Investigation on the Carbon and Nitrogen Transfer from a Terminal Leaf to the Root System of Rice Plant by a Double Tracer Method with $^{13}$C and $^{15}$N.

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It has been recently demonstrated by several workers\(^{6,9,12,23}\) that nitrogen in mature leaves was in a constant partial renewal, and nitrogen once translocated to mature leaves was then retranslocated to new leaves. A large proportion of the nitrogen in the growing leaves was derived from the retranslocated nitrogen originating from the mature leaves. These results suggest that the retranslocated nitrogen may play an important role in building up the new issues of growing leaves. More recently, it has been found that the movement of nitrogen from the leaves to the root also exists in several species of plants, such as field pea\(^ {18}\), white lupin\(^ {16}\), sunflower\(^ {26}\) and rice\(^ {21}\). Transfer of nitrogen from shoot to root took place not only when the roots were kept in medium lacking nitrogen but also when the roots were supplied with enough amount of inorganic nitrogen available for their own use\(^ {16,21}\).

However, the role and significance of the remobilized nitrogen from the leaves to the root have not been fully established. We expected that a part of this question could be ascertained by comparing the movement of nitrogen from the leaf to the root with that of carbon.

Previous work\(^ {22}\), where $^{13}$C-labelled carbon dioxide and $^{15}$N-labelled urea were supplied to the whole leaves of the rice plant at vegetative stage, indicated that the growth of new roots largely depended on the nitrogen translocated from the leaves, and that the mature and old roots also received a substantial amount of nitrogen translocated from the leaves.

In the present study, $^{13}$C-labelled carbon dioxide and $^{15}$N-labelled nitrogen dioxide (NO\(_2\)) were simultaneously administered to a mature terminal leaf of the rice plant at reproductive stage, and the fate of $^{13}$C and $^{15}$N in the plant was followed over 8 days. Special attention was devoted to the transfer of the two isotopes from the leaf to the root system which was classified into three sets of different nodal roots. Gaseous NO\(_2\) would be more suitable form of nitrogenous compound than urea or nitrate in order to introduce an adequate amount of nitrogen into the leaf in a short time\(^ {28}\).

Materials and Methods

Plants

Pre-germinated rice seeds (Oryza sativa L. cv. Nihonbare) were grown on a salan net floating in a vat with a 10-fold dilution of Kasugai's rice culture solution\(^ {29}\) in a naturally-lit growth room with a constant temperature at 25°C and a relative humidity at 70%. The plants were grown under a short-day condition during October to November to prepare morphologically simplified plants which would produce fewer leaves and tillers during the vegetative growth. Such plants would be useful for the clear understanding of the translocation system in the plant. At the 5th leaf emer-
gence (Oct. 27, 1980), 120 seedlings were transplanted spacing 4 cm × 4 cm into a water culture bed (100 l in volume) filled with a 4-fold dilution of Kimura's B culture solution\(^2\) which contained both \(\text{NH}_4\text{-N}\) and \(\text{NO}_3\text{-N}\) as nitrogen source. The culture solution was renewed twice a week and adjusted to pH 5.5 with \(1 \text{ N HCl}\) and \(1 \text{ N KOH}\). The roots of main stem were classified into three sets of different nodal roots by the method of Tatsumi and Kono\(^{20}\). 1) Lower roots (LR): the roots emerged from lower than the 2nd node. 2) Middle roots (MR): the roots from the 2nd and 3rd nodes. 3) Upper roots (UR): the roots from the 4th node.

