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Growth Respiration in Rice Organs as Affected by Nitrogen Content*

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Abstract : The relationship between growth respiration and nitrogen content in rice organs was investigated. Top and root CO_2 exchange rates were continuously measured for 5-6 days under different nutrient concentrations by lowering the light intensity with each passing day. There were significant positive correlations between the growth respiration rate in the top (Rgt) and dry matter increase in the top, and between the growth respiration rate in the root (Rgt) and dry matter increase in the root. Though, there were significant positive correlations between Rgt and leaf area expansion, and leaf dry matter increase, no significant relationship was found between Rgt and dry matter in leaf sheath. The growth respiration rate in each plant part was closely related to the dry matter increase and nitrogen increase. The nitrogen content of the leaf blade was higher than that of the leaf sheath. This suggests that growth respiration in the top is utilized more for the growth of leaf blade than that of leaf sheath. Moreover, the ranges of growth coefficient in the whole plant, top and root were from 0.56 to 1.26, 0.44 to 1.11, and 0.60 to 1.11 g g^{-1}, respectively, under different nutrient conditions. The growth coefficient of each part increased as the result of nitrogen content in new biomass. The growth coefficient in the root was higher than that in the top when compared at the same value of the ratio of the increase in nitrogen. The slope of linear regression in the root was higher than that in the top. In this paper, it was determined quantitatively the relationship between nitrogen increase and growth coefficient in rice organs.
Key words : Growth coefficient, Growth respiration, Nitrogen content, Rice.

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要　旨 : イネの器官別の生長係数と窒素濃度との関係を明らかにするため，培養液濃度の違いによって生育様相を異にしたイネ品種アキヒカリの幼植物を用いて，日毎に光強度を低下させた場合の茎葉部および根部の CO_2 収支を測定，解析した．その結果，茎葉部の生長呼吸量と茎葉部の乾物増加量との間，および根部の生長呼吸量と根の乾物増加量との間に，各々高い正の相関が認められた．茎葉部の生長呼吸量については，葉身の乾物重および葉面積の増加量との間に各々極めて高い正の相関が認められたが，葉鞘の乾物増加量との間には有意な相関は認められなかった．また，個体および各部位の生長呼吸量は，主に乾物増加と窒素増加が関与することが示された．これらのことから，1 g 当たりの乾物増加に関わる生長呼吸量は，窒素含有率の高い葉身では葉鞘より大きいものと考えられた．

一方，生長係数は，異なる培養液濃度条件下において大きく変化し，個体，茎葉部および根部の値はそれぞれ，0.56-1.26，0.44-1.11，0.60-1.11 g g^{-1} であった．また，各部位の生長係数と乾物増加量当たりの窒素増加量（$\Delta N/\Delta W$）との間には正の相関が認められ，根の生長係数は，同じ値の $\Delta N/\Delta W$ で比較すると茎葉部に比べて高く，また，回帰直線の傾きも大きかった．本論文では，イネ器官の生長に伴う窒素増加と生長係数との間の定量的関係が示された．
キーワード : イネ，生長係数，生長呼吸，窒素含有率．

Dark respiration can be divided into two in relation to the growth and maintenance processes[8]. Growth respiration is related to the synthesis of new biomass and maintenance respiration is related to the maintenance of existing biomass. The respiration rate is expressed as the following equation[5] : $R = g(dW/dt) + mW$ (R ; respiration rate, W ; dry weight, g ; growth coefficient, m ; maintenance coefficient). Data on these coefficients is useful to establish growth models and to understand plant growth.

The growth coefficient was found to be influenced by environmental factors such as daylength[4,10] and temperature[11,12]. The growth coefficient is changed by the factor of newly formed biomass[14] and is high when the content of protein is high[15]. But few studies have been done to understand the growth coefficient of organs as related to nitrogen content by measuring the growth respiration

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rate, dry matter increase and nitrogen increase in the same plant.

In this paper, top and root CO_2 exchange rates were continuously measured for 5-6 days under different nutrient concentrations by lowering light intensity day-by-day. The relationships among growth respiration, growth and nitrogen increase in whole plant, top and root of rice seedlings were studied.

