Plant and Soil **165**: 333–337, 1994.

Growth direction of nodal roots in rice: its variation and contribution to root system formation

Jun Abe and Shigenori Morita
Department of Agrobiology, Faculty of Agriculture, The University of Tokyo, Bunkyo-ku, Tokyo 113, Japan

Key words: nodal roots, *Oryza sativa* L., paddy rice, root distribution, root growth direction, root system

Abstract

The root system of a rice plant (*Oryza sativa* L.) consists of numerous nodal roots and their laterals. The growth direction of these nodal roots affects the spatial distribution of the root system in soil, which seems to relate to yield and lodging resistance. The growth angle of a nodal root varies with the type and timing of emergence of the nodal root. The body of a rice plant can be recognized as an integrated set of *shoot units*, each unit consisting of an internode with a leaf and several roots. Nodal roots formed at the apical part of a shoot unit often elongate horizontally, whereas those formed at the basal part of the shoot unit show various growth directions depending on both the growth stages of the plant and the environmental conditions. Moreover, nodal roots that emerge from the most basal shoot unit of a tiller are usually thick and grow downwards. External factors such as planting density and nitrogen application affect the growth direction of nodal roots, probably partly because of the changing tillering pattern of the shoot. In addition to the growth angle of nodal roots, size of nodal roots may be another important factor determining the spatial distribution of the root system in soil.

Introduction

Rice plants (*Oryza sativa* L.) are often grown in a paddy field under flooded conditions. Their root systems comprise numerous nodal roots of relatively short length: a mature rice plant usually has several hundreds of nodal roots, most of which are less than 40 cm in length (Kawata et al., 1963). Therefore, rice plants should form a rather superficial root system compared with wheat (Gregory et al., 1978; Weaver, 1926), maize (Miller, 1916; Weaver, 1926) or millets (Nakamoto et al., 1992), where the seminal and nodal roots are longer.

Although the rooting zone of a rice population is relatively shallow, the vertical distribution of the root system is considered to be important in rice cultivation. It was shown that high-yielding rice plants often had a large proportion of downward-growing nodal roots, which usually developed well in relatively deep layers (Morita et al., 1986, 1988). Moreover, lodging resistance of rice plants partly depends on the rooting depth in the soil (Terashima et al., 1994).

In this paper, we will review the studies of the growth direction of nodal roots in rice plants, because it should be one of the most important factors in determining the spatial distribution of root system. Other possible factors that may determine the distribution of the root system will also be discussed.

Structure of the rice plant body

Before discussing the variation and plasticity of the growth direction of nodal roots, we should explain the structure of rice plants. The body of a rice plant can be considered as an integrated set of *shoot units* (Kawata et al., 1963), which are similar to *leaf-internode units* defined by Sharman (1942). Each shoot unit consists of a stem segment (i.e., an internode and the adjacent node) with a leaf from the distal node and a tiller bud at the basal part (Fig. 1). Nodal roots emerge from both apical and basal sites of each shoot unit and break through the leaf sheaths of the lower shoot units before elongating in the soil. Nodal roots formed at the basal part (*proximal roots*) emerge earlier than those at the apical part (*distal roots*). However, the most basal shoot unit (*prophyll shoot unit*) of each tiller forms only one type of nodal roots, whose diameter is very large (Kawata and Katano, 1976).

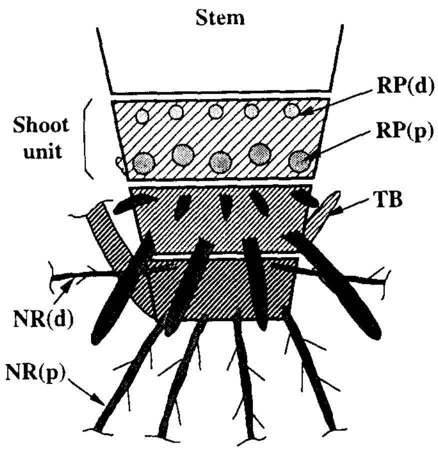

Fig. 1. Schematic illustration of shoot units of a rice plant in the vegetative phase. Main stem and tillers are composed of successive *shoot units*, which develop acropetally. A shoot unit consists of an internode of stem with a leaf at the distal node and a bud of a daughter tiller at the basal end. The leaves of the shoot units are omitted in this illustration. TB, tiller bud; NR(d,p), nodal root (*distal root* and *proximal root* respectively); RP(d,p), root primodia of a distal root and a proximal root respectively.