**Feeding of \(^{13}\text{CO}_2\) and \(^{15}\text{NO}_2\) to single leaves**

On November 20, 1980, when the plants were at boot stage and the 7th leaf (terminal leaf) had fully expanded, 50 plants were selected and transplanted to an another water culture bed in an artificially-lit growth room (30 klx, light/dark 14 h/10 h, 25°C, R.H. 70%). Composition of the nutrient solution was same as before. The feeding experiment was carried out in the same room on the next day. Feeding of \(^{13}\text{CO}_2\) and \(^{15}\text{NO}_2\) to single leaf of each plant was conducted in an assimilation chamber (130 × 50 × 30 cm, made of plexiglass) into which the 7th leaf blades of 50 plants were inserted and sealed in with urethane resin at their basal part. The air in the assimilation chamber was purged by \(\text{CO}_2\)-free air for 10 min and \(\text{CO}_2\) concentration was reduced to around 20 ppm. Then, the evolution of \(^{13}\text{C}\)-labelled \(\text{CO}_2\) was initiated by addition of an appropriate amount of \(1 \text{ N HCl}\) to \(\text{Ba}^{13}\text{CO}_3\) (90.7 atom\% \(^{13}\text{C}\)). The concentration of \(^{13}\text{CO}_2\) in the chamber was monitored with an infrared gas analyzer (Type ZFD, Fuji Electric Co., Ltd., Tokyo), and was maintained between 350 to 400 ppm by occasional addition of \(1 \text{ N HCl}\) to \(\text{Ba}^{13}\text{CO}_3\).

\(^{15}\text{N}\)-labelled \(\text{NO}_2\) was introduced simultaneously with the generation of \(^{13}\text{CO}_2\) by a syringe. \(^{15}\text{NO}_2\) gas was made from \(\text{K}^{15}\text{NO}_3\) (99.7 atom\% \(^{15}\text{N}\)) as described elsewhere\(^3\). The concentration of \(^{15}\text{NO}_2\) in the chamber was monitored continuously every minute with a \(\text{NO}_x\) analyzer (Model 258, Kimoto Electric Co., Ltd., Osaka) and was maintained between 2.5 to 3.5 ppm by additional injection of \(^{15}\text{NO}_2\).

The 7th leaf blades of 50 plants were fed with \(^{13}\text{CO}_2\) and \(^{15}\text{NO}_2\) for two hours in light. At the end of the feeding period, the concentrations of \(^{13}\text{CO}_2\) and \(^{15}\text{NO}_2\) remaining in the chamber were reduced to around 20 ppm and 0.2 ppm respectively through the introduction of \(\text{CO}_2\)-free air for 10 min, then the assimilation chamber was opened. Ten plants were sampled immediately after the termination of isotopes feeding (Day 0). The rest of the plants were kept in the same growth room, then sampled at 1/4 (6 h, Day 1/4), 1 (Day 1), 3 (Day 3) and 8 (Day 8) days after. Roots of the harvested plants were washed with running tap water, then the plants were separated into the fed leaf (FL), the lower leaves (LL, 3rd to 6th leaf), the young panicle (P), the culm (C), the upper roots (UR), the middle roots (MR), the lower roots (LR) and the tillers (T). The leaf sheath was included in each leaf sample. Separated parts of the plant were dried in an oven at 80°C for 3 days, and ground to fine powder with a vibrating sample mill (TI-200, Heiko Scisakusho Ltd., Tokyo).

**Determination of \(^{13}\text{C}\) and \(^{15}\text{N}\)**

Total carbon content of the sample was determined with a Yanaco CN-corder (MT-500, Yanagimoto Co., Ltd., Kyoto), and \(^{13}\text{C}\) content was measured by infrared absorption spectrometry\(^4\) using a JASCO EX-130 \(^{13}\text{CO}_2\) analyzer (Japan Spectroscopic Co., Ltd., Tokyo). Total nitrogen content was determined by the distillation method after Kjeldahl digestion where salicylic acid was used so that the nitrate nitrogen would be measured. \(^{15}\text{N}\) content was measured by emission spectrography\(^5\) with a JASCO NIA-1 \(^{15}\text{N}\) analyzer.

**Results**

**Plant growth**

Since rice plants used in the present experiment were grown under short-day condition during October to November, the young panicle had already differentiated on
the main stem at the 6th leaf stage. The tillers had also formed at the axils of the 4th and 5th leaf at the time of feeding experiment. They developed actively during the experimental period, but had not emerged any roots yet. The upper roots had already ceased to increase the root number at Day 0, but increased their length progressively up to Day 8. The middle and the lower roots did not increase both in number and length throughout the isotope-chase period.

Changes in dry weight of various parts of the plant during the isotope-chase period are shown in Fig. 1. The tillers, the roots, the culm and the young panicle increased their dry weight with their growth, especially in the tillers dry weight increased vigorously. On the contrary, gradual decrease of dry weight was observed in the fed leaf and the lower leaves. Dry weight of the upper roots increased linearly. In contrast, dry weight did not show any significant changes in the middle roots, while some decrease occurred in the lower roots. Changes in total carbon content and total nitrogen content in the various plant parts during the isotope-chase period were similar to those in dry weight, therefore detailed data are not listed here.