Materials and Methods

1. Plant culture

Rice (*Oryza sativa* L. cv. Akihikari) plants were grown in Kimura B solution[3] until the 7-9th leaf stages inside a greenhouse at Okayama University from May to July, 1990, and from June to August, 1992. The procedure for solution culture was as follows. Germinated seeds were put on a saran net fixed on a plastic container (25×32×6 cm) filled with tap water and were grown until the 2nd-leaf stage. The seedlings were then transplanted into the holes, which were 1 cm in diameter and at 4×4 cm spacing, in a styrofoam plate floating on a plastic container (25×32×6 cm) and cultured at three levels of nutrient concentration, i. e., 40%, 100% and 200% of Kimura B standard concentration. The nutrient solution was aerated with an air pump, and renewed every four days. The pH was adjusted to 5.4 daily. Since one apparatus set was available for the measurement of photosynthesis and respiration of the whole plant in this experiment, the seeding dates were then adjusted as shown in Table 1 so that seedlings had the same plant age at the start of measurement.

2. Experimental design

In the 1990 and 1992 experiments, the rates of photosynthesis and top and root respirations were measured at three levels of nutrient concentration, i. e., 40%, 100% and 200% of Kimura B solution. In the 1990 experiment, two more treatments were added. The plants grown in the 40% or 200% nutrient concentration were transferred to the solution with 200% or 40% concentration, respectively (40-200% plot, 200-40% plot), when they were transferred to the growth cabinet (Shimadzu, SCA-001H, Kyoto). In Table 1, nutrient concentration before and after transferring plants to the growth cabinet in all treatments are shown.

Table 1. Culture conditions and rice plant growth during the measurement of photosynthesis and respiration.

Culture conditions	Nutrient concentration[1]		Date of seedling	Period of Pn and R measurement (month/day)	Plant age		Stem number		Leaf area		Dry weight	
	Before measurement (%)	During measurement (%)			(A)[2]	(B)[2]	(A)	(B)	(A) (cm^2)	(B) (cm^2)	(A) (mg)	(B) (mg)
1. Low conc. 1	40	40	'90/5/12	7/ 2~7/ 8	9.0±0.1	0.5	1.0±0.4	0.0	37.5±1.2	10.9	460±19	92
2. Low conc. 2	40	40	'92/6/19	7/24~7/30	7.4±0.1	1.6	1.0±0.0	0.3	26.2±2.9	17.2	213±11	102
3. Low-high conc.	40	200	'90/5/18	7/10~7/16	9.5±0.2	0.5	1.0±0.0	0.3	44.8±3.5	31.3	621±47	117
4. Standard 1	100	100	'90/5/ 6	6/10~6/15	8.0±0.2	1.1	2.9±0.7	0.4	45.3±3.5	40.0	560±11	168
5. Standard 2	100	100	'90/6/18	7/17~7/23	8.1±0.1	1.1	2.8±0.6	0.5	49.6±1.9	48.4	570±10	292
6. Standard 3	100	100	'92/7/ 3	8/10~8/15	7.8±0.0	1.2	2.9±0.0	0.0	36.1±1.3	25.1	251± 9	165
7. High conc. 1	200	200	'90/5/24	6/16~6/22	8.1±0.0	1.0	3.5±0.4	0.0	61.6±4.5	58.9	728±12	300
8. High conc. 2	200	200	'92/7/14	7/31~8/ 5	8.0±0.1	0.8	3.0±0.3	0.3	55.2±1.6	30.6	332±17	244
9. High-low conc.	200	40	'90/5/30	6/25~7/ 1	8.0±0.2	1.3	3.9±0.5	0.6	72.0±4.7	49.6	798±23	311

1) Nutrient condition is expressed as the percentage to the standard concentration of Kimura B solution.
2) (A) : Mean of eight samples and standard error at the start of the measurement, (B) : Increase during the measurement.

3. Measurement of plant photosynthesis and respiration

Forty plants of each plot at the 7-9th leaf stage were placed in growth cabinets for two days prior to the measurement for adaptation to the controlled conditions, i. e., 600 μmol m^{-2} s^{-1} of light intensity, 12 hours of day-length, 26°C, and 75% relative humidity. After that, 12 plants with uniform plant length, leaf age and fresh weight were selected. Four plants were set up in the apparatus for the measurement of photosynthesis and respiration, and the remaining eight plants were used for the estimation of leaf area and dry weight of leaf blade, leaf sheath and root of a plant as the initial values. After the 5-6 day measurement, plants were taken out of the apparatus and their dry weight and leaf area were measured.

