Relationship between Nitrogen Absorption and Growth and Yield of Rice Plants

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Nitrogen requirement of rice plants to produce 100 kg of paddy is about 1.5 to 1.7 kg in Japan,[31] while in the case of high yield rice cultivation at least 1.9 kg of nitrogen is absorbed for the production of 100 kg of paddy.[11] The most important problem in achieving high yields is how to increase nitrogen absorption at each growth stage without disturbing plant growth and without reducing percentage of ripened grains.[11,26]

Many research works concerning effects of nitrogen nutrition on yield determining process have been done. Recently, intensive field studies using ^{15}N have provided a considerable amount of information on soil-plant relationship and agronomy of nitrogen for rice plants.[18]

In the present paper, the relationship between the pattern of nitrogen absorption and the yield determining process is reviewed.

Effects of nitrogen to yield components

1) *Sink size*

In an identical variety, with negligible variation in hull size, the sink size is determined by the number of spikelets. There is a close correlation between the number of spikelets and the amount of nitrogen in the plant at the late stage of spikelet initiation or heading stage.[26] In general, as the number of degenerated spikelets is much smaller than that of differentiated ones, the number of spikelets is mainly determined by the amount of nitrogen absorbed by plants up to the late stage of spikelet initiation, as shown in Fig. 1.

Murayama (1969) and Matsushima (1976) reported that the nitrogen-spikelet number relationship varies in different areas of production (Fig. 2).[11,12,14] In the northern area, more spikelets are produced than in the southern area at the same nitrogen level of plants. Plants grown in the northern area have higher nitrogen content and smaller leaf area. This phenomenon can be explained by the percentage of the number of degenerated spikelets to that of differentiated ones. There is a positive correlation between the ratio of the number of degenerated spikelets to that of differentiated ones and the life span of plants (exclusive of nursery stage)[32] because low nitrogen content in leaves during the period from the late stage of spikelet initiation to the heading stage increases the number of degenerated spikelets.

The number of spikelets is composed of 2 components, i.e., the number of panicles and the number of spikelets per panicle. The number of panicles is correlated with the amount of nitrogen in plants at the necknode initiation stage, because in most cases the necknode initiation stage coincides with the maximum number of tillers stage.[21,26] On the other hand, the number of spikelets per panicle is determined by the ratio of the amount of nitrogen in plants at the late stage of spikelet initiation to the amount of plant nitrogen at the necknode initiation stage.[26] Furthermore, Takahashi et al.[21,23] reported that there is a high correlation coefficient between the number of spikelets and the maximum rate of nitrogen absorption (caused by basal-dressed as well as top-dressed nitrogen)at the time before the necknode initiation stage (hereafter this rate

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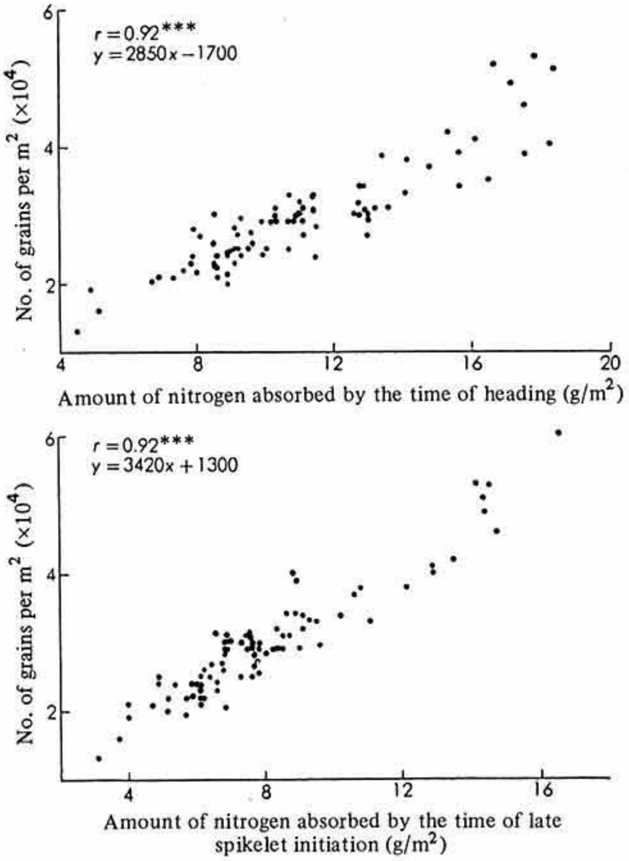

