Structure and Function of Rice Root System as a Basis for Sustainable Agriculture

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1. Introduction

Rice is one of the most important cereal crops in the world, especially in Asia where the population is still rapidly increasing and we have to get higher yield to feed them stably. Although there have been numerous researches on rice, most of them are focusing on their above-ground parts (Matsuo and Hoshikawa 1993a, 1993b, 1993c). We need, at the same time, to examine structure and function of their root systems, because most important management practices including tillage, fertilization and irrigation are actions for the root system which is the dynamic interface between plants and the earth (Morita 2000, Abe 2003). Additionally environment-friendly agriculture is also required recently not to worsen and to solve environmental issues, which is another reason why we must study rice root system. For example, we should reduce fertilizer and water to prevent pollution and to save natural resources respectively, both of which are absorbed by the root system. In this article we would like to review previous and on-going studies on structure and function of rice root system and to propose a viewpoint of designing rice root system for establishment of environment-friendly and sustainable agriculture (Morita 2003).

2. Development of rice root system based on phytomer

A rice root system at harvest consists of several hundreds through over one thousand nodal roots which have numerous lateral roots. Those nodal and lateral roots produce thousands of root hairs which may contribute absorption of water and nutrients through enlargement of surface area. It is already well-known that growth of the rice roots proceeds in harmony with shoot development (Kawata et al. 1963, Hoshikawa 1989). Such coordinate growth of shoot and root can be easily understood based on the concept of phytomer (shoot unit; Kawata et al. 1963, Nemoto et al. 1995). The main stem of a rice plant body is composed of successive morphological units named as phytomer, each of which is a stem segment with one leaf and one tiller bud, and primordia of nodal roots are produced in the stem segment. The tiller bud will grow to be a tiller which also consists of successive phytomers as the main stem.

When the Nth leaf of the main stem unfolds, nodal roots begins to emerge from the (N-3)th phytomer and the first- and second-order lateral roots emerge on the (N-4)th and (N-5)th phytomers, respectively. At the same time, the first leaf of the tiller at the axial of the (N-3) leaf, namely belonging to the (N-2) phytomer, unfolds. Thus growth and development of shoot and roots proceed in harmony with each other in each stem as well as among all the stems in the plant body (Nemoto and Yamazaki 1993). Therefore, observations on shoot growth make us possible to grasp the outline of root system development without digging up.

3. Structure of rice root system based on phytomer

We proposed three questions to understand structure and development of the rice root system (Morita et al. 1995). The first question is how the structural variations of the whole root system in rice can be understood. Our investigations showed that structure of rice root system is possible to be characterized by the combination of two factors, namely the total root length (or root weight) and its vertical distribution pattern in soil. For example, our analysis on varietal differences in root system morphology of rice plants at the harvest which are grown in paddy field shows that Koshihikari bred in Japan has a root system with a small amount and a shallow distribution, Lemont in USA has a root system with large amount and deep distribution and IR36 at IRRI has a root system with large amount and shallow distribution.

The second question is how those two factors, the total root length and its distribution are determined based on growth and development of individual nodal root with laterals. The total root length of the rice plant is determined by combination of the number and length of nodal roots including their lateral roots. And the distribution pattern of roots is influenced by combination of the growth direction and length of nodal roots The growth direction of nodal roots depends on their diameter, namely the nodal roots with larger diameter elongate more downwards, while those with smaller diameter grow more horizontally (Oyanagi et al. 1993, Abe and Morita 1994).

Because primordia of nodal roots are produced in the stem segment of each phytomer, the number, diameter and length of nodal roots might be developmentally interrelated with the morphological traits of the phytomers (Morita et al. 1997, Abe et al. 2000). The third question is how growth of nodal roots relates to morphology of phytomers. Our examination showed that the number of nodal roots mostly depends on the number of the phytomers, and the diameter and length of nodal roots are influenced by the size of the phytomers, respectively. Indeed, there is significant correlation between the length of nodal roots and size of phytomers, and more intimate correlation between the number of nodal roots and the number of phytomers where regression lines between them are not different regardless of cultivars. Thus size and number of phytomers strongly affect structure of root system (Morita and Abe 1999d), though environmental conditions also influence it either directly or indirectly through the influence on shoot growth (Morita and Yamazaki 1993) This means that we can estimate and evaluate root system development without digging if we measure number and size of phytomers in rice plants (Abe et al. 1998).

