Translocation of Foliar-Applied Nitrogen to Rice Roots

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In the course of study on the growth of rice roots we demonstrated that the growing young roots received a considerable amount of nitrogen from the shoot in their early developmental stage, while the root system was fed with inorganic nitrogen through culture solution\(^{15}\). The nitrogen transport to roots from the shoot has been reported by some workers\(^{6,13}\), however, little attention has been given on its significance in relation to the root growth.

Recently much attention has been given on the nitrogen circulation in plants and the role of cycled nitrogen for the plant growth. Kato and Kitada\(^{23}\), and Yoneyama and Sano\(^{20}\) reported that in mature leaves the proteins involved were turned over and that the nitrogen once translocated into mature leaves was retranslocated to young growing leaves. They suggested that the retranslocated nitrogen containing the product of protein degradation might play an important role to build up new tissues of growing leaves. A study on the field pea\(^{7}\) indicated that a considerable proportion of the nitrogen translocated from roots to mature leaves via xylem was subsequently retranslocated downwards to growing lateral roots via phloem. This suggests that the pathway for nitrogenous compounds cycling through mature leaves plays an important role to supply the growing roots with nitrogen.

Rice plants develop the fibrous root system which consists of many adventitious roots emerging from culm nodes. This rooting habit is a characteristic of the Gramineae, suggesting that the shoot-root relationships of rice plant are different from legumes which develop the tap root system.

In this report, the transport of nitrogen to roots from specific leaves of rice plants was investigated using \(^{15}\)N as a tracer, and the role of the leaves for the root growth was discussed in relation to the nitrogen circulation in the plant.

Materials and Methods

Rice seeds (cv. Aichiasahi) were germinated on a salan net floating in tap water in a growth cabinet (temperature: 30°C, light: 10 klx). At the stage of the 5th leaf emergence (May 23, 1978), seedlings were transplanted spacing 4×4 cm into the water culture bed (450 l) filled with a 5-fold dilution of Kasugai rice culture solution; 8 ppm N as (NH\(_4\))\(_2\)SO\(_4\); 4 ppm P\(_2\)O\(_5\) as Na\(_2\)HPO\(_4\); 6 ppm K\(_2\)O as KCl; 0.8 ppm CaO as CaCl\(_2\); 1.2 ppm MgO as MgCl\(_2\); 1.0 ppm Fe\(_2\)O\(_3\) as FeCl\(_3\) (pH 5.5). The plants were grown in a greenhouse under normal light and temperature conditions. The culture solution was renewed every week. On the 22th day after transplanting, when the 9th leaf and the roots from the 6th node began to emerge, 12 plants were selected and prepared for the experiment, and 3 plants were sampled for nitrogen analysis (Day 0).

Foliar feeding of \(^{15}\)N-labeled urea A half of the selected plants was transferred to the pots (10 l) filled with a 5-fold dilution of Kasugai culture solution containing 8 ppm N (plus N medium) and the remainder to the pots filled with the same solution but lacking nitrogen (minus N medium). Under both plus N and minus N medium, the 5th or 8th leaf of the main stem of plants were
fed with $^{15}$N-labeled urea. Their leaf blades were immersed in a solution of 0.2% $^{15}$N-labeled urea ($^{15}$N; 49.63 atom % excess) for 16 hr (from 5:00 p.m. to 9:00 a.m. of the next day) over 7 days. Excess urea was removed from leaf surface by filter papers at the end of each day’s feeding and special care was taken to avoid contamination of other plant parts with the labeled solution. At the end of $^{15}$N-feeding (Day 7), when the 10th leaf and the roots from the 7th node began to emerge, plants were sampled. During this period the culture solution was not renewed and each day’s loss of the solution was supplied with tap water.