Fig. 1. Relationship between the number of grains per m^2 and the amount of nitrogen absorbed by rice plants by the time of heading or the late stage of spikelet initiation[26]

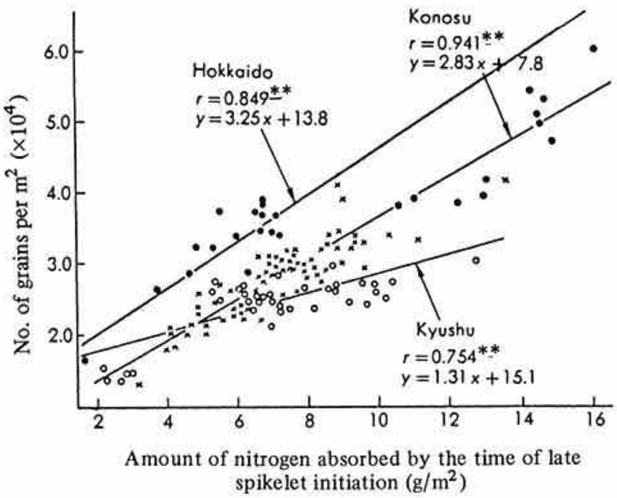

Fig. 2. Relationship between the number of grains per m^2 and the amount of nitrogen absorbed by rice plants by the late stage of spikelet initiation[11]

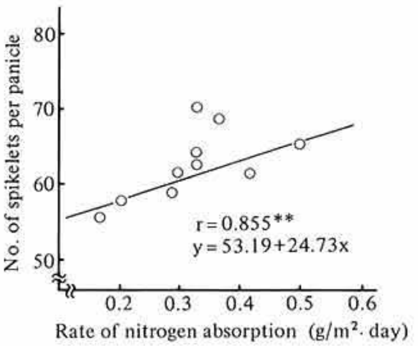

Fig. 3. Relationship between the number of spikelets and the maximum rate of nitrogen absorption[23]

(g/m^2.day) is called the maximum rate of nitrogen absorption) as shown in Fig. 3.

Thus, the components of the number of spikelets are influenced by the nitrogen nutrition of plants. The more the amount of nitrogen absorbed up to the necknode initiation stage, the more the number of panicles. The more the amount of nitrogen absorbed during the period from the necknode initiation stage to the late stage of spikelet initiation, the more the number of spikelets per panicle.

2) *Carbohydrate production and percentage of ripened grains*

Before the late stage of spikelet initiation, nitrogen accelerates vegetative growth and reduces carbohydrate accumulation,[19] whereas after the late stage of spikelet initiation, it promotes carbohydrate accumulation because vegetative growth is limited at this stage.[26] Particularly at the stage after flowering it strongly promotes the carbohydrate accumulation.[26]

The percentage of ripened grains is determined by the ratio of the amount of carbohydrate to the number of spikelets. In general, the percentage of ripened grains has a tendency to decrease with an increase of plant nitrogen content at the late stage of spikelet initiation or at the heading stage. In order to increase the percentage of ripened grains, it is necessary to increase carbohydrate production.

A larger portion of carbohydrates in grains is mainly produced during the ripening period, and the percentage of that amount of carbohydrates in grains increased with an increase of grain yield and the number of spikelets. For high yielding rice cultivation,* therefore, it is necessary to increase the carbohydrate production during the ripening period.[11,26]

Wada concluded based on a number of his experiments that the dry matter production during the ripening period is most closely correlated with the following products: (N + dN)S, where N stands for total nitrogen in leaves at the heading stage, dN for the amount of nitrogen absorbed during the ripening period and S for average solar radiation during the ripening period[26] (Fig. 4). He also emphasized the importance of nitrogen absorption during the ripening period especially in high yielding rice cultivation.

