Partitioning and Utilization of Nitrogen in Rice Plants

By TADAHIKO MAE

Faculty of Agriculture, Tohoku University
(Sendai, 980 Japan)

Among various nutrients, nitrogen has the strongest influence on the growth and yield of rice. Therefore, it is important to understand accurately the dynamic aspects of nitrogen in rice plants. In this paper ^{15}N-studies on partitioning and utilization of nitrogen in rice plants are reviewed.

Partitioning of nitrogen in rice plants

1) Partitioning of absorbed nitrogen in rice plants soon after the absorption

Distribution of nitrogen in a rice plant in a relatively short period after the absorption of the nitrogen has been examined at various growth stages.[1,7,11,12,13,20,25,27,28] The results indicate that the nitrogen is always distributed mostly to new growing organs regardless of growth stages of the plant, while a much smaller amount of nitrogen is also distributed to older parts of the plant.

In plants before the heading stage growing leaves and/or new leaves just developed received the absorbed nitrogen to the greatest extent, while senescent leaves also received the nitrogen but to a limited extent.[7,13,25,27,28] The amount of the absorbed nitrogen partitioned to each leaf already developed was in order of leaf age; the younger the leaf, the larger was the amount. The proportion of the nitrogen partitioned to the roots is larger at younger growth stages. It was 30% of the total amount of absorbed nitrogen in young seedlings[25] and 5–20% in plants at the young panicle formation stage and booting stage.[13]

During the grain-filling period, partitioning of the absorbed nitrogen to ears increased with the development of the ears.[14]

A distribution pattern of the absorbed nitrogen in a plant somewhat differs with the form of nitrogen supplied to the plant: NH_4^+ or NO_3^-.[13,27] Relatively more nitrogen was distributed to developing leaves in the case of ammonium than in that of nitrate, while nitrate-nitrogen was distributed more to actively-functional leaves (the leaves just or a little after the completion of leaf expansion).

2) Partitioning of remobilized nitrogen in rice plants

A large part of nitrogen which had been once a constituent of some organs of rice plants is remobilized and translocated to new growing organs of the plants,[1,7,11–13,16–20,27,28] during their life span.

Remobilized nitrogen, therefore, is translocated very little to old organs.[29] A part of nitrogen in old organs is not remobilized during senescence and remains there until death of the organs. This type of nitrogen is not available for growth of new organs.

Redistribution of ^{15}N, absorbed at the young panicle formation stage, was investigated during the reproductive growth period.[7] After feeding ^{15}N to plants for 5 days at the young panicle formation stage, the plants were cultured until harvest with ^{14}N nutrient. As shown in Fig. 1, just after the labelling, 74% of ^{15}N was contained in leaf blades and 24% in leaf sheaths. At the time of harvest, the amount of ^{15}N decreased to 20% in the leaf blades and to 8% in the leaf sheaths, while ears contained 67% of the total ^{15}N (Fig. 1).

At the time of ^{15}N-feeding, the 12th leaf blades were just growing. Additional 3 leaves developed after the 12th leaf, and then ears grew up. The ^{15}N was preferentially incorporated into consecutive growing leaves and finally into the ear (Fig. 2).

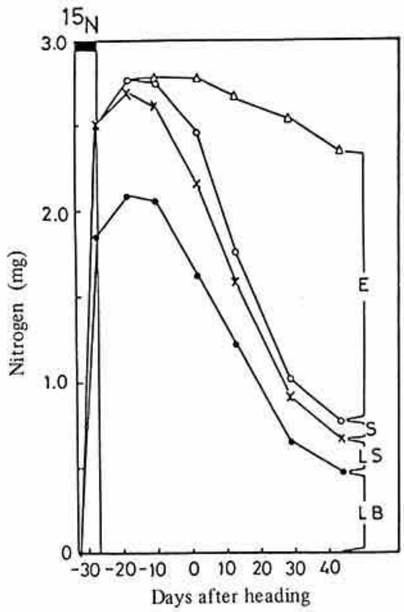

Fig. 1. Redistribution of nitrogen: ^{15}N in each plant part of a rice plant during its reproductive growth
The ^{15}N was derived from ^{15}N absorbed by the plant at the young panicle formation stage. The bar in the top left-hand corner indicates the period of ^{15}N uptake. LB, leaf blades; LS, leaf sheaths; S, stem; E, ear.[7]