Export and respiratory loss of isotopes

Table 1 shows the changes in the amount of $^{14}$C and $^{15}$N recovered in the whole plant during the isotope-chase period. Rapid respiratory loss of $^{14}$C from the whole plant occurred during the first one day, followed by a gradual loss throughout the isotope-chase period. By Day 1, 21% of the origi-

<table>
<thead>
<tr>
<th>Isotopes</th>
<th>0</th>
<th>1/4</th>
<th>1</th>
<th>3</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>$^{14}$C</td>
<td>5,134*</td>
<td>4,476</td>
<td>4,028</td>
<td>3,812</td>
<td>3,481</td>
</tr>
<tr>
<td></td>
<td>(100)***</td>
<td>(87)</td>
<td>(79)</td>
<td>(74)</td>
<td>(68)</td>
</tr>
<tr>
<td>$^{15}$N</td>
<td>236*</td>
<td>229</td>
<td>247</td>
<td>259</td>
<td>225</td>
</tr>
<tr>
<td></td>
<td>(100)***</td>
<td>(97)</td>
<td>(105)</td>
<td>(110)</td>
<td>(95)</td>
</tr>
</tbody>
</table>

* μg/10 plants. ** Relative value to that in Day 0.
Fig. 2. Efflux of $^{13}$C and $^{15}$N from the fed leaf.

Initially assimilated $^{13}$C was respired and a further 11% was lost in the following 7 days. In contrast, $^{15}$N recovered in the whole plant did not show any significant loss over 8 days.

Most of the efflux of $^{13}$C from the fed leaf also took place within one day, and subsequent slow efflux continued thereafter (Fig. 2). In contrast, $^{15}$N was exported more slowly than $^{13}$C from the fed leaf. Gradual decrease of $^{15}$N from the fed leaf was observed throughout the experimental period with a rapid decrease in the first several hours. By Day 1, 75% of the fixed $^{13}$C had been exported to the other parts or lost in respiration, whereas only 21% of the assimilated $^{15}$N was exported to the other parts from the leaf. This general pattern of export of $^{13}$C and $^{15}$N, and of the loss of $^{13}$C in respiration, were very similar to those previously reported on sunflower plant\(^{26}\).

**Distribution of $^{13}$C and $^{15}$N in the plant**

Table 2 shows the changes in $^{13}$C and $^{15}$N abundances (atom % excess) in the various parts of the rice plant. $^{13}$C and $^{15}$N abundances in the fed leaf decreased continuously with the outflow from the leaf or respiratory loss. $^{13}$C abundance in all parts except for the fed leaf increased rapidly up to Day 1 and then decreased mainly due to the dilution by non-labelled carbon newly assimilated. $^{15}$N abundance in vegetative parts also increased up to Day 1, followed by a gradual decrease thereafter. In the young panicle, $^{15}$N abundance increased up to Day 3, then very small changes were observed. The young panicle showed the highest $^{13}$C and $^{15}$N abundances among the plant parts at Day 1, followed by the tillers, the culm and the root. Very low isotopes abundances were detected in the lower mature leaves.

The distributions of the two isotopes in the plant are summarized in Fig. 3. Extremely large amount of $^{13}$C was transported to the tillers. Transfer of $^{13}$C to the tillers continued up to Day 3 when the tillers received more than 50% of the exported $^{13}$C. The amount of $^{13}$C in the young panicle, the culm and the roots increased.