The CO_2 exchange rate of the top and root of the intact plants were measured by the system previously reported[19]. In this system, a stable and continuous measurement of the rate of root respiration was possible since pH and temperature of the solution were well-controlled. The temperature was maintained at 26.0±0.5°C and 23.0±0.1°C for the top air and root solution, respectively, and humidity of top, inlet air was 75% RH. The CO_2 concentration of air in top and root inlet was 335±3 ppm and the air-flow rate for the top and root portion was 12-15 L min^{-1} and 2.5 L min^{-1}, respectively. The pH of the culture solution was 5.35±0.05. The length of day and night was 12 hours. In the 1990 experiment, the rates of photosynthesis and top and root respiration in each of the five treatments, i. e., 40%, 40-200%, 100%, and 200-40% plots were continuously measured for six days, and at the 100% plot for five days. In 1992, measurements were performed for the three treatments, i. e. 40%, 100% and 200% plots for five days. During the 6 day measurement, light intensity was set to 1200 μmol m^{-2} s^{-1} for the first two days, then decreased to 600, 300, 150, 0 μmol m^{-2} s^{-1} on the 3rd, 4th, 5th, and 6th day, respectively. In the five-day measurement, the light intensity was set to 1200 μmol m^{-2} s^{-1} for the first day, then decreased to 600, 300, 150, 0 μmol m^{-2} s^{-1} on the 2nd, 3rd, 4th and 5th day, respectively. Four metal halide lamps (Toshiba D400, Tokyo) were used as the light source.

In the 1992 experiment, thiourea was added in the nutrient solution inside the assimilation chamber to prevent nitrification. The added thiourea was 0.015 times of total nitrogen in the nutrient solution.

4. Measurement of dry matter increase, nitrogen, starch and soluble sugar content

Increases of dry weight and leaf area during the measurement were calculated from the subtraction of the initial values estimated with eight plants. The nitrogen content in each plant part was determined with CN CORDER (Yanaco MT-600, Tokyo) and the amount of nitrogen taken up during the period was estimated in the same way as dry matter increase. Starch and soluble sugar in the leaf sheath were extracted with the method described by Yoshino[22], and their contents were determined using a glucose analyzer (TOA Glu-11, Tokyo).

5. Estimation of the growth and maintenance respiration rate

The gross photosynthesis and respiration were calculated as follows. The top respiration rate in the daytime was assumed to be equal to the top respiration rate at night. The gross photosynthesis rate was the sum of the net photosynthesis rate and the top respiration rate at night. The respiration rate in each plant part through the measurement period was calculated by using the daily respiration rate in each plant part.

The maintenance coefficient in top and root was calculated by dividing the maintenance respiration by the final dry weight in top and root, respectively. Assuming the constant c and the dry matter increase rate, the daily maintenance respiration rate was calculated by multiplying c by the dry weight of the day. The growth respiration rate was calculated by subtracting the maintenance respiration rate from the respiration rate. The growth coefficients in top and root were calculated by dividing the growth respiration rate by the dry matter increase in top and root, respectively.

Results

There were significant positive correlations between the growth respiration rate in top and dry matter increase in top ($r=0.864^{**}$), and between the growth respiration rate in root and dry matter increase in root ($r=0.938^{**}$).

Furthermore, there were significant positive correlations between the growth respiration rate in top and the increase in area and dry matter in leaf blade (Fig. 1). However, there was no significant relationship between the growth respiration rate in top and dry matter increase in leaf sheath ($r=0.574$. Data not shown). There was a positive correlation between the dry-matter increase, apart from starch and soluble sugar in leaf sheath and growth respiration rate in top ($r=0.694^*$. Data not shown).

The nitrogen content and its change in leaf blade were higher than in other two parts (Table 2). Multiple regression analysis was done, using the growth respiration rate in whole plant as a dependent variable, the dry matter increase and the nitrogen increase in whole plant as independent variables. The equation was:

$$Rg=0.35\Delta W+11.9\Delta N+2.6$$

($R^2=0.833^{**}$)

