3. PHYSIOLOGICAL BASIS FOR FERTILIZER RESPONSE OF RICE VARIETIES

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Physiology of Nitrogen Response in the Grain Yield

Among the nutrient elements which limit the grain yield of rice in practical farmers cultivation, nitrogen is most important. On some soils other elements than nitrogen may be the limiting factor : Phosphorus on lateritic soils in the tropics or volcanic ash soils in Japan, potassium on peaty soils or silicic sandy soils, zinc on calcareous soils with high pH, etc. are the examples. However, these cases are rather limited in area. Moreover, our knowledges of varietal difference in response to phosphorus, potassium, etc. are limited. Because of these reasons, in this paper the discussions are limited to nitrogen.

Rice plants growing in submerged soils absorb nitrogen as ammonium ion. Upon absorption ammonia is converted to amino acids in the roots by using carbon and energy derived from carbohydrates, mostly sucrose, which are the photosynthates in the leaves and translocated to the roots. The amino acids thus produced in the roots translocate to the shoots, and are converted to various amino acids and eventually to proteins again by consuming the photosynthates as carbon and energy source.

The proteins synthesized through these processes promote initiation and expansion of various organs including tillers, leaves as well as reproductive organs. An increase of protein synthesis also causes an increase of the protein content of the leaves which generally reasults in accerelated photosynthesis. Active photosynthesis promotes uptake and metabolism of nitrogen as well as the accumulation of carbohydrates, such as starch, depending upon the growth stages and also the status of the plants. In this way, photosynthesis and nitrogen metabolism are closely linked each other.

Protein synthesis takes place at an expense of carbohydrates stored in the plants. An increase of nitrogen uptake cause a decrease of the content of sugar or starch in the straw. When the rate of ammonia absorption exceeds the rate of photosynthesis and the sugars in the straw are depleted to a critical level, asparagin is produced. This is the basis of the asparagine test for a diagnosis of the nitrogen status of the rice plant.[1]

In practical rice production, rice plants always compose a population. Under such conditions, the correlation between the total dry matter production and the grain yield is not always high.[2]

In general, an application of nitrogen causes an increase of the straw weight more than that of the grain weight, and results in a decrease of the grain-straw ratio. The degree of the decrease in the ratio is different among varieties, and under different environmental conditions. An active vegetative growth at early growth stage due to varietal characters, nitrogen application, high temperature, etc. tends to result in a decrease of the dry matter production at later growth stages, and a decrease in the grain-straw ratio.

There is varietal difference in nitrogen response.[3][4][5] The difference had been claimed to be due to varietal differences in the rate of protein synthesis : Varieties which are more active in protein synthesis are the ones which respond to nitrogen better. However, this statement is invalid, because the varietal character in the rate of protein synthesies is not a character which is directly controlled by genes. At early growth stages, there is a close correlation between the growth rate and the rate of protein synthesis. There are

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evidences, however, that the growth rate is directly controlled by genes, and the rate of protein synthesis is the result of the growth rate.[6]

At later growth stages the rate of protein synthesis of the plants in a population is the result of the rate of photosynthesis which is influenced by the degree of mutual shading. Even low-nitrogen-response varietcis respond to nitrogen well, if these are grown under such conditions as there is only limited mutual shading and active photosynthesis can take place ; for example individual plants are planted isolatedly with sufficient solar energy.[2]

The grain yield of the rice plant is controlled by two factors, i.e. "yield container" and "yield content."

The yield container can be expressed as the number of panicles per field area x the number of spikelets per panicle x the size of hulls. These three factors are generally positively correlated with the amount of nitrogen absorbed by the plants at various stages of growth.[7][8] The panicle number is determined by the tiller number which is determined during the tillering stage and by the effective tiller percentage which is decided after the maximum tiller number stage. The spikelet number per panicle and the size of hulls are determined during the period of panicle development.

The yield content is mostly the product after flowering. The production is controlled by photosynthesis and respiration during ripening. Both of them are closely controlled by the status of the plant which is again influenced by the amount and the time of nitrogen absorption by the plants.