**Table 2. Changes in $^{13}$C and $^{15}$N abundance in various parts of rice plant fed from a terminal leaf on the main stem with $^{13}$CO$_2$ and $^{15}$NO$_2$.**

<table>
<thead>
<tr>
<th>Plant part</th>
<th>$^{13}$C abundance (atom % excess)</th>
<th>$^{15}$N abundance (atom % excess)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0*</td>
<td>1/4</td>
</tr>
<tr>
<td>Young panicle</td>
<td>0.58</td>
<td>1.14</td>
</tr>
<tr>
<td>Leaves 7**</td>
<td>2.04</td>
<td>1.50</td>
</tr>
<tr>
<td>6</td>
<td>0.00</td>
<td>0.08</td>
</tr>
<tr>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>3~4</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Culm</td>
<td>0.17</td>
<td>0.38</td>
</tr>
<tr>
<td>Tillers</td>
<td>0.15</td>
<td>0.47</td>
</tr>
<tr>
<td>Roots upper</td>
<td>0.03</td>
<td>0.24</td>
</tr>
<tr>
<td>middle</td>
<td>0.00</td>
<td>0.03</td>
</tr>
<tr>
<td>lower</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>whole</td>
<td>0.01</td>
<td>0.06</td>
</tr>
</tbody>
</table>

* Days after the feeding of isotopes.

**$^{13}$CO$_2$ and $^{15}$NO$_2$ were fed to 7th leaf for two hours.**
rapidly up to Day 1 when the roots received 19% of the exported $^{13}$C. $^{13}$C in the young panicle and the culm tended to increase slightly from Day 1 to Day 8, while significant decrease was observed in the roots during this period.

The amount of $^{15}$N in the tillers and the young panicle continued to increase up to Day 8 with a gradual efflux of $^{15}$N from the fed leaf. The tillers received a large proportion (73%) of exported $^{15}$N at Day 8. $^{15}$N in the roots and the culm increased up to Day 1 when the roots received 17% of the exported $^{15}$N, thereafter $^{15}$N in the roots was maintained at a steady level. Only a small amount of both $^{13}$C and $^{15}$N was translocated to the lower leaves.

**Distribution of $^{13}$C and $^{15}$N in the different nodal roots**

Table 2 shows the changes in $^{13}$C and $^{15}$N abundances in the different nodal roots. Both $^{13}$C and $^{15}$N abundances in all nodal roots increased up to Day 1 and then decreased gradually mainly due to the dilution by non-labelled carbon and nitrogen newly assimilated or absorbed. The highest abundances of both $^{13}$C and $^{15}$N were detected in the upper roots, followed by the middle roots. The lower roots showed very low isotopes abundances.

Changes in the amount of $^{13}$C and $^{15}$N in the different nodal roots are shown in Fig. 4. The amount of $^{13}$C in the upper and middle roots increased rapidly up to Day 1. Transfer of $^{13}$C to the upper roots continued up to Day 3. The upper roots received the $^{13}$C about twice as much as the middle roots at Day 1. From Day 1 or Day 3 to Day 8, the amount of $^{13}$C in the upper and middle roots decreased significantly.

The amount of $^{15}$N in the upper and middle roots also increased rapidly up to Day 1 with the equal amount. From Day 1 to Day 8, a further increase of $^{15}$N was observed in the upper roots, while a nearly same amount of decrease was detected in the middle roots. A very small amount of $^{13}$C and $^{15}$N were detected in the lower roots during the experimental period.

**Discussion**

Efflux of $^{13}$C and $^{15}$N from the fed leaf

Carbon dioxide taken up in rice leaf could be converted into sugars and translocated to the other parts as mainly sucrose\(^1\). Most of the transfer of $^{13}$C from the fed leaf to the other parts took place within one day, and during this time 21% of photoassimilated $^{13}$C was lost from the whole plant through respiration (Table 1, Fig. 2). The end of the rapid phase of respiration was associated with the cessation of export of labelled carbon from the fed leaf. The synchronism between the intense respiratory loss of $^{13}$CO$_2$ and the transloca-
tion of $^{13}$C to the growing tissues observed during one day is indicative of a causal relationship. Although we did not determine the respiratory loss of $^{13}$C by each plant part, the bulk of the respiratory loss of $^{13}$C might occur from the plant parts importing $^{13}$C from the fed leaf. Because GORDON et al. reported on uniculm barley that 36% of the total $^{14}$C originally fixed was respired by 24 h, and the loss of $^{11}$C from the fed leaf itself was only 10% of the total loss of $^{14}$C by the whole plant. The rapid $^{13}$C loss detected during the first one day might be related to the synthetic respiration, and much less intense but continuous respiratory loss of $^{13}$C observed throughout the 8 days-chase period might be associated with the maintenance respiration [17, 18].