(Rg; growth respiration rate in whole plant (mg plant^{-1}), ΔW; dry matter increase (mg), ΔN; nitrogen increase (mg)). This equation indicated that 83% of the total variation in the growth respiration rate in whole plant could explain the dry matter increase and nitrogen increase in whole plant. Multiple regression analysis, also indicated that 89% of the total variation in the growth respiration rate in top could explain the dry matter increase and the nitrogen increase in top. The equation was:

$$Rgt=0.21\Delta Wt+10.7\Delta Nt+0.33$$

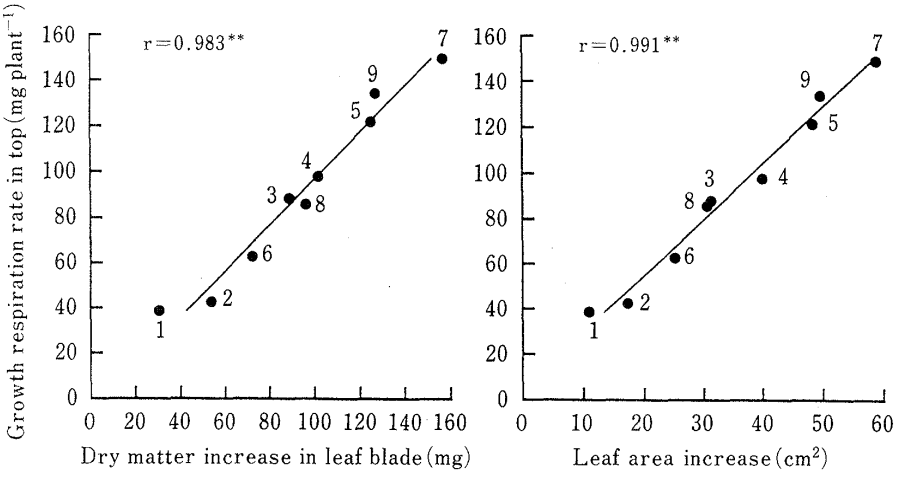

Fig. 1. Relationships between the growth respiration rate in top (Rgt) and the dry matter increase in leaf blade, and between Rgt and the leaf area increase. Numerals beside symbols show the culture conditions as shown in Table 1.

Table 2. Nitrogen content (%) of leaf blade (L.B.), leaf sheath (L.S.) and root at the start and the end of measurement.

Culture condition	A			B		
	L.B.	L.S.	Root	L.B.	L.S.	Root
1. Low conc. 1	3.4	1.4	1.5	3.6	1.5	1.7
2. Low conc. 2	3.9	1.5	1.7	4.3	2.0	1.9
3. Low-high conc.	3.4	1.4	1.9	4.2	1.9	1.8
4. Standard 1	5.0	2.7	2.1	5.0	2.5	1.9
5. Standard 2	5.4	3.3	2.5	4.7	2.4	2.5
6. Standard 3	5.2	2.8	2.2	4.7	2.1	2.1
7. High conc. 1	5.7	3.6	2.6	5.4	2.9	2.5
8. High conc. 2	5.8	3.4	2.6	5.5	2.4	2.3
9. High-low conc.	5.0	2.4	2.0	4.5	2.1	2.1

A: Mean of eight samples at the start of the measurement.

B: Mean of four samples at the end of the measurement.

($R^2=0.886^{**}$)
(Rgt ; growth respiration rate in top (mg plant^{-1}), ΔWt ; dry matter increase in top (mg), ΔNt ; nitrogen increase in top (mg)). In the root, there was a significant positive correlation between the dry matter increase in root and nitrogen increase in root ($r=0.970^{**}$. Data not shown).

The ranges of growth coefficient in the whole plant, top and root were from 0.56 to 1.26, 0.44 to 1.11, and 0.60 to 1.11 g g^{-1}, respectively, under different nutrient conditions. These were within the range of values previously reported[4,6-13,18] (Table 3).

The growth coefficient of each part increased as the nitrogen content of new biomass. The growth coefficient in root was higher than that in the top, when they were compared at the same value of the ratio of the increase of nitrogen to the increase (ΔN/ΔW) (Fig. 2). The slope of the liner regression in root was higher than that in the top. The correlation in top was stronger than that in root.

On the other hand, the range of maintenance coefficient in the whole plant was from 25.6 to 40.7 mg g^{-1} d^{-1} (Table 3). Average maintenance coefficients in top and root were 25.0 and 56.0 mg g^{-1} d^{-1}, respectively. These are similar to the reported values[4,6-13,16,18].