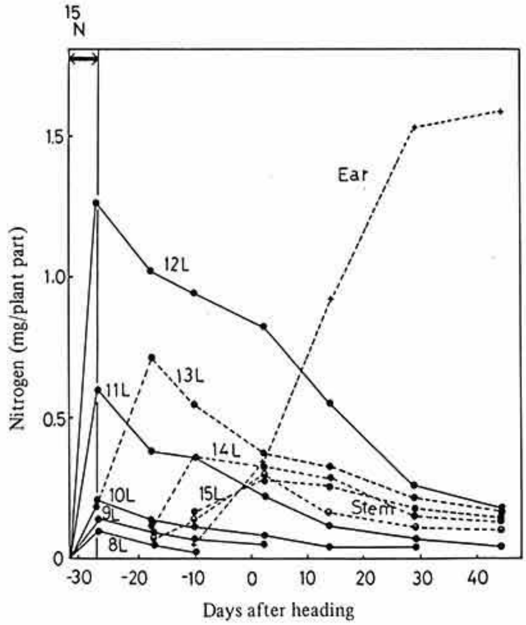

Fig. 2. Redistribution of nitrogen: ^{15}N in each leaf blade, stem, and ear of a rice plant during its reproductive growth
The ^{15}N was derived from ^{15}N absorbed by the plant at the young panicle formation stage. The bar in the top left-hand corner indicates the period of ^{15}N uptake. L, leaf (leaf blade + leaf sheath). (Figured from the data in Ref. 7).

3) Contribution of remobilized nitrogen to the growth of new organs

Nitrogen in a newly growing organ can be divided into 2 groups on the basis of its orgin, i.e., nitrogen newly assimilated and incorporated into that organ during its growing period (absorbed-N), and nitrogen, pre-existed in the plant before that organ starts to grow, and is mobilized and translocated into that new organ during its growing period (remobilized-N). These 2 types of nitrogen could be separated experimentally by the use of ^{15}N as a tracer for the absorbed-N. The evaluation of remobilized-N for growth of a new organ had not been examined quantitatively in rice, before the following studies were made.

The proportion of absorbed-N and remobilized-N in the youngest leaf and the next youngest leaf was examined with rice seedlings[28] and with rice plants at the young panicle formation stage.[7] In these experiments the remobilized-N accounted for 30-64% of the total leaf-N. Similar results were also obtained with growing roots.[23] Then effects of the nitrogen nutrition during leaf development on the proportion of absorbed-N and remobilized-N in the growing 12th leaves were studied[9] and the result is shown in Fig. 3. The remobilized-N accounted for about 50% under the standard culture condition (1 mM ammonium sulfate in the nutrient solution). It accounted for 30% even when the plant was supplied with an excess amount of nitrogen (3-5 mM ammonium sulfate). All these results suggest clearly that remobilized-N plays an important role for growth of new growing organs in rice plants.

Origin of ear nitrogen was studied. Ear nitrogen was composed of nitrogen absorbed by the plant at all growth stages ranged from the young seedling stage to the ripening stage.[16,17] Fig. 4 shows the proportion of each componental nitrogen which was derived from nitrogen absorbed by

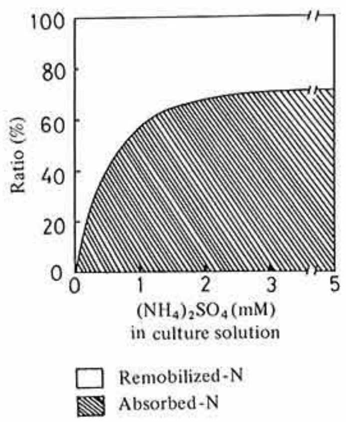

Fig. 3. Effect of nitrogen levels of a nutrient solution on the proportion of absorbed-N and remobilized-N in the growing 12th leaf blades of rice

When the tip of the 12th leaves had emerged from the 11th leaf sheaths, the plants were transferred to the nutrient solutions containing different amounts of nitrogen (^{15}N-labelled), and cultured for 6 days. Then the plants were harvested and total-N and ^{15}N contents of the 12th leaf blades were analyzed. Proportion of absorbed-N and remobilized-N to the increased nitrogen in the leaf during the 6 days was calculated, assuming that the efflux of nitrogen during this period was negligible.[7]

