Effects of Shading on Respiration and Ammonium Uptake of Rice Roots

—Comparison of activity in roots from different nodes—*

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Rice plants develop the fibrous root system which consists of numerous primary roots emerging successively from nodes. All roots are initiated at the stem node, keeping a definite relationship with the emergence and development of the leaves; when the (n)th leaf is developing, roots emerge simultaneously from the (n-3)th node of the same stem, except for the seminal root, and the roots from coleoptile node³⁾.

Several lines of investigation have been carried out on the physiological activities of rice roots in relation to root age^{1,2,5,17)}. Physiological activities and growth of the roots are closely dependent on photosynthesis of leaves to enable the supply of carbohydrates^{4,15,19)}. MURATA et al.¹²⁾ showed an interrelationship between the photosynthetic activity of the shoot and the physiological activity of the root.

To consider the function of a root and root system in rice plant, both the rooting habit and the root-shoot relation seem to be an important aspect. However, very few efforts have been done on the function of a root system in connection with this aspect.

Then, in this paper the characteristics of oxygen and nitrogen uptakes in the roots on definite nodal positions were studied in relation to light condition of the shoot, and the discussion was attempted on the function of a root system in the process of plant growth.

Materials and Methods

Pre-germinated rice seeds (*Oryza sativa* L.

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cv. Aich-asahi) were grown on a salan net floating in a vat with a 10-fold dilution of Kasugai's rice culture solution⁸⁾** for 20 days. At the 5th leaf emergence (Jan. 25, 1977), seedlings were transplanted spacing 4 cm × 4 cm into a water culture bed (200 liter in volume) filled with a 2-fold dilution of the culture solution. Plants were grown in a growth cabinet under natural sun light with a temperature at 27°C in daytime and 19°C at night, conditioning the day length for 16hr and the night length for 8hr by twin reflector lamps (150 W × 2). The culture solution was renewed every week and adjusted to pH 5.0 with 1 N hydrochloric acid.

1. Technique used for sampling the roots from different nodes

The primary roots of a plant attaining a length of 3-4 cm were loosely tied up together by a fine string of nylon, when the 5th, 7th, and 9th leaf emerged. Thus, at the beginning of the experiment, the roots of main stem were classified into four classes as follows; 1) the roots which have elongated before the 5th leaf emergence, designated as seminal root, and the roots from coleoptile and the 1st nodes (S·C·1n), 2) the roots which emerged with the 5th and 6th leaf development and have elongated before the 7th leaf emergence, as the roots from the 2nd and 3rd nodes (2·3n), 3) the roots which emerged with the 7th and 8th leaf development and have elongated before the 9th leaf emergence, as the roots from the 4th

** The full strength solution contained (mg per liter): (NH₄)₂SO₄, 189; Na₂HPO₄, 41; KCl, 48; CaCl₂, 8; MgCl₂, 14; FeCl₃, 10; MnCl₂, 0.75.

and 5th nodes (4·5n), and 4) the roots which emerged with the 9th leaf development, as the roots from the 6th node (6n).

The roots from (n)th node, designated in this report, may correspond to the roots emerging from the (n)th node, which was observed by FUJII³⁾; to the roots emerging from the (n)th nodal region, by INOSAKA⁷⁾; and, to the upper and lower roots emerging from the (n)th shoot unit, by KAWATA et al⁹⁾. The days after emergence of the roots in four classes at the beginning of experiment were as follows; S·C·1n: more than 30 days, 2·3n: 30–16 days, 4·5n: 16–2 days, 6n: 2–0 days.

2. Shading

At the stage of the 9th leaf emergence, 110 plants were selected and prepared for the experiment; 50 plants for control plot (under natural light), 40 plants for shading plot, and 20 plants for removal of shade plot. Shading was carried out for 9 days by using a double black cheesecloth which reduced a light intensity to 36% of natural light. In removal of shade plot, cheesecloth was removed at the 4th day of shading and then a light intensity was recovered to natural light.

3. Sampling

At every 2 days, 10 plants in each plot were sampled. Then the tillers were removed carefully from the main stem. The

roots of main stem were washed with running tap water for 5 min and then rinsed with distilled water. Immediately after washing, the roots which have been classified by the technique mentioned above were cut out and separated under water. For morphological observation of the roots, 3 plants of each plot were sampled and fixed with FAA at the beginning and end of the experiment.

4. Measurement of rate of oxygen uptake in the roots

Each one gram of fresh roots was collected randomly from the separated roots of 3 plants and its oxygen uptake rate was measured in 2 ml of 0.1 M phosphate buffer (pH 7.1) at 30°C, using Warburg manometric technique.