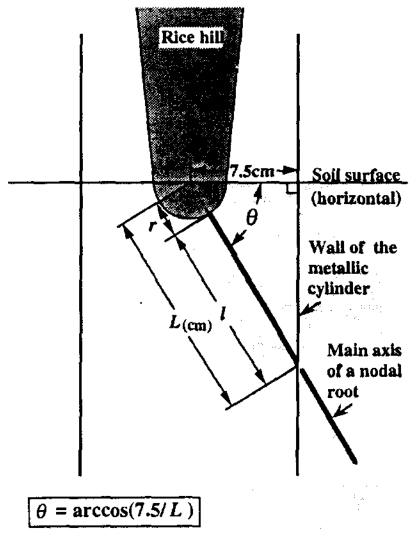

Fig. 2. The method for estimating the growth angle of each nodal root. A metallic cylinder was inserted vertically into the soil with the rice hill at the center. The length of the main axis of a nodal root cut by the cylinder depends on the growth angle of the nodal root. θ, angle of the main axis of a nodal root to the horizontal; r, radius of the crown; l, length of the cut main axis of a nodal root; L, distance between the center of the crown and the site at which the main axis of a nodal root was cut by the cylinder (= $r + l$). After Morita et al. (1987).

Shoot units are formed and mature acropetally in both main stem and tillers with time. The size of successive shoot units increases during the vegetative phase (Fig. 1), resulting in longer nodal roots with larger diameter in upper shoot units. On the other hand, several of the most apical shoot units, that develop and mature in the reproductive phase, have no or few nodal roots with small length and diameter, probably because of the change in the growing pattern of the stem associated with panicle initiation and development.

Method for estimating growth direction of nodal roots

We estimated the growth direction of each nodal root in a rice hill with a cylindrical monolith method (Morita et al., 1986; Yamazaki et al., 1981). Most nodal roots were cut by a metallic cylinder when a soil monolith (i.e., cylindrical soil block) was taken to include a hill at its center. The corrected length of a cut main axis with the radius of the crown (L) is expected to depend on the growth angle of the nodal root to the horizontal (θ) since most nodal roots of rice elongate rather straight throughout the rooting zone. Theoretically, $\cos\theta$ equals the radius of the cylinder divided by L (Fig. 2).

Box monolith methods (Böhm, 1979) were also used to investigate the growth direction and distribution of rice roots in some other researches (Kawata et al., 1969; Kawata and Katono, 1976, 1977).

Variation in growth direction of nodal roots in a plant

There is wide variation in the growth direction of nodal roots in each shoot unit, the mean growth angle depending on the position of the shoot units on the stem with which the roots are associated (Kawata and Katano, 1976; Kawata et al., 1980a; Morita et al., 1992). As a result, rice plants can spread their nodal roots to various regions of soil throughout the growing period (Morita et al., 1992).

It is known that most distal roots on a shoot unit elongate rather horizontally, whereas the growth direction of proximal roots varies with the position of the shoot units on a main stem or a tiller and are much affected by environmental factors (Kawata and Katano, 1976, 1977). The proximal roots of each shoot unit are often much thicker than the distal roots of the same shoot unit in *japonica type* rice varieties (Kawata et al., 1963). Alberda (1953) reported that the root system of

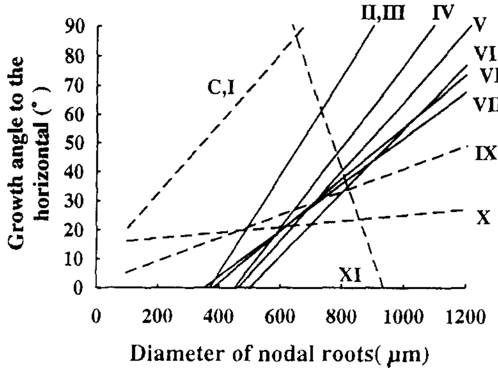

Fig. 3. Regression lines of the growth angle as a function of the diameter of nodal roots in different shoot units of the main stem. Solid lines indicate the regression with significant correlation at 1% level, whereas broken lines indicate no significant correlation. Roman numbers indicate the position of the shoot units counting acropetally (C indicates coleoptile shoot unit with a seminal root). Nodal roots from X and XI shoot units probably emerged in the reproductive phase. After Yamazaki et al. (1981).

