Translocation of Nitrogen Absorbed by the Roots of Specific Tiller in Rice Plant*

Hironori MIMOTO, Mitsunobu HATTORI** and Hiroyoshi CHUJO

(The College of Agriculture, University of Osaka

Prefecture, Sakai 591, Japan)

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Abstract : In order to determine the tiller-to-tiller translocation of nitrogen in rice plants, changes in the percentage content and percentage distribution of absorbed ^{15}N in each tiller and the main stem were investigated by the ^{15}N treatment of the roots of fourth tiller (the fourth tiller in primary tiller was expressed as T4) that emerged from the fourth node of the main stem. The quantity of translocated ^{15}N in tillers after absorption by the roots of T4 was arranged in genealogical order by the site of its distribution as follows : daughter tillers of T4 (T41, T44 ; secondary tillers) > T4 itself > mother stem (main stem) > younger sister tillers (T5, T7 ; primary tillers) that emerged from the upper nodes of the T4 emerging node > elder daughter tillers that emerged from elder sister tiller (niece tiller ; T31, T34) > elder sister tiller (T3) that emerged from the lower node of the T4 emerging node. It was made clear that the nitrogen-distribution from T4 to T3 that emerged from lower node of the T4 emerging node and to secondary tillers on T3 was extremely low. It was, therefore, presumed that a remarkably small quantity of nitrogen was translocated from tillers that emerged from the upper nodes to tillers that emerged from the lower nodes of the stem in rice plant.

Key Words : Distribution, Heavy nitrogen, Rice plant, Tiller, Translocation.

水稻の特定分げつ根より吸収された窒素の転流：三本弘乗・服部三信・中條博良（大阪府立大学農学部）

要 旨： 水稻の主茎および分げつ間における窒素の移動を明らかにするため、主茎の第4葉着生節より発生した1次分げつ（T4）の根群に ^{15}N を施用して、主茎および T4 を含む各分げつにおける ^{15}N の含有率と分配率の推移を調査した。T4 の根群が吸収した ^{15}N の分配の多い順位の傾向は次のとおりとなった。すなわち、T4 から発生した2次分げつ（T41, T44）> T4 自身 > 主茎 > T4 より上位の節から発生した1次分げつ（T5, T7）> T4 より下位の節から発生した1次分げつ上の2次分げつ（T31, T34）> T4 より下位の節から発生した1次分げつ（T3）の順位となった。T4 上の2次分げつへの分配は多いが、T4 より下位の節から発生した1次分げつ並びにその2次分げつへの分配が著しく少ないことが明らかにされたので、水稻では、上位の節の分げつから、それより下位の節の分げつへの窒素の転流は、極めて少ないと推察された。

キーワード： 重窒素、水稻、転流、分げつ、分配。

Influx and efflux of nutrients and water are known to occur repeatedly in plants. Photosynthetic products in the main stem leaves of wheats are translocated to tillers through life^{6,9}). It is considered that the nitrogen compounds in weak tillers are absorbed by strong tillers and are utilized effectively by productive tillers¹⁰). Tillers of Italian ryegrass acquire independence early, and this plant is considered to be a plant in which a nutrient is little translocated from tillers to tillers¹). It has been reported that in rice plants, phosphorus in non-productive tillers was easily translocated to productive tillers⁴). Influx and efflux of nitrogen between old leaves and new leaves on the same tiller has been perceived. New leaves

depended on old leaves for nitrogen supply and nitrogen in old leaves was utilized for the formation of new leaves^{3,8,13}). But, the tiller-to-tiller nitrogen translocation in rice plants has not been clarified. For the purpose of clarification of the tiller-to-tiller nitrogen translocation, the time course of nitrogen distribution was studied by feeding of ^{15}N as a tracer to the roots of a specific tiller.