On the other hand, as the amount of carbohydrates stored in shoots at the heading stage is very small compared with the carbohydrate production during the ripening period, it seems that the former cannot directly influence the yield and the percentage of ripened grains. However, it is notable that the percentage of ripened grains shows a tendency to increase progressively with an increase of the amount of carbohydrate stored

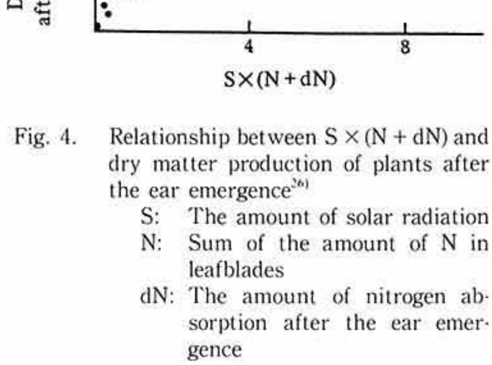

Fig. 4. Relationship between S × (N + dN) and dry matter production of plants after the ear emergence[26]
S: The amount of solar radiation
N: Sum of the amount of N in leafblades
dN: The amount of nitrogen absorption after the ear emergence

* High yielding rice cultivation refers high yielding cultivation of rice, but not cultivation of high-yielding rice, in this paper.

in shoots by the heading stage.[26]

Components of the number of spikelets also affect the percentage of ripened grains. When the number of spikelets is small, there is no relationship between the percentage of ripened grains and the components of the number of spikelets. However, when the number of spikelets increases, the percentage of ripened grains shows a tendency to decrease with an increase in the number of spikelets per panicle. This fact shows that the pattern of nitrogen absorption up to the late stage of spikelet initiation affects the percentage of ripened grains.

Effect of nitrogen on morphological characters

In order to develop a plant type by which light utilization efficiency can be improved and lodging minimized under a high level of nitrogen, it is necessary to reduce the length of culms, the total length of lowermost 3 internodes and that of uppermost 3 leaves, and to increase the specific leaf weight.[11]

A close correlationship exists between the maximum rate of nitrogen absorption and the length of culms, the total length of lowermost 3 internodes or that of uppermost 3 leaves, as shown in Fig. 5.[23] As the length of leaves is influenced not only by nitrogen nutrition, but also by (1) weather conditions[5] and (2) translocation of the large amount of nitrogen from matured organs to newly developing leaves,[1,8,9] the coefficient of regression between the total length of the uppermost 3 leaves and the maximum rate of nitrogen absorption varied year by year.

The nitrogen application during the period from 43 to 33 days before heading increases the culm length, the lengths of lowermost 3 internodes and uppermost 3 leaves, but decreases the specific leaf weight.[11,24,26] On the other hand, the restriction of nitrogen absorption during the period from 42 to 35 days before heading decreases the culm length, the length of lowermost 3 internodes and of uppermost 3 leaves, but increases the specific leaf weight.[11,24]

Therefore, in order to develop a good plant type, it is necessary to control the maximum rates of nitrogen absorption by cultural practices without decreasing the amount of nitrogen absorption.