**Analysis of total-N and $^{15}$N content** Harvested plants were washed by distilled water, cut off and separated into main stems and tillers. The main stem was further separated into roots, the culm, and the leaves. The leaves (leaf blade and leaf sheath) were divided into each leaf position; the 3rd and 4th leaves (leaf 3–4), the 5th leaf (leaf 5), the 6th leaf (leaf 6), the 7th leaf (leaf 7), the 8th leaf (leaf 8), the 9th leaf (leaf 9), and the 10th leaf (leaf 10) (if present). The roots were divided into the roots emerging from nodes lower than the 6th node (the lower roots) and the roots emerging from the 6th and 7th nodes (the upper roots).

Separated plant parts were dried in an oven at 90°C (Day 0 samples) or homogenized in 10 ml of cold M/15 phosphate buffer (pH 7.1). The homogenates were made up to 10% trichloroacetic acid (TCA) concentration with addition of 20% TCA and fractionated into TCA-soluble and -insoluble fractions. Total nitrogen contents of dried and fractionated samples were determined by Kjeldahl method, and their $^{15}$N contents were measured by the emission spectrographic method using a JASCO NIA-1 $^{15}$N-analyzer as described elsewhere.

**Results**

**Plant growth** During the foliar-feeding

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<td>0.83</td>
<td>0.95</td>
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<td>0.20</td>
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<td>0.04</td>
<td>0.36</td>
<td>0.83</td>
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<td>0.97</td>
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<td>Culm</td>
<td>0.61</td>
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<td>0.43</td>
<td>0.15</td>
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<td>0.68</td>
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<td>2.17</td>
<td>0.40</td>
<td>2.57</td>
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<td>3.90</td>
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<td>4.41</td>
<td>9.51</td>
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<td>11.57</td>
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<td>Total</td>
<td>19.70</td>
<td>16.43</td>
<td>2.64</td>
<td>19.07</td>
<td>18.47</td>
<td>2.62</td>
<td>21.09</td>
<td>34.32</td>
<td>5.57</td>
<td>39.89</td>
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</table>

* Every day for a week the specific leaf blades were dipped in a solution of $^{15}$N-labeled urea.
** Plants were pre-cultured with the solution containing 8 ppm N, subsequently transferred into the same solution (plus N medium) or the solution lacking nitrogen (minus N medium) at the start of the foliar application.
Table 2. \(^{15}\text{N}\) abundance (atom \(\%\) excess) in TCA-insoluble and TCA-soluble nitrogen fractions in various parts of the plant after feeding of \(^{15}\text{N}\)-labeled urea to specific leaves for 7 days.

<table>
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<tr>
<th>Plant parts</th>
<th>Minus N medium(^*) (^{15}\text{N}) was fed to</th>
<th>Plus N medium(^*) (^{15}\text{N}) was fed to</th>
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<tbody>
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<td>Leaves</td>
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<tr>
<td>10</td>
<td>0.35</td>
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<td>9</td>
<td>0.10</td>
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<tr>
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<td>7</td>
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<td>6</td>
<td>t</td>
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<td>5</td>
<td>1.27</td>
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<tr>
<td>3-4</td>
<td>t</td>
<td>t</td>
</tr>
<tr>
<td>Culm</td>
<td>0.27</td>
<td>0.26</td>
</tr>
<tr>
<td>Upper roots</td>
<td>0.44</td>
<td>0.31</td>
</tr>
<tr>
<td>Lower roots</td>
<td>0.21</td>
<td>0.31</td>
</tr>
<tr>
<td>Tillers</td>
<td>0.27</td>
<td>0.26</td>
</tr>
</tbody>
</table>

\(^*\) See Table 1. t; trace.

period (from Day 0 to Day 7) leaf 10 newly emerged. Leaf 9 which emerged at Day 0 developed through this period and fully expanded. Leaves lower than leaf 9 did not show any expansion because they had developed before Day 0. The blades of leaf 4 and leaf 3 turned yellow and died, especially in the plant of minus N medium the blade of leaf 5 also became yellowish. The upper roots which had emerged about Day 0 increased their number and length, in contrast the lower roots did not increase their number.