Retransfer of the carbon from once distributed part seemed to be very small, and most of $^{13}$C in the plant appeared to be immobilized at the sites to which it had been translocated during the first one day. Continuous transfer of $^{13}$C to the actively growing parts such as the tillers, the young panicle and the upper roots observed after Day 1 (Fig. 3 and 4) might be due to the transfer of the temporary metabolites accumulated in the fed leaf. These characteristics of carbon transfer in rice plant were very similar to those in uniculm barley [3] and sunflower [20]. It seems that the utilization system of carbon in rice plant may be also organized on a diurnal basis with little carry-over of one day’s assimilates to another as GORDON et al. [3] indicated on uniculm barley.

Nitrogen transfer from the fed leaf occurred gradually throughout the experimental period with a rapid efflux in the first several hours (Fig. 2). Nitrogen dioxide absorbed in the leaf through stomata could be converted into nitrite and nitrate and further assimilated into amino acids via glutamine synthetase and glutamate synthase system [25]. Some of amino acids synthesized may be directly exported from the fed leaf to the other parts through phloem in the first several hours, while others may be incorporated into proteins and other nitrogenous compounds in the fed leaf [6, 14]. The latter could be hydrolyzed later and amino acids produced were exported from the leaf gradually. Yoneyama and Sano [23] reported that in mature rice leaves the proteins involved were turned over and that the nitrogen once incorporated into the constituents of the mature leaves was then retranslocated to the young growing parts. The importance of this kind of remobilized nitrogen from the mature leaves for the growth of new tissues was pointed out by several investigators [8, 9, 12, 23]. Thus, in con-
trast to carbon, nitrogen once incorporated into the leaf constituents may be easily remobilized and utilized repeatedly according to the demand of meristematic tissues. **Partitioning of $^{13}$C and $^{15}$N**

Sink activity for nitrogen expressed as the abundance of $^{15}$N was highest in the young panicle, followed by the tillers, the culm, the whole roots and the lower leaves (Table 2). This labelling pattern of $^{15}$N in the various plant parts was very similar to that of $^{13}$C. Only small amounts of both $^{13}$C and $^{15}$N were translocated to the mature lower leaves where the phloem might be active in export but not in import. These results suggest that the $^{13}$C-labelled sugars and the $^{15}$N-labelled nitrogenous compounds might flow together in the phloem as a bulk stream at least during the phase of primary distribution (probably within the first one day). This assumption may be supported by the finding that the translocation velocities of $^{13}$C-labelled glutamate and proline in phloem were similar to those of $^{14}$CO$_2$ assimilates.

The $^{13}$C/$^{15}$N ratios at Day 1 or Day 3 may indicate the relative requirement of carbon and nitrogen in the various plant parts (Table 3). In the young panicle and the tillers, the ratio decreased from Day 1 to Day 3; this was attributed mainly to a gradual influx of $^{15}$N. A high $^{13}$C/$^{15}$N ratio observed in the young panicle, the culm and the upper roots may reflect the high synthetic activity of cell wall constituents in these parts. Active protein synthesis probably occurred in the tillers might result in a relatively low $^{13}$C/$^{15}$N ratio in this part. The upper roots showed higher $^{13}$C/$^{15}$N ratio than the middle roots. A similar result was also obtained in the previous study. These results imply that the relative distribution of carbon and nitrogen might be partly regulated by the characteristics of the sink organs.

The terminal leaf of rice plant to which the isotope were administered is known to function as a main source of photosynthates for the panicle growth. As was expected, the abundances of both $^{13}$C and $^{15}$N were highest in the young panicle among the plant parts. However, the tillers accumulated the largest amount of isotopes (Fig. 3) because the pools of carbon and nitrogen in this part were relatively large (Fig. 1). Rest parts except for the lower leaves received nearly equal amount of $^{13}$C and $^{15}$N, respectively. Under these physiological conditions, the whole roots received 19% and 17% of the exported $^{13}$C and $^{15}$N respectively at one day after the feeding of isotopes (Fig. 3). Thus, although the roots in the present experiment might compete for the available assimilates with the other strong sinks such as the young panicle and the tillers, they received a considerable amount of carbon and nitrogen translocated from the leaf. The present result and the previous one which was obtained on the plants at vegetative stage suggest that the growth and maintenance of the rice roots may depend not only on the carbon but also on the nitrogen translocated from the leaves throughout the life cycle of the plant. **Fate of $^{13}$C and $^{15}$N in the different nodal roots**