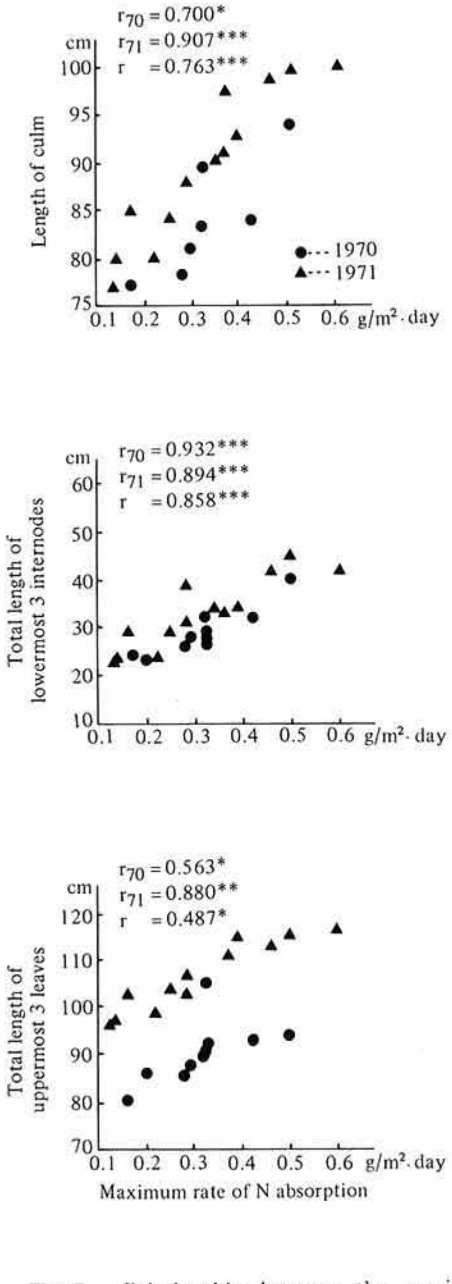

Fig. 5. Relationship between the maximum rate of nitrogen absorption and culm length, total length of lowermost 3 internodes and total length of uppermost 3 leaves[23]

Contribution of nitrogen absorbed at different growth stages to growth and yield of rice plants

1) Tillering stage

During the period from transplanting to the maximum number of tillers stage, plants absorb mainly basal nitrogen (N applied as basal dressing) as well as soil nitrogen which is mineralized from rapidly-decomposable soil organic nitrogen.[3,17,18,22] The pattern of nitrogen absorption during this period is affected by the amount of basal fertilizer, soil chemical characteristics and cultural practices.

Application of a large amount of basal fertilizer increases the absorption of nitrogen derived from the basal fertilizer as well as nitrogen derived from soil, and accelerates plant growh as shown in Table 1.[7,16,27] It also increases the maximum rate of nitrogen absorption.[21,22] The maximum rate of nitrogen absorption is decreased by early transplanting and narrow spacing without decreasing the total amount of nitrogen absorption as shown in Fig. 6.[21,22] And it is also noticed that the maximum rate of nitrogen absorption is increased when the plants are subjected to low solar radiation at the early stage of tillering.[21]

From these facts, one can apply more amount of basal fertilizer under early transplanting or narrow spacing than under conventional cultural practices. On the other hand, under late transplanting or unfavorable weather condition at the early stage of tillering, one must decrease the amount of basal fertilizer.

Behavior of nitrogen top-dressed at the early tillering stage resembles that of basal fertilizer.[28] However, the behavior of nitrogen top-dressed at late tillering stage (10 days before the maximum number of tillers stage) is different from that of basal nitrogen and it increases rapidly the maximum rate of nitrogen absorption.

The amount of nitrogen absorbed during this period contributes mainly to increase the number of tillers and the number of panicles. However, it also contributes to plant growth after the maximum number of tillers stage and, furthermore, to yield components other than the number of panicles by nitrogen translocation to newly developing organs.[1,8,9]

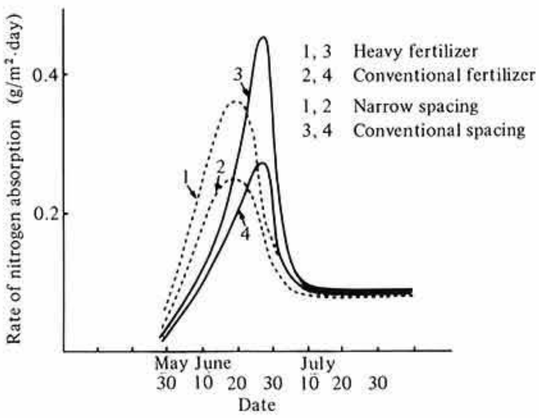

Fig. 6a. Pattern of the rate of nitrogen absorption as influenced by different planting density[21]

Table 1. Relationship between the dose of basal fertilizer and plant growth (Mae et al.)[7]

Dose of basal N (g/m^2)	NH_4-N at just after transplanting (mg/100 g dry soil)	Dry weight (g/m^2)	No. of tillers (m^{-2})	Amount of nitrogen absorption: Total N (g/m^2)	Basal N (g/m^2)	Soil N (g/m^2)
0	0.8	30.0	316	0.68	0	0.68
2	2.3	63.7	608	1.68	0.62	1.06
4	5.9	98.9	799	2.85	1.61	1.24

Cultivar: Sasanishiki. Transplanted on May 10. Harvested on June 20.