Nitrogen contents Table 1 shows the nitrogen content in various parts of the plant at Day 0 and Day 7. During the period of foliar feeding, leaf 9, tillers, and upper roots increased their total nitrogen contents following their growth, especially in the plants of plus N medium. In the newly emerging leaf 10 nitrogen content also increased. On the contrary, nitrogen content decreased in the leaves lower than leaf 8, particularly in the plants of minus N medium. Total nitrogen content of leaf 8 decreased in minus N plants, in contrast to a slight increase in plus N plants. The lower roots gained their total nitrogen contents in plus N plants, however, in minus N plants their contents did not show any significant increment.

Distribution of \(^{15}\text{N}\) Table 2 shows the \(^{15}\text{N}\) abundance in plant parts after plants were fed with \(^{15}\text{N}\)-labeled urea for specific leaves over 7 days (Day 7). From the data shown in Tables 1 and 2, the amount of \(^{15}\text{N}\) in the plant parts was calculated. Fig. 1 shows the distribution of \(^{15}\text{N}\) in the plants of minus N medium.

By the end of the foliar feeding 88.0 \(\mu\)g and 272.4 \(\mu\)g of \(^{15}\text{N}\) was taken up by leaf 5 and leaf 8 respectively, and about 88\% and 71\% of the absorbed \(^{15}\text{N}\) had been exported from leaf 5 and leaf 8 respectively. The remainder was partly incorporated into TCA-insoluble fraction of the fed leaf. In both feeding plants, the growing parts (leaf 10, leaf 9, tillers, upper roots) received large proportions of this exported nitrogen. On the contrary, the leaves below the fed leaf were only sparsely labeled or not labeled at all. The percentage of the \(^{15}\text{N}\) exported from leaf 5 into the roots was 47.3\%, and this value was 1.7 times as large as that from leaf 8 (27.1\%). In contrast, the share of \(^{15}\text{N}\) in the developing leaf 10 was
Fig. 1. Distribution of excess $^{15}$N ($\mu g$) in the rice plant after feeding of $^{15}$N-labeled urea to the 5th leaf (A) or to the 8th leaf (B) for 7 days (minus N medium). ■: TCA-insoluble N, □: TCA-soluble N. Numerals in figures show % distribution of $^{15}$N exported by the fed leaf.

larger in leaf 8-feeding plants than in leaf 5-feeding plants. In both feeding plants the share of $^{15}$N in the upper roots was 1.5–2.6 times as large as that in the lower roots. This is due to not only the substantial mass of the upper roots (Table 1) but also due to the higher rate of $^{15}$N incorporation into the TCA-insoluble fraction of the upper roots (Table 2).

Fig. 2 shows the distribution of $^{15}$N in leaf 8-feeding plants when their roots were fed with the solution containing unlabeled ammonium sulfate during the foliar-feeding period (plus N medium).

By Day 7, 223.5 $\mu g$ of $^{15}$N was absorbed by leaf 8, and 52% of this $^{15}$N had been exported from the leaf. Although the percentage of exported nitrogen from the fed leaf was decreased as compared with that in the plants of minus N medium (Fig. 1), a considerable amount of $^{15}$N was predominantly translocated to the growing plant parts such as leaf 10, leaf 9, roots, and tillers. Particularly the roots received about 25% of the exported $^{15}$N in spite of the effective uptake of inorganic nitrogen from the medium by themselves. The plant absorbed 7 mg of unlabeled nitrogen via root system during the $^{15}$N-feeding period.

**Discussion**

It has been reported that leaves absorb gaseous $^{15}$NH$_3$ and $^{15}$NO$_3^-$ or solution of ($^{15}$NH$_4$)$_2$SO$_4$ and K$^{15}$NO$_3$, and that they assimilate $^{15}$N into amino acids. The
Table 3. Increase or decrease of amount of total nitrogen in various parts of the plants in minus N medium (ΔN−) and in plus N medium (ΔN+), and the increase of amount of retranslocated nitrogen (ΔNR) and that of newly absorbed nitrogen (ΔNA) in the growing organs during the period from Day 0 to Day 7 (mg/3 plants).