5. Measurement of rate of nitrogen uptake in the roots

The cut-out and separated roots of 4 plants were incubated together in a 3 liter glass beaker with a 2-fold dilution of Kasugai's culture solution (pH 5.0) containing ¹⁵N-labelled ammonium sulfate (nitrogen concentration, 20 ppm; ¹⁵N, 19.63 atom % excess) for 3 hr at 30°C. After incubation the roots were washed with running tap water for 10 min, rinsed with distilled water, and then dried in an oven at 90°C for 24 hr.

Total nitrogen contents of the roots were determined by Kjeldahl method and their

Table 1. Effects of shading and of removal of shade on length and number of the roots from different nodes in main stem.*

Total length and number of primary roots/plant	Control	Shading**	Removal of shade***
Leaf number	9.3	9.2	9.5
Root length of the roots from the 6th node (mm)	2056±145	913±92	1346±296
Number of root****			
The roots from the 6th node	13.0±0.0	9.0±0.7	10.3±1.8
The roots from the 4th & 5th nodes	10.3±1.1	10.3±1.8	9.7±0.8
The roots from the 2nd & 3rd nodes	11.7±0.4	10.7±0.8	11.0±0.7
The roots from coleoptile & the 1st nodes, and seminal root	7.0±0.0	8.3±0.4	8.0±0.7

±; Standard error. * At the end of experiment.

** 9 days after shading. *** 5 days after removal of shade.

**** Three or four roots emerged from the 7th node and attained a length of 1~3 mm in control and removal of shade plants.

Fig. 1. Time course of change in dry weight of the roots from different nodes under natural light (○—○), shading (●—●), and removal of shade (○--○) conditions.

—↑; Shows the time of removal of shade.

* S·C·1n; Seminal root, and the roots from coleoptile and the 1st nodes, 2·3n; the roots from the 2nd and 3rd nodes, 4·5n; the roots from the 4th and 5th nodes, 6n; the roots from the 6th node.

^{15}N contents were measured by emission spectrographic method. ^{15}N -analysis was carried out by the method described by OERTLI¹³⁾ with some modification¹⁸⁾ using a JASCO NIA-1 ^{15}N -analyzer. Total amount of absorbed ^{15}N in the roots was calculated from the data of total nitrogen content and abundance of excess ^{15}N in the roots, assuming that 100% of the ^{15}N -labelled ammonium sulfate was applied in absorbing solution.

Results

1. Root growth

Figs. 1 and 2 show the time course of change in dry weight and nitrogen content of the roots during the experiment. In the control plant those of 6n increased during the experimental period. Dry weight of

Fig. 2. Time course of change in nitrogen content of the roots from different nodes under natural light, shading, and removal of shade conditions.

Symbols are the same with Fig. 1.

* See Fig. 1.

4·5n also increased gradually, while the increment of nitrogen content reached plateau at the 2nd day of the experiment. Dry weight and nitrogen content of 2·3n and S·C·1n scarcely showed any increase during the period.

With shading, the increasing rates of dry weight and nitrogen content of 4·5n and 6n were reduced markedly as compared with those of control. After removal of shade and returning the plants to natural light, remarkable increment of dry weight and nitrogen content occurred in both roots, especially in 4·5n. On the other hand shading and removal of shade had little or no effect on both dry weight and nitrogen content of 2·3n and S·C·1n.

Emergence of 6n was retarded by shading and slightly promoted after replacing the plants in natural light (Table 1). There were observed the repression of elongation of 6n under shading and the recovery of its elongation after the removal of shade; in removal of shade, length of the secondary

Fig. 3. Effects of shading and of removal of shade on rates of oxygen (A) and nitrogen uptakes (B) of the root system.

●—●; Shading, ○—○; Removal of shade, —→; Shows the time of removal of shade.

roots of 4.5n which were at vigorous branching stage was longer than that of the roots of control plant at the end of experiment.

From these results as well as those already reported^{8,10}, it is clear that 6n and 4.5n which are growing actively are more susceptible to light condition of shoot for the root growth than 2.3n and S.C.1n.

2. Rates of oxygen and nitrogen uptakes of the root system

The rates of oxygen uptake by the root system decreased through the period of shading, and recovered to the control level at the 5th day after removal of shade (Fig. 3-A). On the other hand the repressive effect of shading on nitrogen uptake rate of the root system coincided with that on oxygen uptake rate till 4 days after shading, however, thereafter the nitrogen uptake rate was returned to increase (Fig. 3-B). It is not clear why the rate of nitrogen uptake of the root system reincreases in spite of its low rate of oxygen uptake. STARCK¹⁶ reported similar phenomena in ³²P uptake by young sunflower, i.e., shading through 7 days reduced root growth, however, the activity of roots as an acceptor of ¹⁴C-assimilates and absorbers of ³²P exceeded that of control plants, in spite of their low respiratory rate.