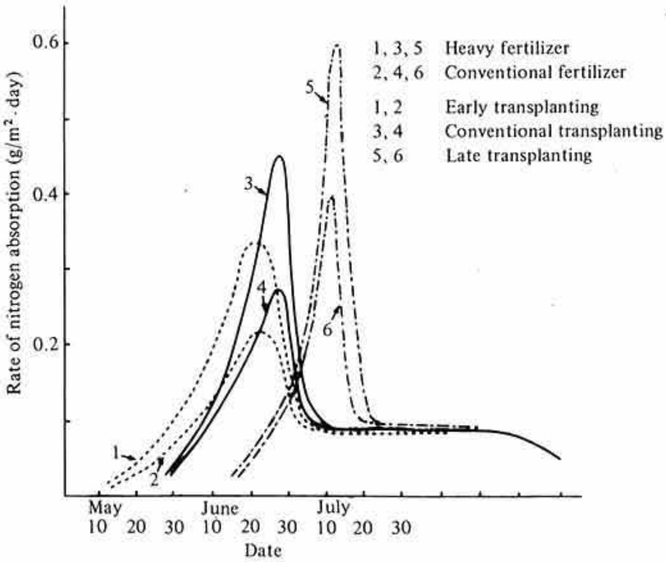

Fig. 6b. Pattern of the rate of nitrogen absorption as influenced by different transplanting time[21]

2) *Early stage of panicle formation*

Ammonium nitrogen derived from basal fertilizer and from rapidly decomposable soil organic nitrogen disappears by the maximum number of tillers stage.[18,22] In general, the necknode initiation stage coincides with the maximum number of tillers stage. After the necknode initiation stage, sources of nitrogen available to rice plants are only slowly-decomposable soil organic nitrogen and top-dressed nitrogen.

During the period from the necknode initiation stage to the late stage of spikelet initiation, the magnitude of plant growth is the largest with rapidly extending leaf area.[11] The amount of nitrogen absorbed during this period gives the most effective contribution to the spikelet production. As the recovery of top-dressed nitrogen at necknode initiation stage is high and almost all the top-dressed nitrogen is absorbed by the late stage of secondary rachis branch initiation stage,[28] the top-dressing at the necknode initiation stage is the most effective for spikelet production.

After the top-dressing given at the necknode initiation stage, the rate of nitrogen absorption is increased, but the increased rate lasts only as long as ammonium nitrogen derived from fertilizer persisting in plow layer is available. After that the rate of nitrogen absorption becomes equal to that of no-top-dressed plants. It happens sometimes that this fact induces an unbalance between 2 major yield components, the number of spikelets produced/m^2, and percentage of ripened grains, especially at a high nitrogen level showing elongation of culm, lower internodes and upper leaves. To increase the nitrogen absorption without any risk, it is necessary to increase the nitrogen supply from slowly-decomposable soil organic matter by increasing nitrogenous fertility of soil, or by deep placement of nitrogen at the necknode initiation stage.[15]

Considering the efficiency of fertilizer application to spikelet production, top-dressing at the necknode initiation stage is the most effective. When the number of spikelets is a limiting factor for increasing yield, or the amount of fertilizer is very limited, the top-dressing at the necknode initiation stage is recommended as the most effective.

As above mentioned, it can be said that to increase the number of panicles is easier than to increase the number of spikelets per panicle for obtaining the target number of spikelets per unit area under high yielding cultivation. However, the contribution of fertilizer nitrogen to spikelet production is greater with the latter than the former, because of the difference in the percentage recoveries of fertilizer between basal and top-dressing.