<table>
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<th>Plant parts</th>
<th>ΔN−</th>
<th>ΔN+</th>
<th>ΔNR*</th>
<th>ΔNA*</th>
<th>ΔNR/ΔNA+ΔNR (%)</th>
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<tr>
<td>9</td>
<td>+1.82</td>
<td>+3.99</td>
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<td>8</td>
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<td>3−7</td>
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<tr>
<td>Culm</td>
<td>−0.03</td>
<td>+0.27</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Upper roots</td>
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<td>+3.49</td>
<td>+2.04</td>
<td>+1.42</td>
<td>58.5</td>
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<tr>
<td>Lower roots</td>
<td>−0.27</td>
<td>+1.10</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Tillers</td>
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<td>+8.45</td>
<td>+0.80</td>
<td>+7.65</td>
<td>9.5</td>
</tr>
<tr>
<td>Total</td>
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<td>+20.19</td>
<td>+1.01</td>
<td>+19.18</td>
<td>5.0</td>
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* ΔNR=ΔN−, ΔNA=(ΔN+)-(ΔN−)
** Proportion of the retranslocated nitrogen to the total incorporated nitrogen in the growing organs.

Foliar-applied urea is also assimilated into amino acids through hydrolysis by the enzyme urease\(^17\). A part of these amino acids is incorporated into insoluble nitrogenous compounds such as proteins, and the remainder is transferred to other plant parts through phloem. This might be true in this experiment also. As shown in Table 2, foliar-applied \(^{15}\)N was intensely incorporated into TCA-insoluble fraction (proteins) in the fed leaf. The soluble fraction showing a high level of \(^{15}\)N may be a pool of amino acids which were recently assimilated from the urea absorbed by the fed leaf. Due to a long-term (over 7 days) foliar-administration of this experiment, the labeled nitrogen incorporated into leaf proteins could be subsequently exported from the fed leaf as the products of protein breakdown together with the recently assimilated amino acids.

*Nitrogen transport from leaves* It was shown in Figs. 1 and 2 that the labeled nitrogen applied to a single upper leaf (leaf 8) was intensively translocated to the growing leaves and incorporated into their TCA-insoluble fractions. This result is in agreement with the other reports\(^4,5,9,22,23\) indicating that the mature leaves are the substantial source of nitrogen for the growing leaves. It is worthy to be mentioned that about 25% of the labeled nitrogen released from leaf 8 was trapped by roots especially by the young upper roots, notwithstanding the fact that the roots were surrounded by ammonium sulfate and could therefore assimilate this nitrogen for their own private use. Similar result was found in our previous experiment for rice plants\(^20\). It is likely that the nitrogen coming from the shoot plays an important role to build up new tissues of young roots, and the result here suggests that the upper leaves are the substantial source to supply the growing roots with nitrogenous compounds.

Although due to their small sizes of nitrogen pool the amount of nitrogen released from the lower leaves was smaller than that from the upper leaves, the lower leaf such as leaf 5 also seem to be a substantial source for the growing roots. About 47% of the exported \(^{15}\)N from the lower leaf (leaf 5) was found in the roots, and this value was 1.7 times as large as that from the upper leaf (leaf 8). This trend of nitrogen movement from leaves of different ages is well associated with that of the carbon; the lower leaves nourished...
principally the roots with supply of photosynthates whereas the upper leaves did for the developing shoots\textsuperscript{16,180}. Presumably the nitrogenous compounds released from the leaves may be translocated along with the sugars and other assimilates in the phloem.