4. Turnover of rice roots

Above-mentioned results from researches on development of the rice root system are based on destructive investigations, because it is not easy to observe and measure non-destructively the same root system *in situ* in paddy field. Instead we usually reconstruct the pattern of root growth and root system development from data of different rice plants which are grown under same or similar conditions in pots or paddy field and taken destructively at several growth stages (Kawata et al. 1963, Morita et al. 1997). The total length of a whole root system is often considered by the standing biomass at each growth stage as a result of formation and death of roots. It is, however, strongly required to examine turnover of roots based on their formation and death, if we would like to understand deeply the function of root system in relation with its structure.

Although several researchers were interested in turnover of rice roots, details of formation and death of rice roots, especially lateral roots, have been still unclear because of destructive methods (Kawata and Soejima 1974). Rhizotron have been sometimes used for non-destructive and continuous observation for the same roots in upland field (Boehm 1974), but it is not good for rice plants because they are grown under flooded condition. Minirhizotron, on the other hand, might be effective to investigate rice roots non-destructively in the paddy field, but there are only few papers on roots of rice plants grown in the United States (Beyrouty et al. 1987, 1988, Salton et. al. 1990) where cultivars, environmental conditions and management practices are quite different from ours in Asia including Japan. Then the authors are now trying to use minirhizotron to investigate rice roots with reference to their formation and death in the paddy field of Japan. After one-year trial we have succeeded to get clear visual images of rice roots and analysis on those data shows detailed formation and death of rice roots with possible relation to their physiological activity (Hasebe et al. 2005a, Hasebe et al. 2005b). Thus minirhizotron can be used for research of rice roots and it is quite effective to study their turnover in relation to their function.

5. Xylem sap rate and root system activity

Then some suitable indicators are necessary to estimate and evaluate function of root system based on its physiological activity. We have been using xylem sap rate (bleeding rate) as an indicator for physiological activity of the root system in rice grown in paddy field (Morita and Abe, 2002, Abe and Morita 2003, Morita et al. 2005). After removal of shoot at certain height (ca. 10 cm) above water surface in the paddy field we put pre-weighed cotton on the cut surface of the stump and wrapped it with plastic film followed by fixation with rubber band. After one hour we take the cotton to weigh and regard the increase as the amount of xylem sap exuded for one hour based on root pressure. Although the detailed mechanism of bleeding is still unclear, xylem sap rate must be a suitable indicator for physiological activity of the root system in rice plants, because bleeding is known to be an energy-dependent physiological activity of the root system. Besides xylem sap rate there are several candidates for indicators to estimate and evaluate physiological activity of the root system including respiration rate, enzyme activity, oxidation and reduction power, but in most cases we have to dig the root system out of the soil and usually sub-samples are used for measurements after destructive procedures. When we measure xylem sap rate of the whole root system, there is, on the contrary, no need to dig out the root system, though we remove the shoot. Additionally it is already known that there often are quite intimate relationships between xylem sap rate and respiration rate, the latter of which relates more directly to physiological activity of roots (Yamaguchi et al. 1995). Because xylem sap rate can be measured more easily without using any sophisticated equipments comparing with respiration rate, we had better measure xylem sap rate instead of respiration rate or other indicators, especially under field conditions.