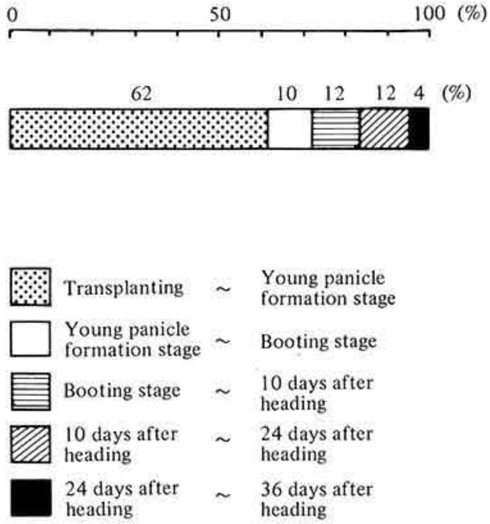

Fig. 4. Origin of ear nitrogen

The plants were grown under the same culture condition until harvest, except that each plant was supplied with ^{15}N-nitrogen during the specific periods indicated in the figure, respectively. After harvest ^{15}N content of each ear was analyzed, and the proportion of nitrogen in the ear absorbed during different periods was calculated. (Mae & Ohira unpublished data).

the plant during different growth periods and which constituted the ear nitrogen at the time of harvest (Mae & Ohira unpublished data). The amount of nitrogen derived from that absorbed during the grain filling period was only 30% of the total ear-N. Thus the remobilized-N from the vegetative organs accounted for 70%. Leaf blades were the major source of remobilized nitrogen, followed by leaf sheaths and stems. Roots were of little importance in this process.[7]

Although rice plants are usually exposed to considerable changes in the amount of nitrogen available for their growth during their growth period, they can, in general, complete well-balanced growth. One of the reasons for such a characteristic could be explained by the fact that growth of new organs depends strongly on remobilized-N. If growth of new organs is dependent entirely or mostly on absorbed-N, it would not be possible for the plant to keep its well-balanced growth against large changes in the amount of absorbed-N, especially caused by the application of nitrogen fertilizer. This fact is important to understand the relation between plant growth and nitrogen nutrition.

Nitrogen flows in rice plants

1) Nitrogen flows in a whole plant

Most of the nitrogen absorbed by roots is translocated to top parts with a transpiration stream via xylem. Utilization of nitrogen in each plant part is different depending on its organ specificity, such as leaf, stem, ear, and root, age of the organ, the growth stage of the plant and the nutritional condition of the plant. In each organ a part of the nitrogen would be incorporated into cellular constituents or a storage pool, and remain there.

The rest of them would be transported immediately from the organ to growing organs of the plant via phloem. The nitrogen which has been once incorporated into the cellular constituents is remobilized as the results of their own turnover or by the degradation during senescence, and transported to new organs via phloem. Recently it was shown that nitrogen of growing roots of rice is originated partially from the top part of the plant,[15,22-24] suggesting that some nitrogen is circulated in a plant during its life. Recently, chemical composition of rice phloem sap exuded from the cut end of insect stylets was analyzed in detail.[2-5]

Distribution and redistribution of the nitrogen absorbed at the young panicle formation stage were followed in a rice plant during panicle development. It was suggested that some of the nitrogen is directly transported to panicles from roots.[1,16,17]

2) *Nitrogen flows in mature leaves*

The nitrogen content of a leaf is balanced by the amounts of influx and efflux of nitrogen in the leaf. Yoneyama and Sano (1978)[28] examined the influx and efflux of nitrogen in the leaves of young rice seedlings for 10 days, and proposed a model for the influx and efflux of nitrogen during the life span of a rice leaf. Later, nitrogen flows in mature leaves were analyzed by multi-compartment analyses of data from the above ^{15}N tracer experiment.[29] According to their analyses, the 4-compartment model, which consisted of the compartment of the pool for N influx from xylem, that for efflux from the leaf, that for the temporary storage pool, and that for the insoluble-N (protein), fits the measured data better than the 2- or 3-compartment models (Fig. 5). Results of computation indicated the following: The flow of nitrogen through the protein pool was larger than the direct flow in newly matured leaves, whereas the reverse was true in senescent leaves. The presence of a temporary storage pool of soluble-N was suggested. Half-lives of insoluble N pools were 90–150 hr. The pool for N efflux from the leaves was small with the shortest half-lives (less than 2.1 hr) of N turnover. The extent of N recycling during protein turnover was estimated to be little.