As shown in Fig. 3-B, this reincrease of the nitrogen uptake rate at the 4th day after shading was further promoted when

Fig. 4. Rate of oxygen uptake in the roots from different nodes under natural light (○—○), shading (●—●), and removal of shade (○—○) conditions.

Numerals in the figure show the days after shading.

* See Fig. 1.

Fig. 5. Rate of nitrogen uptake in the roots from different nodes under natural light, shading, and removal of shade conditions.

Symbols are the same with Fig. 4.

* See Fig. 1.

shade was removed, and then the rate was greater than the control at the 2nd and 5th day after removal of shade.

3. Rate of oxygen uptake of the roots from different nodes

Figs. 4 and 6-A show the effects of shading and of removal of shade on oxygen uptake rate of the roots from different nodes. In control plant the oxygen uptake rate decreased from upper roots to lower roots, showing the highest value at the uppermost roots (6n) (Fig. 4). This pattern of oxygen

Fig. 6. Effects of shading and of removal of shade on rates of oxygen uptake (A) and nitrogen uptake (B) of the roots from different nodes.

×; Seminal root, and the roots from coleoptile and the 1st nodes, ●; the roots from the 2nd and 3rd nodes, △; the roots from the 4th and 5th nodes, ○; the roots from the 6th node. →; Shows the time of removal of shade.

uptake rate which increased toward upper nodal roots corresponds to FUJII's result³⁾, and this pattern was not changed by shading and removal of shade.

However, the effects of shading and of removal of shade on oxygen uptake rate in the respective roots were characteristically different with their ages and nodal positions (Fig. 6-A); at the end of experiment, the rate of oxygen uptake of 2·3n and 4·5n decreased to about 40% of the control, however, that of S·C·1n and of 6n remained in about 80% of the control. At the 5th day after removal of shade, the oxygen uptake rate of respective roots increased and recovered to the control level, especially those of 6n and S·C·1n exceeded conspicuously the control. These results show that the rate of oxygen uptake suppressed by

Table 2. R.Q. of the roots from different nodes in control plant.

	Position of the roots*			
	S·C·1n	2·3n	4·5n	6n
O ₂ uptake (μl/hr/plant)	1.34	12.5	22.1	20.9
CO ₂ evolution (μl/hr/plant)	1.64	11.4	18.5	17.9
R.Q.	1.22	0.91	0.84	0.86

At the end of experiment.

* See Fig. 1.

shading of the shoot was greater in 4·5n and 2·3n than in S·C·1n and 6n. However, the promotion of oxygen uptake by removal of shade was more remarkable in the latter.

Table 2 shows the respiratory quotient (R.Q.) in the roots of the control plant. Value of R.Q. in 2·3n and S·C·1n was higher than that of 4·5n and 6n, especially S·C·1n showed high value over 1.0. It seems to be possible that the respiration in S·C·1n having a high R.Q. may be dependent on the oxidative breakdown of organic acids.

4. Rate of nitrogen uptake of the roots from different nodes

Figs. 5 and 6-B show the effects of shading and of removal of shade on the rate of nitrogen uptake of the roots from different nodes. In control plant 6n showed the highest rate of the uptake during the experimental period. The rate of nitrogen uptake of the respective roots decreased successively toward lower nodal roots. This pattern is similar to that of the rate of oxygen uptake (Fig. 4).

In shaded plant the grade of decrease in rate of nitrogen uptake in 6n was less than that in the other roots, i.e., the rate was reduced to 80% of the control in 6n and to 46% to 53% in the other roots at the 4th day after shading. The reincrease of rate of nitrogen uptake on the 4th day after shading occurred clearly in the respective roots, especially in 6n the uptake rate was superior than that of the control. The rate of nitrogen uptake of the roots in shaded

Fig. 7. Relations between rates of oxygen and nitrogen uptakes in the roots from different nodes.

Symbols are the same with Fig. 6.

(A); $Y=0.41X+17.8$, $r=0.60^*$

(B); $Y=0.43X-0.48$, $r=0.73^{**}$

(C); $Y=0.29X-6.67$, $r=0.73^{**}$

(D); $Y=0.30X-16.8$, $r=0.83^{**}$

plants was accelerated by returning the plants to natural light. At the 5th day after removal of shade the rate of the respective roots exceeded that of control (Fig. 6-B). These results show that the suppressive effect of shading on the rate of nitrogen uptake is less in 6n than in the other roots, and the promotive effect at the 2nd day after removal of shade was notable in all the roots.