The amount of $^{13}$C in the whole roots increased rapidly up to Day 1, thereafter gradual but significant decrease of $^{13}$C was observed over the experimental period (Fig. 3). The upper, the middle and the lower roots received 62%, 34% and 4% of the $^{13}$C at Day 1, respectively (Fig. 4). $^{13}$C in the upper roots continued to increase up to Day 3. Similar results were also obtained in the uppermost nodal roots of rice plant at vegetative stage. Labelled carbon entering to the upper roots which were actively developing would be utilized for construction of new tissues. Some of $^{13}$C in all nodal roots might be lost through respiration which produced the energy required for growth and maintenance of the various functions. A part of $^{13}$C might be retranslocated to the shoot as carbon skeleton of organic nitrogenous compounds synthesized in the roots.

The amount of $^{15}$N in the whole roots also increased rapidly during the first one day, thereafter no apparent changes were observed (Fig. 3). However, the behaviours of $^{15}$N were not same among the different nodal roots. All nodal roots in-
Table 3. The C/N and $^{15}C/^{15}N$ ratios in the various parts of rice plant fed $^{15}CO_2$ and $^{15}NO_3$ from a terminal leaf on the main stem.

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Days after the feeding of isotopes</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C/N</td>
<td>$^{15}C/^{15}N$</td>
<td></td>
</tr>
<tr>
<td>Young panicle</td>
<td>12.4</td>
<td>49.8</td>
<td>12.8</td>
</tr>
<tr>
<td>7 th leaf*</td>
<td>11.2</td>
<td>9.4</td>
<td>11.4</td>
</tr>
<tr>
<td>Lower leaves</td>
<td>12.4</td>
<td>—</td>
<td>12.7</td>
</tr>
<tr>
<td>Culm</td>
<td>17.1</td>
<td>42.3</td>
<td>20.3</td>
</tr>
<tr>
<td>Tillers</td>
<td>9.3</td>
<td>31.2</td>
<td>9.5</td>
</tr>
<tr>
<td>Roots upper</td>
<td>10.8</td>
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<tr>
<td>middle</td>
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<td>31.9</td>
<td>14.2</td>
</tr>
<tr>
<td>lower</td>
<td>21.1</td>
<td>—</td>
<td>28.4</td>
</tr>
</tbody>
</table>

* $^{15}CO_2$ and $^{15}NO_3$ were fed to 7 th leaf for two hours.

increased their $^{15}N$ contents until Day 1, at this time the upper roots and the middle roots received almost equal amount of $^{15}N$. From Day 1 to Day 8, a further gradual increase of $^{15}N$ was observed in the upper roots, while a nearly same amount of decrease was detected in the middle and the lower roots (Fig. 4). A rapid transfer of $^{15}N$ to the all nodal roots up to Day 1 would be related to a rapid efflux of $^{15}N$ from the fed leaf observed in the first several hours. A gradual increase of $^{15}N$ in the upper roots from Day 1 to Day 8 might be due to both the continuous transfer from the fed leaf and the retranslocation from the middle and the lower roots. A gradual decline of $^{15}N$ observed after Day 1 in the middle and the lower roots might result from the unbalance between a rapid efflux and a slow influx of $^{15}N$ probably occurred in these parts. A part of the remobilized nitrogen from these roots might be transported to the upper roots maybe by-passed through the shoot. TATSUI and KONO reported that in rice plant labelled nitrogen taken up by the lower roots from the medium could be transported not only to the shoot but also to the other roots, especially to the upper roots. As a result, 87% of $^{15}N$ transferred to the whole roots was distributed to the upper roots at Day 8 (Fig. 4).

Thus, $^{15}N$ translocated from the terminal leaf to the root system was distributed not only to the new roots but also to the mature roots which had already ceased to increase their nitrogen content. The labelled nitrogen entering to the new roots would be utilized for the protein synthesis. The significance of the labelled nitrogen transported to the mature roots could not be fully defined from the restricted results obtained here. The transfer of $^{15}N$ from the leaf to the mature roots may be merely attendant to that of $^{13}C$, assuming that a mass flow system would operate in long-distance transport. However, the labelled nitrogen imported to the mature roots would be also incorporated into the protein fraction, and then retranslocated to the new roots and the shoot. These patterns of nitrogen movement among the different nodal roots seem to be analogous to that observed among the leaves with different ages or positions on the stem. Mature roots may also act in the same manner as the mature leaves do in the utilization process of nitrogen in the whole root system.