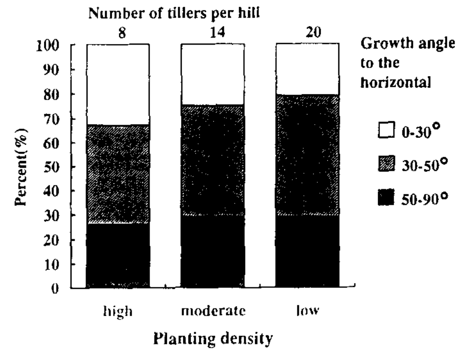

Fig. 4. Effects of planting density on the growth direction of nodal roots. The columns indicate the percentage of the total number of nodal roots in a rice hill with various root angles in plants grown at different planting densities. The numbers above the columns indicate the mean number of tillers alive at the harvesting stage (i.e., panicles) per hill. A rice hill consisted of 3 plants in all the three plots. **high**, high planting density (11.1 hills m^{-2}; 30cm × 30cm spacing); **moderate**, moderate planting density (22.7 hills m^{-2}; 21cm × 21cm spacing); **low**, low planting density (44.4 hills m^{-2}; 15cm × 15cm spacing). After Morita et al. (1987).

the "Bengawan" rice variety consisted of "coaser type" and "finer type" of roots, which grew downwards and horizontally respectively. Although he did not describe the exact positions at which the nodal roots emerged, these two types of roots could correspond to the proximal and distal roots respectively. These facts suggest a possible relation of root diameter to growth direction of nodal roots. In fact, close positive correlation was found between the diameter and growth angle of nodal roots in each shoot unit during the vegetative phase of plant growth (Fig. 3; Yamazaki et al., 1981). In addition, the thick nodal roots from prophyll shoot unit usually elongate vertically (Kawata and Katano, 1976, 1977; Kawata et al., 1980a).

Although the mechanism of the plagiogravitropic response of roots is still unknown, the size of the root cap and/or the proportion of columella in a root cap are thought to be affecting factors (Moore and Pasieniuk, 1984a, b; Pillet, 1982; Ransom and Moore, 1985). It was reported that root diameter correlates with the size of root cap and columella in rice nodal roots, and that root caps of proximal roots have a greater length and diameter than those of distal roots (Kawata et al., 1977).

At the same time, it may be significant that the regression lines of growth direction as a function of the diameter of nodal roots had different coefficients depending on the position of the shoot units on the stem (Fig. 3). Moreover, nodal roots formed in the reproductive phase (i.e., after panicle initiation stage) rarely grow vertically (Kawata et al., 1980a). It is suggested that the growth direction of nodal roots may be determined not only by root diameter but also by internal conditions related to the growth of the whole plant body.

Plasticity of the growth direction of nodal roots in response to external factors

The rooting pattern of rice varies not only with the variety (Abe et al., 1990; Morita et al., 1993) but also with the growing conditions. For example, high planting density seemed to increase the proportion of nodal roots growing horizontally (Fig. 4; Morita et al., 1987). Morita et al. (1986) reported that high levels of nitrogen resulted in an increase of nodal roots with large diameter and large growth angle to the horizontal. On the other hand, fertilization of a paddy field in Thailand with inorganic nitrogen resulted in a high proportion of horizontal roots, while application of organic materials promoted downward growth of nodal roots (Abe et al., 1994). Redox conditions and/or organic acids in the soil may also influence root growth direction in rice plants, since different water management in paddies resulted in different distributions of root systems as shown in Figure 5 (Kawata et al., 1969; Kawata and Katano, 1977).

It is still unknown how these external factors cause the differences in the proportion of nodal roots with