3) Late stage of panicle formation

During the period from the late stage of spikelet initiation to the heading stage, an increase of nitrogen absorption can influence only to a small extent growth of vegetative organs and sink size[26] because the differentiation of vegetative organs and spikelets has almost finished and growth of vegetative organ is limited. Nitrogen contributes to sink size by only decreasing the number of degenerated spikelets and increasing the hull size. It also contributes to ripening by increasing specific leaf weight, nitrogen content in leaves and by promoting carbohydrate accumulation.[4,26]

Top-dressing at the late stage of spikelet initiation or just before the reduction division stage of pollen mother cell, increases rapidly the rate of nitrogen absorption, resulting in a very high percentage recovery of the nitrogen,[28] but it does not induce any unbalance between the 2 major yield components. Therefore, the effect of the top-dressing at the late stage of spikelet initiation is not so obvious but not risky.

4) Ripening stage

After heading, nitrogen contributes to carbohydrate production. In most cases, as the amount of nitrogen which can be absorbed during the ripening period is very small compared to the nitrogen requirement of grains, a large amount of nitrogen is translocated from leaves to grains with the advance of ripening.[26,29] For keeping leaves at high rate of photosynthesis with long leaf duration, it is important to prevent the decrease of nitrogen in leaves by increasing the rate of nitrogen absorption.[26] Decrease of leaf area is correlated with the difference between the amount of nitrogen required by grains and that absorbed during the ripening period.[30] To increase the nitrogen absorption, top-dressing at the heading stage is effective. The merits and demerits of the top-dressing at the heading stage was compiled by Wada.[26] The effect of the top-dressing at the heading stage is not necessarily large, namely within 10% in most cases, but with very little risk of yield decrease.[26]

Contribution of nitrogen from different origins absorbed at different growth stages to total nitrogen in plants

Contribution of nitrogen absorbed at different growth stages from different origins to total nitrogen varies with cultural practices. One example calculated from the data of Wada et al.[27,28] and Ando and Shoji[2,3] is shown in Fig. 7. Only 26% of nitrogen in a plant is originated from fertilizer nitrogen, 11% is originated from soil by priming effect of fertilizer, and the balance is originated from soil. Soil-originated nitrogen in a plant is composed of 2 parts, one from rapidly-decomposable soil organic nitrogen and the other from slowly-decomposable organic nitrogen.[3] One third of it is derived from rapidly-decomposable organic nitrogen.

As already reported,[17,22] the limiting factor for absorption of soil nitrogen is nitrogen absorption ability during a period up to the maximum number of tillers stage and mineralization rate of soil organic nitrogen in a period after the maximum number of tillers stage. As the percentage recovery of basal fertilizer is about 30% and the percentage recovery of slowly-decomposable organic nitrogen can be assumed to be 50 to 80%, there is little difference between the amount of ammonium nitrogen released from rapidly-decomposable soil organic nitrogen and that from slowly-decomposable soil organic nitrogen. The coefficient of yearly variance of the percentage recovery of basal- and top-dressed nitrogen is small.[10] To increase the soil nitrogen absorption, it is necessary to improve cultural practices (fertilizer application method) or to increase the supply of nitrogen from soil.

It is possible to increase the absorption of soil nitrogen by increasing the absorption of nitrogen released from rapidly-decomposable soil organic nitrogen by cultural practices[20] such as narrow spacing or early transplanting. However, there is very limited space to increase the absorption of soil nitrogen released from slowly-decomposable soil organic nitrogen by cultural practices.