Materials and Methods

Oryza sativa L. cv. Koganenishiki (heavy panicle type) and cv. Nakateshinsenbon (panicle number type) were used. Rice seeds were sown on a sand bed after 2 days soaking and 1 day incubation at 30°C on May 25, 1987. The seedlings were grown by water culture method in a greenhouse. On June 28, when the 1st leaf of the 4th primary tiller (T4) that emerged from the 4th node of main stem developed (plant age in leaf number was

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** Present address : Sennan-district Agriculture Extension Office of Osaka Prefecture, Kishiwada-shi, Osaka 596, Japan.

about 7.0), the seedlings were transplanted into the plastic pots (diameter ; 8 cm, height ; 8 cm) after removing the T2 and 2nd leaf of main stem. Many holes were made in the bottom of plastic pot for the purpose of easy development of roots, and a square hole (1 × 2 cm) was made in the side of 5 cm height of pot in order to separate the T4 and the roots of T4 from other tillers and roots (Fig. 1). Seedlings were fixed with gravels and cultivated by water culture method in a vinyl house. On July 25, each plastic pot with a seedling was set into a plastic container which was divided into two compartments, I and II (Fig. 1), and the roots of T4 were dipped in the solution of container I and others were in container II, respectively. Three sorts of nutrient solution ; the Kimura B nutrient solution ($(\text{NH}_4)_2\text{SO}_4$; 48.2, KH_2PO_4 ; 24.8, KNO_3 ; 18.5, $\text{Ca}(\text{NO}_3)_2$; 59.9, MgSO_4 ; 65.9, Fe-EDTA ; 22.0 (mg/l)), ^{15}N -labeled ammonium nitrogen solution ($(^{15}\text{NH}_4)_2\text{SO}_4$; 107.5, KH_2PO_4 ; 24.8, K_2SO_4 ; 15.9, $\text{CaCl}_2\cdot 2\text{H}_2\text{O}$; 53.7, MgSO_4 ; 65.9, Fe-EDTA ; 22.0 (mg/l)) and nitrogen-free solution (minus nitrogen solution of the preceding ^{15}N -labeled ammonium nitrogen solution) were used, and three degrees of concentration of culture solution (standard concentration, 2-fold dilution and 4-fold dilution) were prepared. From seeding day (on May 25) to setting day (on July 25), plants were grown in a 2-fold dilution of Kimura B. During the following 9 days, container I was filled with a 4-fold dilution of Kimura B, and container II was filled with a standard ^{15}N -labeled ammonium nitrogen solution ; then the solutions of container I and II were changed to the nitrogen-free solution and cultured for the subsequent 14 days. The solution was renewed about once a week and pH was adjusted to 5.0 every other day.

Three plants were sampled every 2 or 7 days, washed by running tap water and separated into each tiller according to the nodal position. Then the tillers were separated into the leaf blades, the leaf-sheaths+culms and the roots. Separated plant parts were dried in an oven at 70°C for 3 days, and ground to fine powder. Total nitrogen content was determined with a N.C-analyzer (SUMIGRAPH Model. NC-80), and ^{15}N content was measured by emission spectrography with a

Fig. 1. Method of ^{15}N -feeding treatment. MS and T3 to T5 indicate the main stem and primary tillers on the 3rd to 5th nodes of the main stem, respectively.

JASCO N-150 ^{15}N -analyzer. The atom% of ^{15}N -labeled ammonium sulphate was 16.93. But, all data gained by using ^{15}N tracer technique were translated into the numbers assuming that 100 atom% excess ^{15}N was administered.

Results

1. Change in total nitrogen concentration

The total nitrogen concentrations in the leaf blades, leaf sheaths+culms and roots are shown in Table 1. The total nitrogen concentrations slightly increased in the shoots of each tiller until 4 days after ^{15}N feeding. The total nitrogen concentration in T4 whose roots were treated with 4 times higher concentration of nitrogen showed the highest value, compared with all other tillers. When the culture solution was changed to a nitrogen-free solution, the total nitrogen concentrations in the shoots and roots decreased gradually. The total nitrogen concentrations in the leaf blades, leaf sheaths+culms, and roots in panicle number type cv. Nakateshinsenbon were higher than in heavy panicle type cv. Koganenishiki.

2. Ratio of absorbed ^{15}N content to total nitrogen content in each plant part

The change in the percentage of ^{15}N content to total nitrogen content in each part of the main stem and each tiller when the roots of T4 were treated with ^{15}N is shown in Fig. 2

Table 1. Changes in the total nitrogen concentration (%) in various plant parts after ⁵ N-feeding to the roots of T4.