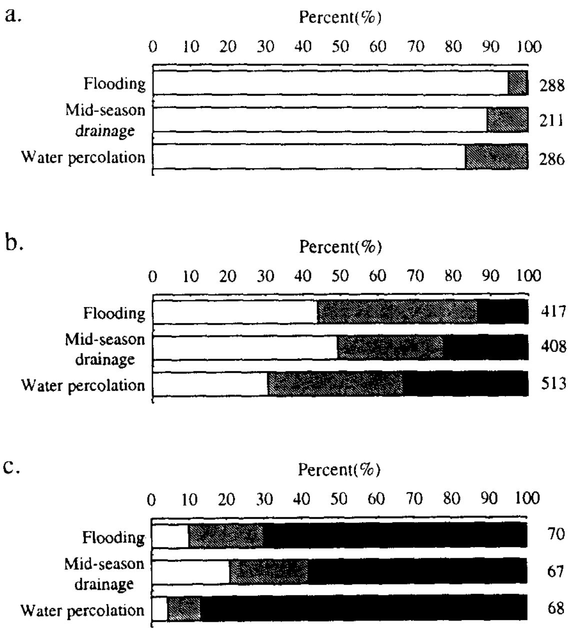

Fig. 5. Effects of different water managements on growth direction of nodal roots. The horizontal bars indicate the percentages of nodal roots per hill growing at three different inclinations (square, 0-35°; shaded square, 35-55°; dark square, 55-90° to the horizontal). The number of roots measured is indicated by the number on the right of the bar. **a**, distal roots; **b**, proximal roots; **c**, nodal roots elongating from prophyll shoot units. **Flooding**, flooding the paddy without drainage or water percolation; **Mid-season drainage**, draining the paddy for three weeks at the mid-season of the cultivation, **Water percolation**, flooding the paddy with percolating of the water through the soil at the rate of 3cm per day. After Kawata and Katano (1977).

various growth directions in a root system. It should be noted that low planting densities and high rate of nitrogen application often increase the number of tillers per plant (Fig. 3). The large number of tillers is due to an increased number of the secondary and tertiary tillers, which themselves often have a rather small number and size of shoot units. Such differences in number and size of shoot units should change the number and the distribution pattern of the diameter of nodal roots in a whole plant, perhaps resulting in a modification of the rooting pattern.

Furthermore, the growth direction of nodal roots in a single shoot unit could also be affected by environmental factors. It was shown that the light conditions experienced by the leaf changed the growth direction of elongating nodal roots in a water-cultured shoot unit (Morita and Yamazaki, 1992). Therefore, the growth direction of nodal roots might depend on the amount of substrates (e.g., photosynthetic assimilates) translocated from the leaf to elongating nodal roots.

We suppose that the translocation of substrates may be affected by both the root diameter, as a limiting factor of transportation, and the potential amount of substrates that could be partitioned to roots. Our working hypothesis on the plagiogravitropic response of rice nodal roots is as follows. 1) The growth direction of nodal roots may be primarily limited by their diameter, which is determined before and/or just after their emergence. 2) The growth direction of nodal roots may also be influenced by the amount of substrates able to be partitioned to roots, that varies considerably with the developmental stages of shoot as well as the environmental conditions. In summary, the relationship between the amount of substrates translocated to the roots and the root diameter is the most important factor regarding to plagiogravitropic response of rice nodal roots.

Growth direction of nodal roots and the spatial distribution of a root system

We have also investigated the spatial distribution of rice root systems, including lateral roots, in paddy fields. As the row and hill spacing are usually 30 cm and 15 cm respectively, cylindrical monoliths 15 cm in diameter were taken at two locations - one including a rice hill at the center and the other at the mid-point between four neighboring hills (Morita et al., 1988). The monoliths were sliced with 5 or 10 cm increments of soil depth, and the length and/or weight of roots in each soil block were measured. Therefore we could calculate a "*root depth index*" of the root system using estimated rooting densities at each depth of the soil just below a hill and between four hills (Murita et al., 1993). The "root depth index" is the weighted average of root depth in soil (Oyanagi et al., 1993; Oyanagi, 1994), which is something like the depth of the centroid in a root system.

In the results, the "root depth index", did not always correlate with the mean growth angle of nodal roots in the rice plants taken from the same plots. For example, Dobashi 1, an old Japanese variety, had a larger "root depth index" (7.9cm from soil surface) than IR36 (7.3 cm), a semi-dwarf modern variety bred by the International Rice Research Institute, though Dobashi 1 had a smaller mean growth angle of nodal roots (29.4° to the horizontal) than IR36 (33.0°). The difference in "root depth index" seemed to be due to the large size of the nodal roots in Dobashi 1 (Morita et al., 1993). Dobashi 1 had a greater root length per nodal root (2.35 m) than IR36 (1.25 m), indicating the long main axes of nodal roots and well-developed laterals of Dubashi 1. On the other hand, Lemont, one of the most popular varieties in the United States of America, showed a large "root depth index" (9.0 cm) with large mean growth angle of nodal roots (37.9°). These results suggest that there may be several strategies by which rice varieties form a root system with a deep distribution in soil. Neither growth direction nor size of nodal roots alone determines the root distribution; it is their combination which is important.

Environmental conditions could affect the elongation of nodal roots as well as the root growth direction. Soil conditions, such as the depth of plow-pan, soil hardness and the development of soil pores, seem to be some important factors affecting vertical distribution of root systems in a paddy (Kawata et al., 1969, 1980b).

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Section editor: H Lambers