5. Relations between rates of oxygen and nitrogen uptakes in the roots from different nodes

There were found close correlations between rates of oxygen and nitrogen uptakes of the roots from different nodes; $r=0.60^*$ in S·C·1n, $r=0.73^{**}$ in 2·3n, $r=0.73^{**}$ in 4·5n, and $r=0.83^{**}$ in 6n (Fig. 7). The regression lines were different among the respective roots; $Y=0.41X+17.8$ in S·C·1n, $Y=0.43X-0.48$ in 2·3n, $Y=0.29X-6.67$ in 4·5n, and $Y=0.30X-16.8$ in 6n. They could be divided into two groups by regression coefficients, i.e., one consisted of 0.41 and 0.43 in 2·3n and S·C·1n, respectively, with relatively high coefficients, and the other consisted of 0.29 and 0.30 in 4·5n and 6n, respectively, with relatively low coefficients. The difference of these regres-

Fig. 8. Effects of shading and of removal of shade on the ratio of rate of nitrogen uptake to rate of oxygen uptake in the roots from different nodes.

Symbols are the same with Fig. 6.

sion coefficients between the two groups may suggest that the ratio of nitrogen uptake rate to oxygen uptake rate (efficiency of nitrogen uptake) was larger in the lower roots (S·C·1n, 2·3n) than in the upper roots (4·5n, 6n).

Fig. 8 shows the ratio of nitrogen uptake rate to oxygen uptake rate (efficiency of nitrogen uptake) in the roots. The ratio in the control plant increased markedly toward lower roots. By shading the ratio decreased greater in the lower roots than in the upper roots, then the difference in the value among the roots from different nodes diminished at the 4th day after shading. On the other hand, by returning the plants to natural light, the ratio of lower roots increased greater than that of the upper roots. Then the difference in the ratio among the roots from different nodes increased and became similar pattern to the control. Above result shows that the lower roots are more susceptible in the efficiency of nitrogen uptake than the upper roots as the light condition of shoot changes.

Discussion

In this experiment all the roots of main

stem of a plant in vegetative stage were classified into four classes not only by their nodal positions but also by their chronological ages after rooting.

As shown in Figs. 4 and 5, rates of oxygen and nitrogen uptakes were highest in the uppermost roots (youngest roots) and decreased toward the lower roots (older roots). This pattern among the different aged roots in rates of oxygen and nitrogen uptakes is in agreement with the result reported by BABA and INADA¹⁾ in measuring the activities of the roots classified with their color and lateral root appearance.

It was shown in Fig. 6-A that the effect of shading on the rate of oxygen uptake was lesser in the uppermost roots than in the other roots, except for the lowermost roots. This difference may be due to the change in demands for photosynthate in the roots with ageing. YOSHIDA and MIYAMATSU¹⁹⁾ reported that the rapidly growing parts of the root such as root tip and apical region of lateral root accumulated ¹⁴C-labelled photosynthate more actively than the other older parts.

It is well known that root respiration is closely dependent on the carbohydrate supply from the shoot^{4,12,15,19)}, and also reported that the uptake rate of nutrients such as nitrogen, phosphorus, and potassium was closely dependent on root respiration⁶⁾. This experiment suggests a close correlation between rates of oxygen and nitrogen uptakes in the roots from different nodes (Fig. 7), and moreover clearly indicates that the efficiency of nitrogen uptake is higher in the lower roots (older roots) than in the upper roots (young roots). This difference in the efficiency between upper and lower roots may be due to the change in respiratory system with ageing. According to BABA and INADA¹⁾, an active respiration through the cytochrome-cytochrome oxidase system was responsible for the active absorption of nitrogen and phosphorous by new roots, and INADA⁶⁾ suggested that energy for nutrient uptake might be supplied more efficiently through cytochrome oxidase system in new roots. However, the respiratory energy in the roots is believed to be con-

sumed not only by uptake of nutrients but also by other energy dependent activities such as root growth.

These facts indicate that less respiratory energy is consumed for nitrogen uptake in the young roots in spite of their high net efficiency of uptake, thus apparent efficiency of nitrogen uptake in the young roots may become lower than that in the older roots.