There is diurnal pattern in xylem sap rate of rice plants grown in the paddy field and it will reach the max in the early morning (Morita and Abe 2002). Developmentally the xylem sap rate of rice plants transplanted in the paddy field will gradually increase to reach the maximum value at around the heading and then decrease rapidly during ripening period (Morita and Abe 2002). Because xylem sap rate must depend on both the total root length and its physiological activity during the growing period, we analyze xylem sap rate on the basis of the equation as follows:

Xylem sap rate = total root length x physiological activity

Because it is quite tedious and time-consuming to examine the total length of the whole root system developmentally, we estimate the total root biomass based on the relationship between the total root number and total phytomer number. Because there is quite intimate relationship between those two morphological traits as mentioned in section 3, we can estimate the total root number from the total phytomer number which is fundamentally the same as the accumulated total leaf number. Then we calculated physiological activity of an individual root as the xylem sap rate divided by the accumulated leaf number which is proportional to the total root number. Physiological activity of each root already starts to decrease much earlier than the heading when the xylem sap rate of the whole root system reaches the max. Before the heading there successively come larger and longer nodal roots with more lateral roots and the xylem sap rate of the whole root system gradually increase by the increasing total root biomass in spite of decrease in physiological activity of individual roots. After the heading xylem sap rate rapidly decreases, probably because there is almost no emergence of new nodal roots and ageing of all the nodal roots with their laterals proceeds to decrease their physiological activity.

6. Xylem sap rate and yield in rice

Xylem sap rate during the grain-filling period was measured to examine physiological activity of the root system and its contribution to yield. As a result, we found quite intimate negative correlation between xylem sap rate and head weight, and the xylem sap rate decrease while the head weight increase after the heading (Morita and Abe 1999a). Xylem sap rate decreased more gradually than that in the control when all the heads were removed at anthesis (Morita and Abe 1999b). These results suggest that there might be competition for photosythate between heads and the root system during the grain-filling period.

Then we examined the relationship between xylem sap rate and head weight with reference to yield level. Rice plants at the border of paddy field usually have larger shoot with larger heads comparing with those in the center of paddy field, which is called as border effects. Border plants have higher xylem sap rate, possibly because of larger root system and higher physiological activity, and there might be positive correlation between head weight and xylem sap rate at harvest (Morita and Abe 1999c).

In addition, when two rows of rice plants were removed at certain sites in the paddy after transplanting or at the heading, there were variations among treatments and significant negative correlations between xylem sap rate and ripening head weight during grain-filling in all the treatments including the control. However, regression lines were different depending on yield level and final grain yield showed rather positive relation with the xylem sap rate (Morita and Abe 2001). Similar results were obtained when we examined the relationship between yield and xylem sap rate at the harvest in Thailand and China (Morita 2000). Furthermore, we compared several cultivars with different yield level and there were also significant negative correlations between them, though regression lines were different among cultivars depending yield level (Abe and Morita 2004).

Above-mentioned results strongly suggest that function of the root system may contribute yield formation during grain-filling, and that we possibly get higher yield if we can decrease the xylem sap rate more gradually during grain-filling.

7. Xylem sap analysis for plant nutrition

As is well-known nitrogen absorption has great influence for yield, but at the same time we have to control and reduce nitrogen fertilization to establish environment-friendly agriculture. Nitrogen uptake of rice plants have been examined by measuring nitrogen concentration in shoot as well as leaf color. Recently we tried to monitor nitrogen absorption more directly by analysis on concentration and amount of nitrogen in xylem sap as follows:

Amount of nitrogen absorbed = xylem sap rate x nitrogen concentration

As a result, clear diurnal change existed in the nitrogen concentration of xylem sap with much higher value in light phase than dark phase. The nitrogen concentration in xylem sap also showed clear phenological change with high value at early growth stage of rice plants and gradual decrease with time. This decrease is likely due to the decline of both soil nitrogen content and physiological activity of root system with ageing of individual roots. Because xylem sap rate had different phenological change with a peak at around the heading, the nitrogen content (i.e., xylem sap rate x nitrogen concentration) presented a peak at around the panicle initiation stage.