Shoot ^c	Plant parts ^c	Koganeishiki ^a					Nakateshinsenbon				
		2 ^b	4	10	16	23	2	4	10	16	23
MS	Leaf blades	3.39	3.46	3.25	3.05	2.61	3.50	3.56	3.55	3.01	2.67
	Leaf s. + c.	1.66	1.66	1.45	1.12	0.76	1.53	1.54	1.58	1.14	0.92
	Roots	1.46	1.68	1.61	1.57	1.10	1.60	1.78	1.73	1.61	0.81
T3	Leaf blades	3.60	3.55	3.29	3.02	2.49	3.54	3.71	3.65	3.02	2.54
	Leaf s. + c.	1.92	1.62	1.47	1.06	0.72	1.54	1.73	1.60	1.27	0.78
	Roots	1.60	1.37	1.34	1.13	0.86	1.56	1.44	1.44	1.23	0.85
T4	Leaf blades	3.63	3.84	3.47	3.11	2.59	4.16	4.24	3.86	3.12	2.70
	Leaf s. + c.	1.95	2.17	1.77	1.31	0.82	2.31	2.43	1.92	1.38	0.87
	Roots	1.92	2.13	1.80	1.77	1.21	2.42	2.16	1.98	1.58	1.23
T5	Leaf blades	3.48	3.60	— ^d	2.99	—	3.67	3.77	3.51	3.07	2.65
	Leaf s. + c.	1.59	2.00	—	1.03	—	1.62	1.61	1.57	1.26	0.85
	Roots	1.60	1.49	—	0.92	—	1.42	1.38	1.41	0.99	0.83
T7	Leaf blades	3.33	3.60	3.35	3.07	2.54	3.34	—	3.68	3.02	2.67
	Leaf s. + c.	1.97	2.00	1.43	1.11	0.76	1.74	—	2.28	1.21	0.92
	Roots	1.51	1.49	1.11	0.99	0.80	1.03	—	1.67	0.97	0.81

^a Rice cultivars.^b Days after the ¹⁵N-feeding (0~9 days ; ¹⁵N-feeding treatment, 9~23 days ; N-free treatment).^c See Fig. 1 (Leaf s. + c. indicates leaf sheaths + culms).^d — means that less than three tillers in the sampling three plants were emerged out, and N concentration could not be determined.

and Table 2. The mean values of the percentage ¹⁵N contents in the leaf blades of the two cultivars at the 23rd day (on Aug. 17) after the start of ¹⁵N feeding (¹⁵N treatment for 9 days followed by treatment with nitrogen-free solution for 14 days) are shown as follows: about 14% for the main stem, about 2% for T3, about 40% for T4, about 7% for T5, about 9% for T7, about 2% for T31, about 4% for T34, about 47% for T41 and about 49% for T44 (Table 2 and Fig. 2). The percentage ¹⁵N content in T4 whose roots were fed with ¹⁵N solution, and those in T41 and T44 that emerged from T4 itself showed extremely high values respectively. The percentage ¹⁵N content was in the order of T44 > T41 > T4 > MS (main stem) > T7 > T5 > T34 > T31 = T3.

Because of the fact that T34 and T44 had not yet grown roots at 10th day (Table 2), which was, moreover, 1 days after cultivation in nitrogen-free solution, all the nitrogen con-

tents in these shoots at the 10th, 16th and 23rd day were probably translocated from their mother tillers (T3 for T34 and T4 for T44).

From the investigation of the ¹⁵N content in each part, it was found that the ¹⁵N contents in the leaf blades, leaf sheaths + culms and roots began to increase gradually immediately after the ¹⁵N feeding, but the pattern of change in the ¹⁵N distribution varied with the position of tillers and the parts of tillers, when cultivation was switched to a nitrogen-free solution (Fig. 2). Namely, the percentage ¹⁵N contents in leaf blades varied only slightly in T3 and T5 which had low contents of ¹⁵N. On the 7th day after changing the culture medium to nitrogen-free solution, the ¹⁵N contents in T7 which had a slightly higher level of nitrogen than other primary tillers except T4 and in the main stem increased slightly compared to those in other primary tillers except T4. On the 14th day, however, the ¹⁵N content in cv. Koganeishiki de-

Table 2. Changes in the percentage of ^{15}N contents to total nitrogen contents in the leaf blades and the number of roots after ^{15}N -feeding to the roots of T4.