On the other hand, the change in oxygen uptake rate of the roots from different nodes by shading did not take place in the same manner as that in nitrogen uptake (Figs. 6-A, 6-B). As shown in Fig. 8, the (apparent) efficiency of nitrogen uptake in the older roots was more susceptible than that in the younger roots to the light condition of shoot. This result may clearly characterize the difference in root-shoot relationship between younger roots (upper roots) and older roots (lower roots).

The reason why the efficiency of the older roots is more sensitive than that of the younger roots is still not clear, however, a high efficiency of nitrogen uptake in the older roots seems to be actively maintained by sufficient supply of the photosynthate from shoot in favourable light conditions. This may suggest a specific role of the older roots in nitrogen uptake of the root system.

According to OKAJIMA¹⁴⁾, water and salt absorption by the old roots was superior to those by the young ones in intact rice roots under sufficient supply of nitrogen. LEE and OTA¹¹⁾ demonstrated that the elimination of nitrogen application reduced the root activity especially in lower nodal roots. These reports suggest an important role of old roots in nutrient uptake under favourable nutrient conditions. In this experiment nutrients were supplied sufficiently by water culture, then the older roots also seem to play a significant role in nitrogen uptake (ca. 20% of total uptake) in spite of their relatively low uptake rate.

Roots function not only as an acceptor of carbohydrate from shoot but also as a donor of mineral nutrients to shoot. It has been widely believed that the young roots play an important role in nutrient supply to shoot because of their active nutrient

uptake measured by detached roots. On the contrary, as mentioned above, OKAJIMA's result¹⁴⁾ examined in attached roots shows that the old roots absorb nutrients more actively than the young roots. This difference in activity of nutrient uptake between detached and attached roots may suggest that the transport is an important process in nutrient uptake by roots.

Further analysis of intact root system may be needed to make clear how the nutrient uptake by different aged roots is accomplished in relation to shoot.

Summary

The effects of shading of shoot on respiration and ammonium uptake of rice roots from different nodes were explored. 1. The rates of oxygen and nitrogen uptakes were highest in the roots from the uppermost node and decreased toward the lower roots. 2. The rates of oxygen and nitrogen uptakes were less susceptible to the light condition of shoot in the roots from the uppermost node than in the other roots, except for the roots lower than the

2nd node. 3. There were close correlations between rates of oxygen and nitrogen uptakes of the roots from different nodes. 4. The ratio of nitrogen uptake rate to oxygen uptake rate (efficiency of nitrogen uptake) was higher in the roots from lower nodes than in the roots from upper nodes. 5. The roots from lower nodes were more susceptible than the roots from upper nodes in the efficiency of nitrogen uptake as light condition of shoot changed. The data are discussed in relation to root age and root-shoot relationship.

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〔和 文 摘 要〕

地上部の遮光が水稻根系の呼吸とアンモニア吸収力に及ぼす影響 —とくに節位別に分級した根群間の比較—

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水稻根系を構成する発根節位の異なる根群間の生理機能の特徴を比較するために、地上部の遮光処理がそれらの根群の呼吸とアンモニア吸収活性に及ぼす影響を調べた。葉と根の出現・伸長の規則性を利用してあらかじめ分級した第1節以下、第2・3節、第4・5節および第6節から出現・伸長した1次根(節根)をもつ第9葉期的水稻を用いた。

遮光は最上位節根(第6節根)の出現・伸長を遅延させ、遮光解除はそれらを促進した(第1表)。また、これらの処理は、上位節根(第4・5節根、第6節根)の乾物重・窒素含有量に対しても同様の影響を与えた(第1, 2図)。

酸素吸収力と窒素吸収力の両者はともに、最上位節根でもっとも高く、下位の節根になるにしたがって低かった。遮光によるこれらの活性低下は最上位節根でもっとも小さく、中位の節根(第2・3節根、第4・5節根)でもっとも大きかった。最下位節根の窒素吸収力の低下は酸素吸収力の低下に比して顕著であった(第4, 5, 6図)。

各節根の酸素吸収力と窒素吸収力との間に高い正の相関が認められた。その回帰係数は、より上位の節根(第4・5節根、第6節根)とより下位の節根(第1節以下の節根、第2・3節根)とで異なり、後者で大きかった(第7図)。

酸素吸収力に対する窒素吸収力の比(窒素吸収効率)は最下位節根でもっとも大きく、上位の節根になるに従って小さくなった。窒素吸収効率に対する遮光と遮光解除の影響は、上位の節根(第4・5節根、第6節根)に比較して下位の節根(第1節以下の節根、第2・3節根)でより大きくあらわれた(第8図)。

これらの結果にもとづき、水稻の生長における根系の役割について若干の考察を行った。