10% of the water contents was given to each tube as top dressing at days 38–39. One tube without plants was prepared, and the soil mechanical impedance was measured with a developed penetrometer device (Iijima et al., 1990) equipped with a 2.0 mm metal probe. The diameter of soil column in the tube was more than 20 times that of the probe, so that there would be no edge effect (Whiteley et al., 1981) for the measurement of soil mechanical impedance.

Roots of rice are supposed to reach its maximum length at the panicle initiation period or after heading (Beyrouty et al., 1988; Cruz et al., 1986). Mengel and Barber (1974) showed that the maize root system reaches its maximum extension a few days after silking. Whole root systems were therefore sampled after heading for rice and tasseling for maize. The sampling days of maize and rice were day 59 and day 73, respectively. The average air temperature during the experimental period was 28.6 ± 3.1°C (Average ± S.D.).

The whole root system was sampled by washing carefully from the vertical half of the tube had been removed. All axile roots were tied with a thread at 0.5, 1.0 and 1.5 m depth in the control, and 0.2 and 0.5 m depth in the compact to classify the rooting depth. Then they samples were preserved in FAA solution (formalin : acetic acid : 70% ethanol = 1 : 1 : 18), and rooting node and the depth of root apex were examined for each axile root.

In this study, each axile root which penetrated below 1 m depth in the control and below 0.5 m in the compact is called “deep root”, although in many reports all roots in the deeper soil layer are called deep roots without distinguishing root components. Furthermore, the soil layers where root apices existed were categorized into three groups: deep (1.0–2.0 m in the control, 0.5–1.0 m in the compact), medium (0.5–1.0 m in the control, 0.2–0.5 m in the compact) and shallow (0–0.5 m in the control, 0–0.2 m in the compact) soil layers. We will refer to the three deepest roots in each plant “deepest roots” because with the compact treatment three to seven roots in each root system penetrated into the deep soil.

In rice, there are two kinds of nodal roots, those which emerge from the upper portion of the nodes (upper roots) and those which emerge from the lower portion of the nodes (lower roots). In this study, these two kinds of roots were distinguished, by preparing successive cross sections manually. We also have surveyed roots emerging from tillers as well as those from main stems. However, roots emerged from tillers did not elongate as much as those from the main stem, and we measured only the roots emerged from the main stem in three replicate plants.

Results and Discussion

1. Soil physical condition

The water content of each soil layer in the soil column had reduced to approximately 5–10% during a 7-day irrigation interval (Fig. 1). The soil water content in the soil column was high, the deeper the soil layer. The soil water contents in the soil at a depth of 1.5 and 1.8 m were particularly high: about 35–40% one day after irrigation and about 25–35% before irrigation, which were 83–95% and 60–83% of the maximum water holding capacity, respectively. Such high water contents indicated that roots had been probably subjected to anaerobic stress in the deep soil layer.

In the control, mechanical impedance at 0.1 m depth was relatively higher than in other layers (Fig. 1). However, the inhibition of root elongation was not observed in that layer. This higher mechanical impedance might be caused by the relatively low soil water contents and the method to fill the soil. Mechanical impedance in the compacted soil layer was approximately 3 times greater than that in the control. The morphology of the roots in the compacted soil indicated that mechanical impedance was high enough to inhibit root elongation. The axile root diameter in the compacted soil was much larger than that in the control.

2. Lateral root growth

Several axile roots stopped elongation at a depth of around 0.4–1.2 m in the control and 0.2–0.5 m in the compact, and then, branched 1st order lateral roots which penetrated much deeper. Some of these lateral roots in the control were nearly 1 m long. Morphological characteristics of these 1st order laterals such as root
diameter and branching ability of higher order lateral roots were similar to those of axile roots. We therefore assumed that these 1st order laterals should be included in the category of deep root. The depth of those lateral roots was regarded as the rooting depth of the axile root from which they branched.

The appearance of lateral roots in the medium soil layer in the compact was marked different from that in the other soil layers. Elongation of lateral roots was inhibited and their diameter increased in the compacted soil in both species. Several axile roots and the 1st order laterals, however, penetrated through the compacted soil, and higher order laterals on these roots notably proliferated in the 0.5—1.0 m control soil layer.

3. Rooting nodes of the deep root

The numbers of root apices existing in the three soil layers (deep, medium and shallow soil layers) were examined separately for each seminal or nodal root (Fig. 2). The deep roots were found to have emerged at a relatively early growth stage, namely from coleoptilar root to 2nd nodal root in rice, and from seminal root to 2nd nodal roots in maize except seminal adventitious root. The number of roots in the deep soil layer decreased as rooting node advanced. The node that produced the highest number of the deep roots was the 1st node in rice and coleoptilar node in maize either with or without soil compaction. In the compact, the tendency of deep rooting was similar to that in the control, although elongation was inhibited by compacted soil stress. This indicated that soil mechanical stress does not modify the deep rooting habit.

4. Rooting node of the deepest root

In the control, rooting nodes of the deepest root were coleoptilar to the 2nd node in rice, and from seminal to the 2nd node in maize (Table 1). The first node in rice and coleoptilar node in maize developed the largest number of the deepest roots, which was the same as for the deep roots. A similar tendency was observed in the compact, although the rooting node of the deepest roots in rice was slightly shifted to a higher node.

Seminal and seminal adventitious roots emerging from the seeds are considered to play an important role during the plant establishment when the shoot is not fully developed. On the other hand, the nodal roots may function to support the subsequent vegetative growth.