It was shown in Table 2 that the detectable
\[ ^{15}\text{N} \text{translocated from the upper leaf was absent of sparsely found in the lower leaves which were aged but still green. Similar results have been found in the } ^{15}\text{N}-\text{feeding experiments for sunflower}\textsuperscript{23}, corn (Yoneyama and Arak unpublished data) and Lupinus}\textsuperscript{99}. This may partly due to the absence of the active connection of the phloem between upper leaves and lower leaves in culm nodes. In this experiment the roots received considerable amounts of labeled nitrogen from the upper leaf, therefore the lower leaves had the possibility to receive some of this labeled nitrogen from roots through xylem with the transpiration stream. This implies that there is no effective pathway for nitrogenous solutes passing through the roots from the downward phloem stream to the upward xylem stream. The result here for nitrogen is in contrast to the case for carbon\textsuperscript{14} and phosphorus\textsuperscript{1} circulating through the root system.

\textit{Estimate of the proportion of retranslocated nitrogen in the growing roots} Table 3 shows the increase or decrease of amount of nitrogen in plant parts from Day 0 to Day 7. In the plants of minus N medium, nitrogen content was increased in leaf 10, leaf 9, tillers, and upper roots. On the contrary it was decreased in the other parts especially in leaf 8 and leaf 3–7. This indicates that nitrogen which had been incorporated into leaf 8 and leaf 3–7 before Day 0 was subsequently retranslocated into growing plant parts (leaf 10, leaf 9, tillers, and upper roots). In these nitrogen-starved plants the bulk of nitrogen released from the plant parts in which considerable amounts of nitrogen losses occurred may be composed of the nitrogenous product arising from the protein breakdown.

From data in Table 3 the amount of nitrogen retranslocated to the growing plant parts during the experimental period (7 days) was estimated assuming that; in the plants of plus N medium the nitrogen retranslocation occurred in the same manner as that in the plants of minus N medium. Thus increment of the amount of retranslocated nitrogen ($\Delta N_R$) and of newly absorbed nitrogen ($\Delta N_A$) in growing organs was calculated as follows, and summarized in Table 3.

\[ \Delta N_R = \Delta N - , \quad \Delta N_R + \Delta N_A = \Delta N + \]

where $\Delta N -$; increment of amount of nitrogen in plant parts of minus N plants. $\Delta N +$; increment of amount of nitrogen in plant parts of plus N plants.

The result shows that 46–52\% of the incorporated nitrogen in the developing leaves was retranslocated from other parts of the plant, chiefly from the developed leaves (leaf 8 and leaf 3–7). Although the nitrogen starvation might accelerate the protein breakdown which made the increase of retranslocated nitrogen from the developed leaves, the value here obtained is in agreement with the result obtained by a previous
\[ ^{15}\text{N} \text{tracer experiment of rice leaves: about } 30–50\% \text{ of the incorporated nitrogen in the developing leaves comes from other parts of the plant}\textsuperscript{22}.\]

In the developing upper roots it was shown that the proportion of the retranslocated nitrogen was about 59\% (Table 3). This value accords substantially with that calculated in the developing leaves of this experiment. By analyzing the phloem and xylem exudates of Lupinus Pate et al.\textsuperscript{12} reported that more than 80\% of the incorporated nitrogen in the roots was translocated from the mature leaves, and less than 7\% was directly transferred from the assimilating sites within the root system, whether the legume was nodulated or non-nodulated. A study on cotton plants\textsuperscript{23} has indicated that 10–36\% of the reduced nitrogen available to the roots was imported from the shoot. These differences among plants imply that not all plant species may be in the same situation. The nutritional level may also affect the nitrogen transport to the roots, as suggested by RADIN\textsuperscript{15} in cotton plants.