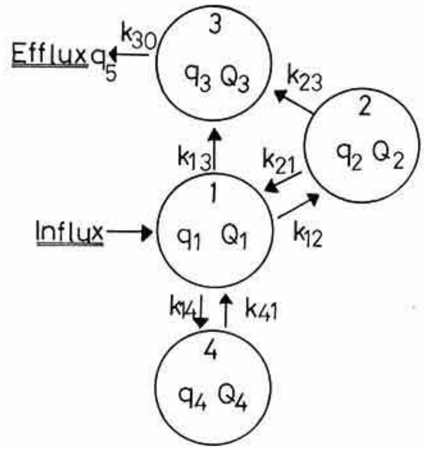

Fig. 5. Compartment model of N flows in mature rice leaves
Xylem N comes into compartment 1 and N is transferred from this compartment to compartments 2, 3, and 4. Compartment 3 is the soluble-N pool for the N efflux from the leaf. Compartment 4 is the temporary storage pool for soluble-N. Compartment 2 is the insoluble-N (protein) pool. K_{ij} is the transfer rate constant for the N flow from compartment i to j. K_{30} is transfer rate constant from compartment 3 to the outside of the leaf. q_m is the amount of labelled N in each compartment, q_5 is the label lost from the leaf. Q_m is the amount of N in each compartment. Rate constants of nitrogen flows, transfers with protein turnover and flow through a storage pool of soluble-N were derived from a least-squares fit between the mathematical expressions and the corresponding data (See Ref. 29 for details).

Mae et al. (1983, 1984)[6,10] studied in detail the influx and efflux of nitrogen in the 12th leaf blades of rice throughout the leaf's whole life. Effects of nitrogen nutrition on the influx and efflux were also investigated. As shown in Fig. 6, the influx was maximal in the very early stage of the leaf's life, and then decreased although it was observed until the late stage. About 90% of the total influx was finished until about the time when the nitrogen content of the leaf reached the maximum amount (1–2 weeks after the completion of leaf expansion) regardless of the levels of the nitrogen nutrition during and after the grow-

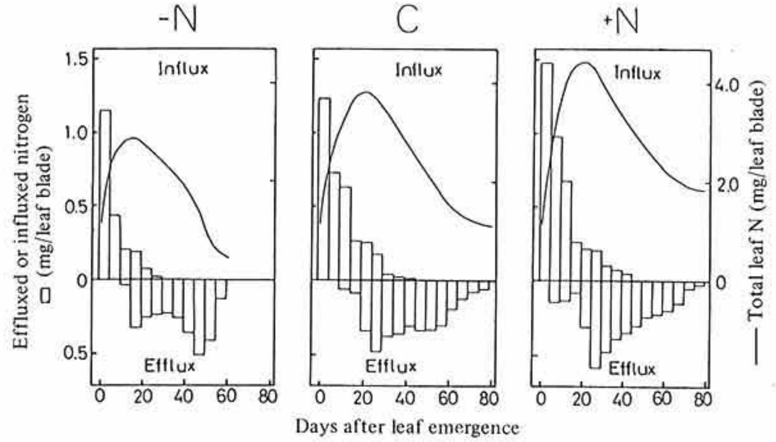

Fig. 6. Changes in the influx and efflux of N in the 12th leaf blades of rice from leaf emergence through senescence
Plants were grown with different amounts of N (N-deficient [−N], control [C], and N-sufficient [+N]). The solid curved lines represent the regression curves for changes in the total leaf-N.[10]

ing period of the leaf, indicating that the nitrogen content of mature leaf is determined mostly by the amount of nitrogen which flowed in the leaves until a little after the completion of leaf expansion.

Protein metabolism in rice leaves

Incorporation of ^{15}N nitrogen into the subcellular and protein fractions was examined in rice leaves at various leaf ages.[21] ^{15}N nitrogen was incorporated into all the fractions examined but the extent of the incorporation differed among them by leaf age. The nitrogen was incorporated into Fraction 1 protein (ribulose bisphosphate carboxylase) more extensively in growing leaves than senescing ones.[8,21] In senescing leaves the nitrogen was incorporated more into the other soluble proteins except Fraction 1 protein. Synthesis and degradation of ribulose bisphosphate carboxylase, which is a key enzyme for photosynthesis and photorespiration, were studied precisely in the 12th leaf of rice throughout its whole life.[6,10] Synthesis of the enzyme was almost proportional to the amount of the nitrogen which flowed in the leaf; about 90% of the enzyme was synthesized until a little after the completion of leaf expansion. The patterns of its synthesis did not differ largely among the leaves of the plants grown under different nitrogen nutritions.

The origin of amino-acid nitrogen in developing leaves was investigated.[26] Amounts of glutamic acid, aspartic acid, and alanine were relatively dependent upon the newly-absorbed nitrogen and, on the contrary, arginine, lysine, proline, and valine were dependent on the retranslocated nitrogen.

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