As a complete review of literatures related to the yield container and the content has recently been made by Dr. Murata, the readers may refer to his paper.[9]

The Yield Container Related to Varietal Response to Nitrogen

At rather low levels of nitrogen application, hence at rather low grain yield levels, the grain yield is positively correlated with the size of the yield container. As such conditions prevailed in the past, varietal differences in nitrogen response in these days were considered to be derived from varietal differences in the components of the yield container.

Rice varieties are loosely classified into two groups ; i.e. the panicle weight type and the panicle number type.[10] It is said that under ordinary field conditions the increment of the increase caused by nitrogen application is generally larger in the number of panicles than in the panicle size. There is a tendency that the more the panicle number of a variety, the smaller the panicle size. Moreover, there is a genetic association between the plant height and the panicle size : The larger the panicle size, the taller the plant. Thus, the panicle weight type is more prone to lodge, especially at high nitrogen levels. Due to these reasons nitrogen response of the panicle number type is higher than that of the panicle weight type.

The degree of nitrogen response has been improved during the past history of varietal improvement in Japan.[5] The improvement occurred in association with the shift of varieties from the panicle weight type to the panicle number type.

It should be borne in mind that an increase of the yield container can be accomplished by a heavy nitrogen application combined with a dense planting. However, as under such conditions lodging become more serious problems, the significance of lodging resistance is especially important. Thus, the shift of the types has been closely related to agronomic practices. The change from the panicle weight type to the panicle number type occurred in association with an increase of nitrogen level and also an increase of spacing. With lodging resistant varieties further increase in the spikelet number can be accomplished by increasing the planting density.

The breakthrough in maximizing the grain yield after having varieties of the panicle number type with small panicles is to convert these varieties to the panicle number type with larger panicles. However, the probability of success in this approach is somewhat doubtful.

When the level of nitrogen application was rather low, the studies on the yield components was very important. Breeders sought to produce varieties of the panicle number type, and agronomists also concentrated their efforts to manipulate the plants to have a best combination among the yield components. However, the present situation is different. With presently available varieties and also with the use of sufficient fertilizers it become not at all difficult to increase the size of the yield container. Thus, the studies on the yield container is loosing significance, and those on the yield content is gaining importance.

There is another factor controlling the actual size of container. Under some circumstances the sterility percentage may be high. Sterile spikelets have no facility to act as the container. The sterility percantage is generally increased with an increased nitrogen application. The growth stage when the sterility percent is decided is from about 10 days before flowering to flowering. Most of the physiological factors determining the sterility percentage are more or less common with those determining the yield content.

The Yield Content Related to Varietal Response to Nitrogen

There is a close correlation between the grain yield and the dry matter production after flowering.

When a population has a potentiality to produce the content more than the size of the container, the size of the container controls the amount of the conetnt and the grain yield. This situation is frequent at low nitrogen levels as discussed previously. In the rice plant the size of the yield container, which means the number and the size of hulls, gives mechanical limitation to the amount of the content.[8] The rate of photosynthesis decreases when the hulls have been filled up. In other words the size of the sink limits the rate of photosynthesis.

At high nitrogen levels, where the container tends to be larger than the content, the size of the yield container does not directly decide the grain yield, because the container is not necessarily filled up. The capacity to produce the content is the factor which decides the grain yield.

These facts demonstrate the importance of critical studies on the yield content, i. e. the rate and the duration of the dry matter production after flowering.

The yield content can be classified into two categories : (a) the substances stored in the straw till flowering and then translocate to the grains, and (b) the products after flowering.[11]

At low nitrogen levels the proportion of (a) to the total amount of the content is larger than at high nitrogen levels.[12] Generally speaking, a high grain yield is associated with a large proportion of (b), and when the growth duration is long the proportion of (a) tends to be larger than when it is short.[13] Due to these reasons long duration varieties are generally low nitrogen responding and short duration varieties have more chances to respond well to nitrogen.[2]

The dry matter production of a population after flowering is the function of the rates of photosynthesis and respiration of the population. Of course, these are influenced by the climatic condition during the period.