The upper roots in the present study might be equivalent to the superficial roots which were known to develop continuously until full-ripe stage, and were considered to be concerned physiologically in ripening. Centralization of the retranslocated nitrogen into the upper roots may be an example of the elaborate system of nitrogen utilization in rice plant at reproductive stage when nitrogen supply from leaves to roots would be insufficient for the root growth due to the competition with the other strong sinks. Further investigation using the rice plant grown under usual
long-day condition should be conducted to ascertain those speculations.

Summary

To investigate the translocation of carbon and nitrogen from leaves to roots, $^{13}$C-labelled carbon dioxide and $^{15}$N-labelled nitrogen dioxide were simultaneously administered to a mature terminal leaf of rice plants at boot stage, and the fates of the two isotopes in the plants were followed over 8 days. The roots were classified into three sets of different nodal roots.

Most of the transfer of $^{13}$C from the fed leaf to the other parts took place within one day, and during this time 21% of the photoassimilated $^{13}$C was lost through respiration. Transfer of $^{15}$N from the fed leaf occurred gradually throughout the experimental period with a rapid efflux in the first several hours.

The close similarity of labelling patterns of $^{13}$C and $^{15}$N in the various plant parts suggested that the two isotopes might flow together in the phloem as a bulk stream at least during the phase of primary distribution. The $^{13}$C/$^{15}$N ratios in the various plant parts indicated that the relative distribution of carbon and nitrogen might be partly regulated by the characteristics of the sink organs.

Although the roots at reproductive stage of rice plant might compete for the available assimilates with the other strong sinks, they received a considerable proportion of $^{13}$C (19%) and $^{15}$N (17%) exported from the fed leaf at Day 1. Both $^{13}$C and $^{15}$N were translocated not only to the new roots but also to the mature roots which had already ceased to develop. Labelled carbon in the all nodal roots decreased gradually after Day 1 maybe due to the respiration and the retranslocation to the shoot. Labelled nitrogen entering to the mature roots was then retranslocated to the new roots and the shoot. Most of the $^{15}$N transported from the leaf to the root system was finally accumulated in the new roots which were developing actively.

References


* In Japanese with English summary.

** In Japanese.
[和文摘要]

$^{13}$C と $^{15}$N のダブルトレーサー法による水稲の葉から根系への炭素と窒素の転流の研究

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葉から根へ送られる窒素の意義を明らかにする目的で、穂まし期の水稲の最上位葉に $^{13}$C 標識の炭酸ガスと $^{15}$N 標識の二酸化窒素を同時に取り込み、$^{13}$C と $^{15}$N の体内移動および部位別に分級した根中での動態を 8 日間追跡した。

同化葉からの $^{13}$C の転流は 1 日で大部分が終了し、その間に固定された $^{13}$C の 21% が呼吸により失われた。一方、$^{15}$N の同化葉からの流出は $^{13}$C に比べ遅く、かつ実験期間中継続して起った。

$^{13}$C と $^{15}$N の体内分布パターンの類似性から、少なくとも一次分配過程では $^{13}$C と $^{15}$N は一緒に根管中を動くと考えられる。一方、各部位の $^{13}$C/$^{15}$N 比に違いが認められたことから、炭素と窒素の相対的分布はシングル器官の性格によっても影響されていると思われた。

同化後 1 日目には葉から転流した $^{13}$C の 19% と $^{15}$N の 17% が根系へ分布した。$^{13}$C と $^{15}$N は生長中の上位節根（新根）ばかりでなく、発育を完了した下位節根へも転流した。根中の $^{13}$C 量は呼吸による放出や地上部への再転流のため、1 日目以降明らかに減少した。下位節根へ転流した $^{15}$N は、その後上位節根や地上部に再転流し、最終的には根系中の $^{15}$N の大部分は上位節根へ集中し、その生長に使われた。