Shoot*	^{15}N contents (%)						Number of roots					
	Kogane-nishiki*			Nakateshinsenbon			Kogane-nishiki			Nakateshinsenbon		
	10*	16	23	10	16	23	10	16	23	10	16	23
MS	6.9	15.7	12.2	6.3	9.4	16.2	49	53	67	49	42	49
T3	1.4	2.1	1.9	3.0	1.8	2.3	51	53	59	39	46	50
T31	0.8	2.1	1.4	1.5	0.8	2.4	19	24	33	15	16	35
T34	1.3	4.7	2.9	3.5	2.1	4.0	0	6	12	3	9	11
T4	30.6	35.7	38.0	33.2	37.2	42.2	18	13	29	26	16	20
T41	45.8	58.5	45.9	41.9	43.8	48.1	3	9	16	12	7	32
T44	56.2	52.9	45.5	52.9	54.0	51.6	0	2	8	0	1	7

*See Fig. 1 and Table 1 (T31 and T34 indicate secondary tillers on the 1st and 4th nodes of the 3rd primary tillers).

creased while it continued to increase in cv. Nakateshinsenbon. The ^{15}N content in T4 which had a remarkably high level of ^{15}N , increased in its leaf blades by the nitrogen-free treatment, but decreased rapidly in its leaf sheaths+culms and roots. The rate of decrease in ^{15}N was larger in roots than in the leaf sheaths+culms.

3. Percentage distribution of ^{15}N in each plant part

The percentage distribution of ^{15}N in various parts of shoots absorbed from the T4 roots are shown in Table 3. The percentage distribution of ^{15}N in T4 whose roots were treated with ^{15}N and in secondary tillers of T4 was remarkably high in both cultivars. The percentage distribution of ^{15}N in the leaf blades was highest, followed by the leaf sheaths+culms, and it was lowest in the roots. The decreasing tendency of percentage distribution of ^{15}N in the leaf sheaths of T4 after the nitrogen-free treatment became more pronounced than that in the roots. The percentage distribution of ^{15}N in T3 and T5 was low and the range of their variations was narrow. In cv. Nakateshinsenbon, the percentage distribution of ^{15}N in the main stem and T7 that had slightly high levels of ^{15}N showed an increasing tendency after nitrogen-free treatment; whereas in cv. Koganenishiki showed a decreasing tendency.

Discussion

The nitrogen content in a shoot is remarkably affected by the nitrogen condition of root sphere⁷⁾. In ordinary rice plant cultivation, the

total nitrogen content in a shoot decreases with growth after establishment, and temporarily increases by topdressing⁵⁾. In this experiment, the total nitrogen contents increased in all the tillers until 4 days after the beginning of ^{15}N treatment. It was presumed that the high concentration of total nitrogen in T4 was owing to exposure of its roots to nutrient solution which contained four times as much concentration of nitrogen as the cultivation solution used for other tillers, and the increase in total nitrogen concentration in the tillers, except T4, cultured in a 4-fold dilution was owing to the renewal of solution. The percentage contents of total nitrogen in the leaf blades, leaf sheaths+culms and roots in panicle number type cv. Nakateshinsenbon which easily produced tillers were constantly higher than those in heavy panicle type cv. Koganenishiki. As a high nitrogen content in shoots generally contributes to the growth of tillers, it is presumed that tillers and panicles develop easily in cv. Nakateshinsenbon.

The change in the percentage of ^{15}N contents to total nitrogen contents in various parts of tillers and the main stem differed remarkably with the nodal position of tillers and plant parts when the roots of specific tiller (T4) were fed with ^{15}N . The percentage of ^{15}N contents to total nitrogen contents in the leaf blades of the main stem and tillers at the 23rd day after the start of ^{15}N feeding (^{15}N feeding for the first 9 days followed by cultivation in nitrogen-free solution for 14 days) was in the order of daughter tillers (T44, T41) of T4, T4

Table 3. Changes in the percentage distribution of ^{15}N in various plant parts after ^{15}N -feeding to the roots of T4.