We also examined absorption of nitrogen top-dressed from the nitrogen concentration in xylem sap and xylem sap rate of a lowland rice variety Koshihikari grown in pots and paddy field (Sakaigaichi et al. 2005). The concentration of nitrogen began to increase 6 h after top-dressing as ammonium sulfate, reached the maximum value at 24 h, and decreased thereafter. It took more than 6 h to increase in nitrogen uptake, probably because the time was required for diffusion of ammonium into the soil and movement into the xylem vessel. The nitrogen concentration in xylem sap decreased to the same level as the control 168 h after top-dressing in the field experiment, which indicates the uptake of top-dressed nitrogen by the rice plants completed in 7 days. Approximately 55 % of top-dressed nitrogen was absorbed by the rice plants in those 7 days. The onset of increase in xylem sap rate was more than 12 h after top-dressing, which was later than that of the nitrogen concentration in the xylem sap in both pot and field experiments. This time lag suggests that the xylem sap rate was promoted not simply by an increase of nitrogen compounds as osmotic solutes in the xylem sap but through an increase of physiological activity in roots caused by the top-dressed nitrogen. The SPAD values of leaf color, which is often used for nutritional diagnosis, responded to the top-dressing rather late, even behind xylem sap rate. The analysis of nitrogen in xylem sap offered an effective method to illustrate the dynamics of top-dressed nitrogen in detail.

8. Rice root system under FACE condition

Global warming is one of the most serious environmental issues in the world, though its detailed mechanism has been unknown. The concentration of CO_2 , one of the greenhouse effect gasses, in the air is still increasing and it may influence to air temperature which is one of the important environmental factors in agriculture. Therefore, there are numerous studies on effect of CO_2 enrichment on crop growth, but most of them are experiments in closed system including growth chamber where crop growth is somewhat different from that in open field called as chamber effect. In order to overcome such chamber effect, FACE (free-air CO_2 enrichment) projects are going at several sites in the world, especially in USA and EU (Norby et al. 2001).

FACE project had been proceeded for rice plants grown under flooded condition in Japan for the first time in the world (Kobayashi et al. 1999). We took part in the project to examine effects of CO_2 enrichment on rice root system in 1999, 2000 and 2003 (Morita et al. 2005). A japonica rice variety Akitakomachi was grown in irrigated lowland paddy field. The CO_2 concentration in the FACE plots was controlled at 200 $\mu mol \cdot mol^{-1}$ above the ambient level. The length and weight of roots were measured at the heading stage, but they were not significantly increased by elevated CO_2 except for the root weight in 1999. The specific root length was smaller in the FACE plots than in the ambient plots, suggesting thicker and /or less branching roots under FACE condition. The xylem sap rate was measured by using cotton trap as an index of the physiological activity of the whole root system at the heading and the mid-ripening stages. The xylem sap rate per stem was lightly smaller in the FACE than in the ambient plots. In addition, the xylem sap was analyzed to determine nitrogen content in 2003. The nitrogen content in the xylem sap at the heading stage was significantly smaller in the FACE plots. These results suggest that physiological activity of rice roots is not enhanced or somewhat declined by elevated CO_2 concentration. Therefore, we make efforts to improve structure and function of rice root system in order to get higher yield stably under higher concentration of CO_2

9. Designing rice root system for sustainable agriculture

In this paper we briefly review researches on structure and function of roots in lowland rice grown in irrigated paddy field, though there might be different approaches to improve cultivation of rice plants with different genetic background grown under different ecological environments. At present development of rice root system are studied from the viewpoints of turnover using minirhizotron, which is quite helpful to understand the dynamic aspects of root system. Such understanding of dynamics in structure and morphology of root system is necessary to examine function of root system, and measurement and analysis of xylem sap rate are effective to estimate and evaluate physiological activity of the whole root system. Deeper understanding of relationships between structure and function of root system must be helpful to improve rice cultivation and to establish more environment-friendly and sustainable one through designing and control of structure and function of root system.

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