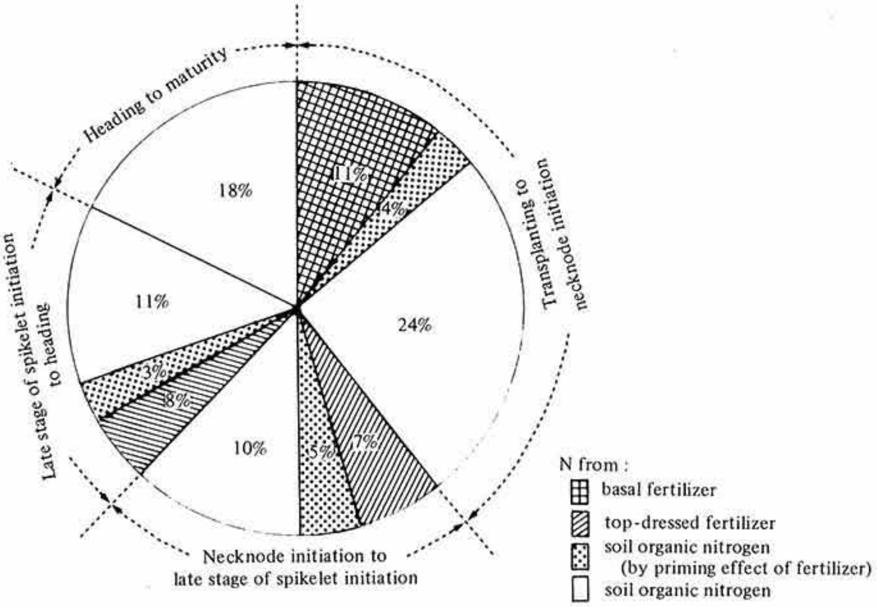

Fig. 7. Ratio of the amount of nitrogen absorbed from different origins and at different growth stages to the amount of the total nitrogen in plants
Basal fertilizer — 7 g/m^2
Top-dressed fertilizer — 2.5 g × 2/m^2
Top-dressed at the secondary rachis branch initiation stage and at the late stage of spikelet initiation.

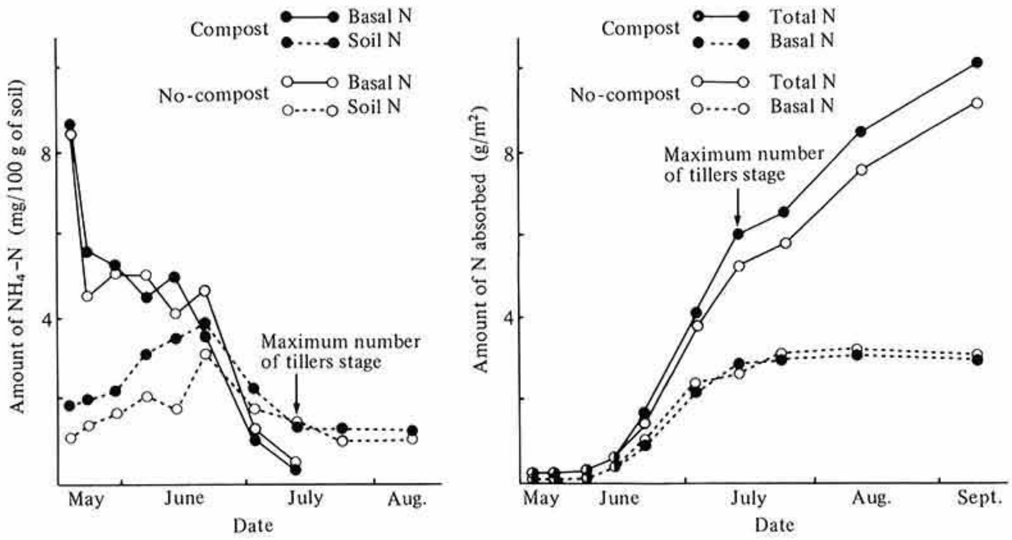

Fig. 8. Differences in the amount of soil NH$_4$-N and in N absorption by rice plants between the compost plot and the no-compost (control) plot (Data of Aomori Agr. Exp. Sta.)
In the compost plot, compost application at the rate of 10 t/ha/yr has been repeated continuously for 50 years.
Basal N: 100 kg N/ha was applied
Cultivar: Mutsuhonami
Date of transplanting: May 14

For increasing the amount of available soil nitrogen, it is important to increase the rate of mineralization of soil organic nitrogen by increasing the nitrogenous fertility of soil.