Shoot ^a	Plant parts ^a	Koganenishiki ^a					Nakateshinsenbon				
		2 ^a	4	10	16	23	2	4	10	16	23
MS	Leaf blades	4.4	3.6	4.8	6.6	5.7	3.3	3.1	2.5	4.1	5.0
	Leaf s. + c.	4.4	3.6	3.7	2.8	2.1	3.9	2.9	1.7	2.0	2.3
	Roots	0.9	1.2	1.2	1.8	1.1	0.9	1.3	0.3	1.2	1.2
	Total	9.7	8.4	9.7	11.2	8.9	8.1	7.3	4.5	7.3	8.5
T3	Leaf blades	1.3	1.1	0.8	0.8	0.9	0.5	1.0	1.3	0.8	0.7
	Leaf s. + c.	0.8	1.0	0.3	0.3	0.4	0.6	0.7	0.6	0.3	0.3
	Roots	0.4	0.2	0.2	0.3	0.2	0.2	0.2	0.2	0.1	0.1
	Total	2.5	2.3	1.3	1.4	1.5	1.3	1.9	2.1	1.2	1.1
T4	Leaf blades	16.5	19.2	22.4	17.0	18.8	20.3	17.7	17.1	19.7	14.6
	Leaf s. + c.	21.4	20.6	12.1	7.4	6.7	19.8	19.7	10.3	8.5	5.0
	Roots	7.0	8.8	5.3	4.3	3.2	7.0	5.2	4.2	2.6	2.3
	Total	44.9	48.6	39.8	28.7	28.7	47.1	42.6	31.6	30.8	21.9
T5	Leaf blades	1.0	0.7	— ^a	1.6	—	1.6	2.1	2.2	2.1	1.9
	Leaf s. + c.	0.9	0.7	—	0.6	—	2.4	1.4	0.9	1.1	0.8
	Roots	0.2	0.1	—	0.1	—	0.4	0.3	0.2	0.1	0.2
	Total	2.1	1.5	—	2.3	—	4.4	3.8	3.3	3.3	2.9
T7	Leaf blades	0.9	2.0	1.1	2.6	1.8	0.6	—	0.2	1.5	2.5
	Leaf s. + c.	0.8	1.4	0.6	1.2	0.9	0.5	—	0.1	0.5	1.0
	Roots	0.0	0.2	0.6	0.1	0.1	0.1	—	0.0	0.1	0.2
	Total	1.7	3.6	2.3	3.9	2.8	1.2	—	0.3	2.1	3.7
T31 ^b ~ T52	Leaf blades	0.4	0.0	0.9	2.1	2.8	0.9	0.6	2.3	1.8	2.3
	Leaf s. + c.	0.3	0.6	0.3	0.7	1.1	1.2	0.6	1.1	0.9	1.0
	Roots	0.1	0.3	0.1	0.2	0.4	0.0	0.1	0.2	0.2	0.4
	Total	0.8	0.9	1.2	3.0	4.3	2.1	1.3	3.6	2.9	3.7
T41 ^c ~ T43	Leaf blades	15.6	13.7	22.4	32.6	35.1	15.7	17.8	27.9	31.7	41.7
	Leaf s. + c.	18.7	15.0	17.7	13.2	13.2	16.8	19.8	19.8	16.4	12.1
	Roots	4.0	5.8	6.0	3.6	5.4	3.5	5.7	7.0	4.1	4.6
	Total	38.3	34.5	46.1	49.4	53.7	36.0	43.3	54.7	52.2	58.4

^a See Fig. 1 and Table 1.^b T31~T52 ; Secondary tillers of T3 and T5 (T31, T32, T33, T34, T51, T52).^c T41~T44 ; Secondary tillers of T4 (T41, T42, T43, T44).

itself (the roots of T4 were treated with ^{15}N solution), the main stem, younger sister tillers (T7, T5) that emerged from the upper node of T4, daughter tillers (T31, T34) of T3 and elder sister tiller (T3) that emerged from the lower node of T4 (Table 2 and Fig. 2). The percentage distribution of ^{15}N in each tiller at

the 23 days after the start of ^{15}N feeding showed almost the same order as the percentage of ^{15}N content to total nitrogen contents (Table 3).

The results regarding the percentage of ^{15}N contents to total nitrogen contents and percentage distributions of ^{15}N in the plant parts

Fig. 2. Changes in the percentage of ^{15}N contents to total nitrogen contents in each plant part after ^{15}N -feeding to the roots of T4.