Seminal roots of rice and seminal adventitious roots of maize did not penetrate into deeper layer in both the compact and control (Fig. 2 and Table 1). This indicated that rooting depth is not simply proportional to the growth duration of each root, and some axile roots which do not become the deep roots exist even though they emerge at the beginning of plant establishment. However the cause of the difference in rooting depth remains unknown, and requires further study, such as examination of the translocation of carbon and nitrogen, production of endogenous plant growth regulators and root elongation rate.

The deepest roots may have been subjected to an anaerobic stress due to the high soil water content in the deep soil layer. The deep roots have tolerance to the anaerobic condition. This should also be examined further to clarify the physiological characteristic of deep roots.

Kawata et al. (1963) reported that the roots emerging
from the 6th to 9th nodes were longer than other roots in lowland rice grown under a submerged condition in a 0.3 m deep wagner pot. The longest root was around 0.4 m in their report. The difference between the node position from which the longest root developed in their report and in the present experiment may be attributed to the difference in ecotype of rice cultivar, soil water regime and size of rooting container used.

5. Upper and lower roots in rice root system

In the rice root system, the upper roots which emerged from the upper portion of the node penetrated deeper than the lower roots which emerged from the lower portion of the same node (Table 2). This is in agreement with the results obtained on lowland rice grown in a paddy field (Kawata et al., 1963), and in a 1/2000 a wagner pot (Kawata and Katano, 1976). The average value given here is the ratio of all upper roots to all lower roots emerging from the same node. Thus, a value higher than the average indicates that more upper roots elongated to that layer. The values in the deep soil layer were higher than the average value in both the compact and control except for the value of the 2nd node in the control. This quantitatively demonstrated that the upper roots tended to penetrate more deeply than the lower roots. In the compact, this tendency was clearer.

Table 1. Rooting nodes of the deepest roots.

<table>
<thead>
<tr>
<th>Component</th>
<th>Rice</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Compact</td>
</tr>
<tr>
<td>Seminal root</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Seminal adventitious root</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coeloptilar nodal root</td>
<td>3</td>
<td>3*</td>
</tr>
<tr>
<td>1st nodal root</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>2nd nodal root</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

Three of the deepest roots in each plant were included in the deepest roots.
Nine deepest roots from three replicate plants are shown in each column.
Values with # and $ include one and two axile roots whose 1st order lateral roots penetrated into deep soil layer, respectively.
Table 2. The ratio of the number of upper roots* to that of lower roots at various depths in the rice root system.

<table>
<thead>
<tr>
<th>Soil layer</th>
<th>Node</th>
<th>*Co</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
</tr>
</thead>
<tbody>
<tr>
<td>(m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>lower</td>
<td>lower</td>
<td>upper</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.62</td>
<td>lower</td>
<td></td>
</tr>
<tr>
<td>0.5—1.0</td>
<td>0.67</td>
<td>1.00</td>
<td>1.50</td>
<td>2.67</td>
<td>0.40</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.0—</td>
<td>2.50</td>
<td>1.80</td>
<td>1.00</td>
<td>upper</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.70</td>
<td>1.30</td>
<td>1.43</td>
<td>1.86</td>
<td>0.79</td>
<td>1.00</td>
<td>0.62</td>
<td>lower</td>
<td></td>
</tr>
<tr>
<td>Compact</td>
<td>lower</td>
<td>lower</td>
<td>0.50</td>
<td>0.50</td>
<td>0.60</td>
<td>0.89</td>
<td>1.07</td>
<td>lower</td>
<td></td>
</tr>
<tr>
<td>0.2—0.5</td>
<td>1.67</td>
<td>2.50</td>
<td>1.60</td>
<td>9.00</td>
<td>upper</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5—</td>
<td>2.00</td>
<td>6.00</td>
<td>3.00</td>
<td>upper</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>1.33</td>
<td>1.57</td>
<td>1.30</td>
<td>1.56</td>
<td>1.30</td>
<td>0.90</td>
<td>1.07</td>
<td>lower</td>
<td></td>
</tr>
</tbody>
</table>

*: The roots which emerged from upper portion of each node.
Average indicates the ratio of the number of all upper roots to that of all lower roots emerged from the same node.
*: Co, coleoptilar node; 1st—7th, 1st—7th node.
lower: no upper root existed; upper, no lower root existed.

values in the deep soil layer were significantly higher than that in the control at the 1st and 2nd node nodal roots.

6. The direction of the root elongation

The root distribution pattern in the soil is mainly determined by the direction of root elongation and the length of each root system component. These two factors should be included to clarify which roots in a root system become the deep root. The direction of roots was not measured in this study because of the small diameter of the tube. However, it is clear that the direction of axile root varies with the node from which it emerged. In maize root system, for instance, roots occurring from lower nodes elongated more horizontally and those from upper nodes penetrated more vertically around the base of a stem in the soil (Yamazaki and Kaeriya, 1982; Kaeriya and Yamazaki, 1983; Tradiou and Pellerin, 1991). In contrast to maize, the reverse trend was observed in the roots emerging from a main stem in lowland rice (Oyanagi et al., 1993). Many of the roots emerging from lower nodes of the tillers including the prophylls penetrated vertically (Kawata and Katano, 1976). However, whether these results could be applied to the deep soil layer was not quantitatively analyzed. The relationship between the rooting node and deep root should be studied further taking the direction of root elongation into consideration.

Acknowledgment

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References


*In Japanese with English summary.