One way for increasing soil fertility is application of a large amount of organic matter. Behavior of nitrogen derived from organic matter in paddy fields is still not yet clarified because of the difficulty of determination. It has been believed that effect of organic fertilizers appears only at the middle and late growth stage of plants. But, recently experimental data of Aomori Agricultural Experiment Station[47] showed that there is no difference in the pattern of behavior of NH_4-N in soil between the compost plot (application of 10 t of compost/ha/yr continued for 50 years) and the non-compost plot. However, the amount of NH_4-N in soil is always higher in the compost plot than in the no-compost plot at tillering stage. It was also clearly shown that rice plants in the compost plot absorbed more nitrogen throughout the whole growth period from tillering stage to maturity as given in Fig. 8. Therefore, continuous application of compost is a good method to increase the nitrogenous fertility of soil.

The increased amount of nitrogen absorption caused by the practice of continuous compost application was about 10 to 15 kg-N/ha/yr. It varied with different paddy fields and different cultural practices.

Patterns of nitrogen absorption in high yielding rice cultivation

To achieve high yields, plants must absorb a large amount of nitrogen and have well balanced yield components.[11] In the case of plants holding a large number of spikelets, the percentage of ripened grains generally shows a tendency to decrease with an increase of nitrogen. The pattern of nitrogen absorption must be suitable to make plants increase their percentage of ripened grains. For this purpose, plants must absorb a large amount of nitrogen after the late stage of spikelet initiation, because the nitrogen absorbed after that stage largely contributes to the ripening without any risk. Top-dressing after the late stage of spikelet initiation is useful because it increases the amount of nitrogen without any risk to the ripening.

On the other hand, during the period from transplanting to the late stage of spikelet initiation, the most elaborate technology of nitrogen application is required because nitrogen promotes plant growth and increases the sink size, but it sometimes disturbs plant growth as already mentioned. The adequate amount of basal fertilizer depends on cultural practices and weather condition. However, since the top-dressing at this period sometimes disturbs plant growth and induces an unbalance between yield components, it is quite reasonable to attempt to increase the amount of nitrogen absorption during the period from the necknode initiation stage to the late stage of spikelet initiation by strengthening the nitrogenous fertility of soil. Critical examination of results of farmers' contests for maximizing yield revealed that winners of the contests concentrated their efforts to strengthen soil fertility.

Tsuboi[25] and Murayama[13] compiled the data of high yielding rice cultivations and demonstrated the expected nitrogen nutrition for high yielding rice cultivation. With plants grown in northern areas of Japan, the ratio of the amount of nitrogen absorbed by plants at different growth stages to the amount of nitrogen at maturity is as follows: 35-50% for a vegetative period up to the panicle initiation stage, 30-40 for the panicle initiation stage to the heading stage, and 15-30% for the ripening stage. Data[34] of Yamagata Agricultural Experiment Station from 1979 to 1982 shows 40% for transplanting to the maximum number of tillers stage, 20% for the necknode initiation stage to the late stage of spikelet initiation, 20-25% for the late stage of spikelet initiation to the heading stage and 15-20% for the ripening stage. Kamada et al.[6] reported that 35% for transplanting to the tillering stage, 55% for the tillering stage to heading, and 15% for the ripening stage. Recently, transplanting has come to be mechanized, and younger seedlings are planted at narrow spacing. In response to such changes, the pattern of nitrogen absorption is also changing. The ratio of the amount of nitrogen absorbed at early growth stage to the total amount of plant nitrogen at maturity is higher with plants grown in 1980's than with plants grown before 1960's and early 1970's.

Based on these facts, the ideal pattern of nitrogen absorption to obtain the yield of 9 tons-brown rice per hectare can be assumed as follows: As the optimum percentage of ripened grains is said to be about 80%[26] calculation is carried out under the following condition: percentage ripened grains is 80%, and the average number of spikelet per panicle is 80. According to this calculation, the plants must absorb the following amount of nitrogen: 10.5 g/m^2 by the necknode initiation stage (40%), 14.6 g/m^2 by the late stage of spikelet initiation (60%), 18.3 g/m^2 by the heading stage (80%), and 22.8 g/m^2 by the maturity.

This calculation is only one example. The method of fertilizer application should be determined by considering the pattern of nitrogen supply from soils, cultural practices to be adopted, and weather conditions.

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