Under a given set of climatic conditions, the rate of photosynthesis is the function of the leaf area index (LAI), the potential photosynthetic rate per unit leaf area, and the light receiving coefficient.[14][15]

The LAI has an influence on the coefficient. At high nitrogen levels, the LAI tends to be large, mutual shading increases and the coefficient decreases. The lower leaves in a population with a large LAI are shaded by the upper leaves, and can not express the capacity to photosynthesize because of limited supply of solar energy to them. Moreover, the leaves which are kept under mutually shaded condition for a prolonged period, especially those leaves which have high nitrogen content, loose their capacity to photosynthesize.[16] These facts demonstrate that the degree of mutual shading is one of the critical factors for the rate of photosynthesis of a population.

The degree of mutual shading is the function of the LAI and the extinction coefficient. Varieties excessively vigorous in the vegetative growth tend to produce an excessive leaf area at high nitrogen levels, loose their capacity to produce dry matter vigorously after flowering due to severe mutual shading, and produce a low grain yield.[17]

With a given LAI the degree of mutual shading is not constant, because there are varietal differences in the extinction coefficient. The coefficient is large when the leaves are holizontally displayed. The leaves which are long and thin tend to bend and become holizontal. Thus, the mutual shading is less when leaves are short, thick and erect.[18] With these characters the problems due to mutual shading is less even if the LAI is fairly large. Due to these reasons varieties with short and erect leaves are more responsive to nitrogen than varieties with long and droopy leaves.[19]

Respiration is indispensable for the dry matter production, because the energy needed for the production is generated by respiration. Under normal conditions, with materials of 100 parts 60 parts of new materials are produced at the expense of energy which is generated by 40 parts. In this case the growth efficiency is 60%. However, if there is respiration in the organs which are not directly linked with growth, the value of the growth efficiency decreases.[20] Such type of wasteful respiration occurs in the mutually shaded lower leaves. Excessively elongated internodes at the base of culms also respire without direct contribution to the dry matter production. Moreover, these make the plants taller and more susceptible to lodging.

The balance between photosynthesis and respiration controls the dry matter production. If the balance become unfavorable before or at the time of flowering the sterility percentage increases, and if it is small during ripening the 1000 grain weight decreases. At any rate, with a large balance between photosynthesis and respiration during the period between about 10 days before flowering to maturity a high grain yield is possible provided with a container which is adequate to accept the content.

Another factor which controls the total amount of the dry matter production during ripening is the duration from flowering to maturity.[18] Varietal difference in this duration appears to be small. However, since there are some differences, there may be possibility to extend the duration with breeding efforts, though the feasibility of the efforts is not certain. Of course, if the plants become deficient in some of indispensable elements, such as nitrogen or potassium, the longevity of the leaves decreases[21] and results in a shortend duration from flowering to harvest. Thus, to keep the plants adequately supplied with these elements till maturity is important to express genetic potentiality in the duration of the ripening period.

To summarize these discussions, desirable characters for a high-nitrogen-response varieties are short duration from sowing to flowering, long duration from flowering to maturity, not excessively vigorous in the vegetative growth, adequate LAI, short clum, and short and erect leaves.

Environmental Conditions Realted to Varietal Response to Nitrogen

Photosynthesis is the function of solar radiation. The more the solar radiation, the higher the rate of photosynthesis. An abundant supply of solar energy favors the grain yield.[15]

The rate of respiration is increased by an increase of temperature. This is true not only in the respiration which is linked with the growth, but also in that which has nothing to do directly with the growth. Due to this reason, importance of the plant type prevails when the solar radiation is limited and the temperature is high.[2] The improvement of the plant type is especially important in the tropical monsoon area where the solar radiation is limited and the temperature is high. Of coures, it is also a necessary factor in any rice area. With a desirable plant type even in the tropics the growth efficiency is kept high and a reasonably high grain yield is possible with a high level of nitrogen application.