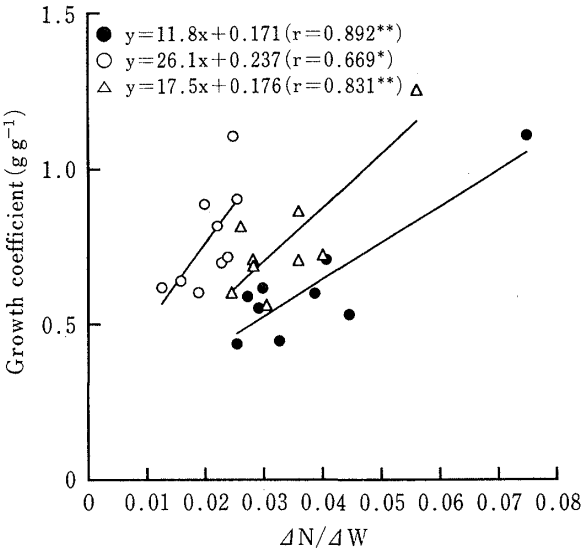

Fig. 2. Relationship between the ratio of the nitrogen increase to the dry matter increase (ΔN/ΔW) and the growth coefficient in top, root and whole plant.
● : Top, ○ : Root, △ : Whole plant.

Discussion

The production of proteins needs higher energy than the production of carbohydrates[13,14,20,21]. It is suggested that the growth coefficient is different in each plant part. Some reports[4,18] show that the growth coefficient in root is higher than that in top. The reason may be that the growth respiration in the root includes the cost of ion uptake. In our experiment, the average of the growth coefficient was higher in root, but exceptions were observed. The ΔNt/ΔWt in the top of those plants was high. The growth coefficient in root is not always higher than that in top.

The growth coefficient in root was higher than that in top, when they were compared at the same value of ΔN/ΔW. And the slope of the liner regression in root was higher than that in top. Two explanations may relate : One explanation is that the cost of components of newly formed biomass of root is higher than

Table 3. Growth coefficient (g) and maintenance coefficient (m) in top, root and whole plant grown under different nutrient concentrations.

Culture condition	g (g g^{-1})			m (mg g^{-1} d^{-1})		
	Top	Root	Whole plant	Top	Root	Whole plant
1. Low conc. 1	0.62	1.11	0.71	26.4	65.9	38.9
2. Low conc. 2	0.53	0.71	0.72	30.0	69.2	40.7
3. Low-high conc.	1.11	0.64	1.26	22.7	43.7	28.7
4. Standard 1	0.71	0.62	0.87	21.5	37.8	25.6
5. Standard 2	0.55	0.90	0.69	20.7	63.2	30.9
6. Standard 3	0.44	0.60	0.60	19.8	53.2	26.3
7. High conc. 1	0.60	0.82	0.70	27.6	53.9	33.1
8. High conc. 2	0.45	0.89	0.56	27.5	54.0	32.5
9. High-low conc.	0.59	0.70	0.81	28.8	63.4	37.3
Average	0.62	0.78	0.77	25.0	56.0	32.7

that of top. Another explanation is that the growth respiration in root includes the cost of ion uptake. However, in this experiment, ion uptake was not measured, so discussion of explanation of those results could not take place.

In intact rice plants, it is difficult to measure the respiration rate of leaf blade and leaf sheath separately because the newly formed leaf is inside the leaf sheath. In our experiment, the estimate of the respiration rate of leaf blade and leaf sheath was done by measuring together. The growth respiration rate in top increased in proportion to dry matter increase and the nitrogen increase, and it was closely connected with leaf area expansion and leaf dry matter increase. The reason may be that the growth respiration in top is utilized more for the growth of leaf blade than that of leaf sheath, because the nitrogen content of leaf blade is higher than that of leaf sheath. However, Yamaguchi et al.[21] reported that the respiration rate of leaf blade in the vegetative stage was lower than that of the other parts. In this case, the leaf sheath included the newly formed leaf inside the leaf sheath. The different conclusion may be caused by the difference in measuring method.

On the other hand, some reports show[4,16,18] that the maintenance coefficient in root was higher than that in top. Amthor[2] outlines two reasons : One possible explanation is that much biosynthesis is occurring at sites remote from active photosynthesis. Another explanation is the possibility of the greater engagement of the alternative pathway in root. Penning de Vries[15] showed maintenance respiration relates to active transport processes to maintain certain ion concentrations in the cell. So the other possible explanation is that the cost of maintenance in certain ion concentrations in root is higher than that in top, because roots are soaked in nutrient solution.

The relationship between protein content and maintenance coefficient had been reported[1,15]. However, in the present experiment, no relationship was found between nitrogen content and maintenance coefficient in top and root. The reason might relate that a regression method involving changes in light level must account for a possible loss of a steady state of substrate production and utilization[2]. In this experiment, the maintenance coefficient was assumed constant during the measurement. However, nitrogen, starch and soluble sugar content changed. Then, the maintenance coefficient might contain errors in using the regression method.

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