● ; leaf blade, ○ ; leaf sheath+culm, ▲ ; root.

*Kogane ; Koganenishiki, Nakate ; Nakateshinsenbon.

suggested that nitrogen was distributed from the specific tiller (T4) whose roots were treated with ^{15}N to the daughter tillers of T4 itself > mother stem > > sister tillers > niece tillers in the order of priority named. Among the sister tillers of the same primary tillers, the youngest sister which emerged latest was given the top priority over other tillers, and the eldest sister which emerged earliest was given the least distribution of ^{15}N . In the secondary tillers, the grandchild tillers were given a priority, while the daughters of the sisters were given an extremely small share of ^{15}N .

Wang et al.¹¹⁾ reported that younger tillers were more affected by the defoliation of main stem and tillers that emerged from the upper node were more affected by tillers that emerged from the lower node, and that the order of nutrient distribution was related to the nodal position and the emerging order of tillers. Furthermore, in a study of $^{14}\text{CO}_2$ -treatment of

primary tillers, Wang et al.¹²⁾ reported that assimilated and translocated ^{14}C from the exposed primary tiller was distributed mostly to secondary tillers (daughter tillers of the ^{14}C -exposed tiller), followed by main stem (mother stem), other primary tillers, and other secondary tillers in the order named. The decrease in the percentage distribution of ^{15}N to the main stem and tillers showed precisely the same pattern of order as the decrease in the distribution of $^{14}\text{CO}_2$ described by Wang et al.¹²⁾.

The patterns of the percentage distribution of ^{15}N by the parts (leaf blades, leaf sheaths+culms, roots) of the plant seemed to be identical to those of the percentage content. The percentage distributions of ^{15}N in the leaf sheaths+culms and roots of T4 which contained the highest concentration of ^{15}N , decreased by the nitrogen-free culture, and efflux of ^{15}N was perceived. However, in the

leaves, the percentage distribution of ^{15}N increased continuously by preferential distribution. The increase in ^{15}N in the leaves after the nitrogen-free culture seemed to be due to the translocation of ^{15}N from the leaf sheaths and roots in which the nitrogen concentrations were decreased. Because the percentage distribution of ^{15}N in the leaf sheaths+culms was about two times of that in the roots, and the percentage distribution of ^{15}N in these parts (estimated from Table 3) decreased at a higher rate than in the roots, the leaf sheaths+culms seemed to be quantitatively more contributory than the roots. However, as the rate of decrease (the slopes of percentage of ^{15}N contents in Fig. 2) was larger in the roots, the roots may be more contributory than the leaf sheaths+culms, if measured by time.

Yoneyama¹³⁾ reported that the increase in ^{15}N contents in newly developing leaves even during nitrogen-free culture occurred by influx of ^{15}N from old leaves. If the leaf sheaths+culms are regarded as old leaves in this experiment, the results obtained here are completely consistent with the results of Yoneyama¹³⁾.

After discontinuation of the nitrogen-treatment, the percentage of ^{15}N contents in all the parts of T7 which contained slightly higher quantity of ^{15}N and the main stem increased in cv. Nakateshinsenbon but decreased in cv. Koganenishiki (Fig. 2). This finding may suggest that the nitrogen content in the shoot of cv. Koganenishiki is more liable to change than in cv. Nakateshinsenbon.

The distribution in T3 and its secondary tillers was far less compared to that in T5 or T7, and the distribution to the lower nodal tillers which emerged earlier than T4 was very scarce. These results seem to indicate that nitrogen is rarely translocated from upper nodal non-productive tillers to lower nodal productive tillers. However, Nakamura⁴⁾ reported that absorbed ^{32}P was transferred from non-productive tillers to productive tillers, but not from the later to the former.

In general, tillers of a plant depend nutritionally on the main stem until independence is acquired by rooting^{1,2)}. The degree and pattern of dependence on other tiller differ with plants. Some plants are liable to depend

on mother stem even after independence or are little dependent, and some others acquire early independence from mother stem^{1,6,9)}. Wheats are late in acquiring independence and rely on other tillers^{6,9)}. Italian ryegrass is early in acquiring independence¹⁾. From the results of this experiment, it was assumed that the rice plant is a plant less dependent on other tillers after independence.

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