The exportable nitrogen in the developed
leaves consists of (1) nitrogenous compounds arising from protein turnover or discharge of storage pools, and (2) nitrogenous solutes which are in the process of cycling through the leaf. The significance of the nitrogen category (1) in the formation and the growth of developing organs has been indicated by several workers, and the retranslocated nitrogen we discussed in this paper is the nitrogen of category (1) also. Studies on legumes have indicated that the leaves are active centers of the xylem to phloem exchange of nitrogenous solutes originating from the root system, and that this pathway through the leaves may be the major route to provide the growing parts of shoots and roots with a variety of nitrogenous compounds available to protein synthesis.

Unfortunately it is impossible to estimate the quantity of the nitrogen of category (2) in this experiment. In rice plants, however, Yoneyama and Sano indicated that a considerable amount of nitrogen transported to the developed leaves was moved out before it was incorporated into the protein. We have reported in another paper that a substantial amount of 15N taken up by the aged roots of rice plants was rapidly transferred to the young developing roots via shoot. These results suggest that there exists a possible route for nitrogenous solutes transferring from xylem to phloem in developed leaves and returning back to the growing roots in rice plants.

Summary

Translocation of nitrogen from leaves to roots in rice plants at the 9th leaf stage was investigated using 15N as a tracer. Feeding a single upper leaf (the 8th leaf) or a lower leaf (the 5th leaf) with 15N-labeled urea (0.2% solution) over 7 days resulted in intensive incorporation of 15N into TCA-insoluble fraction of the growing centers of shoots and roots. About 25% of 15N exported from the upper leaf was incorporated into roots especially into the growing upper roots, notwithstanding the fact that the roots were simultaneously fed with non-labeled ammonium sulfate (8 ppm N). The percentage of amount of 15N exported to the roots was larger from the lower leaf than from the upper leaf.

Compared the plants of minus N medium with that of plus N medium (8 ppm N) for the change in nitrogen contents of plant parts over 7 days, the amounts of retranslocated nitrogen and of the newly absorbed nitrogen in the growing organs were estimated; 59% of the incorporated nitrogen in the growing upper roots was chiefly retranslocated from the developed leaves.

These results suggest that in rice plants the developed leaves are the major source to supply the growing roots with nitrogenous compounds.

Acknowledgment

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* In Japanese with English summary, ** in German with English summary, *** in Russian with English summary.
水稲の葉から根への窒素の転流

森二郎・河野 榊広
（名古屋大学農学部）

第9葉抽出期の水稲の第8葉身（成熟葉）または第5葉身（古葉）を、$^{15}$Nで標識した0.2％尿素溶液に浸漬し吸収させ、7日後の植物体各部分への$^{15}$Nの分布状態を調べた。

第5、8葉身から吸収された$^{15}$Nの一部は$^{15}$N供与葉中に、他は生長の活発な新葉（第9、第10葉）、分けつ、新根（第6、第7節根）へ転流し、それぞれTCA不溶態窒素画分にとり込まれた。これとは対照的に供与葉より下位の葉への$^{15}$Nの転流は不活発であった（第1、第2図）。

供与葉から転流した$^{15}$Nの根への分配割合は、培養液中に窒素が存在しない条件下（−N区）において、第8葉（約27％）よりも第5葉（約47％）で明らかに高かった。培養液中に窒素が存在する条件（8ppm、+N区）でも、第8葉から転流した$^{15}$Nのうち約25％が根へ分配され、培地中の窒素の有無は葉から根への窒素の転流割合にほとんど影響を与えてなかった（第1、第2図）。

実験期間中の−N、+N両区の水稲体各部分の窒素含量の増減から、この期間中に生長した新葉ならび
に新根へそれぞれとり込まれた窒素のうち、根から新たに吸収された窒素と植物体中の他の部分から転流し
た窒素の割合を推定した（第3表）。その結果、新葉と新根における他の部分から転流してきた窒素（再転
流窒素）の割合は、それぞれ約46～52％と約59％であった。

以上の結果より、とくに根の生長に必要な窒素のかなりの部分が地上部から供給されており、成熟葉なら
びに古葉が新根への窒素供給器官として重要な役割を果していると推論した。