Nitrogen application causes delay in the growth duration. In cool areas, where the rice season is limited, shortness in the growth duration is one of the important factors of high-nitrogen-response varieties. With long duration verieties there are more chances to fail to mature completely till frost comes in autumn when nitrogen is applied at a high level. The same statement can be made in dry areas where the period of water supply is limited.

The rice plant become more susceptible to blast with nitrogen application. Blast resistance is a prerequisite for high-nitrogen-response varieties. Silica is considered to be important in resisting blast. With nitrogen application silica content decreases and plants become more susceptible to blast. Silica also makes the plant type better by making the leaves more erect.[22]

Weeds compete with rice. Proper weeding is a prerequisite to have good nitrogen response, because weeds become more active and more seriously compete with rice plants by nitrogen application. With no or incomplete weeding, vegetatively active rice varieties are favorable, because they are stronger in competing with weeds. However, if such varieties are planted with heavy fertilizer application and with proper weeding, they can not produce good yield due to too vigorous vegetative growth.

The competitive ability is also a important character in breeding practices. By bulk selections vegetatively vigorous varieties are favored because of their competing ability and only low-nitrogen-response varieties survive.[23]

There are also chances to have more insect damage with nitrogen application, because rice population become more crouded and insects have more places to live in and also the plants become more palatable to insects. If insect resistance can be expected, it is a desirable character for high-nitrogen-response varieties.

In conclusion high-nitrogen-responce varieties planted with heavy nitrogen application is the key to have a high rice grain yield. However, to accomplish this goal, proper managements, such as good water management, good weeding, perfect pest and disease control, etc. are the prerequisites.

Discussion

N. Murayama, Japan : You sound pessimistic about the breeding of new varieties that have large panicles in addition to such characters as high-tillering, short stature, etc. Is it impossible to breed a variety that have larger panicles with less weight of leaves or larger yield container per unit leaf area?

Answer : It is possible. However, in order to realize this combination, it is necessary to increase the content.

A. Suzuki, Japan : At what growth stage does the mutual shading give the worst influence on the yield of grain?

Answer : The mutual shading is the results of leaf expansion. Thus, it is impossible to have mutual shading at early growth stages and generally it becomes a problem after the ear-initiation stage. The mutual shading at flowering poses its adverse effect on the grain yield.

S. **Yoshida**, IRRI : Are there any data from the field experiment that increased application of nitrogen increases percentage of unfilled grains before lodging ?

Answer : There are such data at least in temperate area. In the tropics such data are not many. One of the possible reasons for it in the tropics is that, instead of increasing sterile spiklet number, degenerated spikelet number increases.

S. **Tsunoda**, Japan : You mentioned the optimum LAI is different among varieties. Let me know the actual values of optimum LAI for IR 8 and for Peta under normal climatic conditions in the rice growing season in Philippines.

Answer : For Peta it is 4-5 and for IR 8 there seems to be no optimum LAI.

S. **Matsushima**, Japan : Which is more important character, lodging resistance or plant type for the variety of high fertilizer response ?

Answer : Both characters are important and also it is somewhat difficult to differentiate these characters. With bad plant type, the base of the culms are shaded the plants tend to elongate, and become susceptible to lodging.

S. **K. De Datta**, IRRI : (1) The association between the plant height and panicle weight you indicated — should not be the association between the plant height and panicle length ? Generally longer panicls are also heavier, am I correct ?

(2) Should not your correlation value in Fig. 1 be increased if you take the dry-matter increased following panicle initiation than after flowgring and the grain yield ?

Answer : (1) You may be correct. Anyway there are associations and there is no easy physiological explanation to it.

(2) It depends upon the situation. However, the point which I wanted to make clear is majority of the starch in the grain is photosynthetic products after flowering.

M. W. Thenabadu, Ceylon : Is asparagine production always an indication of adequate or excess nitrogen in plants ? Will asparagine be produced under conditions of nutrition also ?

Answer : Asparagine test is used to diagnose the rice plants in the field whether nitrogen top-dressing is necessary or not. I do not know if asparagine exists in the plants when these are deficient or excess in nutrients other than nitrogen. However, under ordinary field conditions the test is good enough for the diagnosis.

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