Physiological Study on the Ripening of Rice

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The ripening process of rice should be properly investigated dividing it into two developmental stages; that is, one from young panicle formation to heading and flowering, and the other from fertilization to grain maturation.

The former, including flower bud differentiation which is an important and interesting physiological problem of plant, is a very significant period from the viewpoint of productivity where the number of spikelet of one panicle, the size of spikelet and its soundness are determined. But generally only the latter is regarded as the ripening stage of rice in a narrow sense.

Translocation and accumulation of substances into grain

One of the essential and characteristic phenomena of the ripening stage of rice is the translocation and accumulation of substances in plant body. This is a process to transport and accumulate the substances, which had been absorbed and assimilated by plant, into grain in a very short period; therefore, its complicated mechanism is a very important problem to clarify.

As the results of the investigation used several radioisotopes as tracers on the movement of the inorganic substances undesirable substances, absorbed by crop plant, and assimilation products, the author and his colleagues have emphasized and established the importance of plant morphology, nutrition and metabolism in plant body, and environmental conditions on these processes.

In the present article the author would like to summarize some of the results of the investigations at the ripening stage of rice.

1) Translocation and distribution of phosphosynthetic products into panicle

The most important constituent of rice grain as a food is starch, and the carbon of which derives from the sugars assimilated by the photosynthesis in leaves. Asada found that 5 per cent of the assimilation products of the flag leaf, which was exposed to ${}^{14}CO_2$ gas, translocated into grains at the end of three hours, and 15 per cent of that translocated into grains after five hours.

Morooka found that the panicle immediately after heading possesses the ability of carbon dioxide assimilation of which assimilated products contribute to grain formation. Contribution of the assimilation by panicle to the carbon in grains was estimated to be about 5 per cent.

The assimilation products of a flag leaf moves to descend along a leaf sheath and turn to upward at a node to ascend to a panicle. Asada et al. manifested that the distribution of assimilation products in a panicle depends on the mutual positions of leaves and panicles on the stem.

It is proved that the assimilation products are translocated almost in the form of sucrose. The site of biosynthesis of sucrose is thought to be at the step where assimilation products are moved from mesophyll to leaf vein. But the mechanism of the translocation of the assimilation products still remained obscure.

2) Translocation of the inorganic substances absorbed by plant at each growing stage and its accumulation into grain

At the ripening stage of rice the yellowing of leaves begins to develop gradually from the lower part of plant to upward. Several inorganic substances which had been absorbed into the leaves start to translocate from these yellow leaves into grains. And the substances absorbed by the root at this stage also transport into grains directly. Especially as to phosphorus, more than 80 per cent of the whole contents of the plant are accumulated in grains.

Asada et al. investigated the absorption time of the phosphorus accumulated in grains and on the difference of phosphorus effect on grain formation owing to the difference of absorption time. Their results showed that from 60 to 80 per cent of the phosphorus absorbed even during tillering and flowering stages are accumulated in grains in the same rate at the other stage.

On the other hand, Doi and Sakaguchi reported that calcium and strontium were scarcely translocated from the absorbed position in the plant except those of absorbed around heading stage which were accumulated in abundance in grains. Thus the movements of elements in the plant are different by their specificities, especially the movement of phosphorus is in striking contrast with that of calcium; that is, the movement of the former is closely related to the metabolism of plant but that of the latter is rather confined by environmental conditions.

The lower leaves, which are the main organs of nutrition supply, are needed to die withering normally at the ripening stage of rice. In this case, if magnesium is deficient in the plant, the translocation of phosphorus would be restrained causing the abnormal withering of lower leaves resulting in low production of grain.

Thus, the physiology of ripening must be considered not only with the grain formation but also with the whole living phenomena (especially on nutrition) and the growing behavior of the plant.

Biosynthesis and histological development in grain

1) Biosynthesis of starch

Many precious studies on starch as the most important staple food for human being have been conducted up to now. But the oldest and most intimate problem for human life, that is, the mechanism of starch formation in grain, is still unsolved.

We have had an interest in the biochemical relation between the phosphorus metabolism in grain which shall be described later and the starch formation in grain, and have performed some experiments on this problem but details shall be skipped from description here because of space limitation.

2) Biosynthesis of phytin

A large amount of phosphorus accumulates in the grain of rice at the ripening stage. This is a peculiar phenomenon which cannot be found in the other parts of plant. The study on the phosphorus metabolism under such condition must be very interesting.

As to the change of the amount of phosphorus compounds in grain at the ripening stage, acid insoluble phosphorus is generally formed at the early ripening stage and no change of its amount was caused by phosphorus nutrition.

The existence of phytin, myo-inositol hexaphosphate, in plant has been recognized from of old, but its biosynthetic pathway and physiological function still remain obscure.

Asada and Tanaka studied the problem since 1959, and disclosed several points as follow; as the results of the trace of labelled inorganic phosphate or glucose-1-phosphate which was administered to the grain at the ripening stage, it was recognized that these phosphorus compounds form, at first, a pool of inorganic phosphorus and phosphorus esters which could exchange with each other, then they were taken up into acid insoluble phosphorus and phytin which did not change further.

On the other hand, it was also proved that inositol is biosynthesized from sucrose and glucose in grain, and that more than 80 per cent of which are transformed into phytin at the ripening stage. Myo-inositol monophosphate exists also in ripening rice grain. This resulted from the phosphorylation of just one esterification at C_2 hydroxyl groups of myoinositol.

From the results on the incorporation experiments of ³²P inorganic phosphate, ³H-myoinositol or ¹⁴C-myo-inositol which was fed to the grain or rice or of wheat at their ripening stage, it was found that among possible myoinositol phosphates only myo-inositol monophosphate and phytic acid incorporated these radioactive substances.

Thus, it was substantiated that the phosphorylation of myo-inositol does not proceed in free state but it is performed by the effect of some unknown intermediate. Therefore, we must consider more complicated mechanism than that presumed at first.

Tanaka and Yoshida have recently investigated the distribution of P, K and Mg in the matured grain of rice by electron microprobe X-ray analysis and have revealed that these elements are found almost in the aleurone layer of the grains (Fig. 1), and also they manifested, by the microautoradiography with ³H-myo-inositol that myo-inositol is concentrated in aleurone particles (Fig. 2).

Furthermore, they have concluded that phytic acid exists in the aleurone particles as the salt of K and Mg according to the result described above and the chemical analysis of the isolated aleurone particles. For this study, they established the procedure of the isolation of intact aleurone particles from the grains.

They also have indicated the catalylic action of the isolated aleurone particles on the phosphorylation of myo-inositol.



endosperm aleurone layer pericarp

Fig. 1. Distribution of P and Mg in the cross section of rice grain examined by the electron microprobe X-ray analysis : Scanning line



Fig. 2. The radio-autogram of aleuron-cell from the rice grain labelled with ³H-myoinositol at the ripening stage

From these results, it is considered that the phytic acid is biosynthesized through the phosphorylation of myo-inositol which is performed by the catalytic action of the aleurone particles in the grain or rice at the ripening stage, and is accumulated in this particle as the salt of K and Mg. It is presumed that the aleurone particles have an important function not only on the phosphorus metabolism at the ripening stage but also on the phosphorus metabolism accompanied with germination because K and Mg, which are the important necessary elements for phosphorus metabolism coexist with phytic acid in the aleurone particles. Some interesting experimental results which can support this presumption have really being obtained.

Thus, as the accumulation of substances in

the grain at the ripening stage can be also regarded as the formation of tissue in the grain, this may not be a more accumulation of substances but may be a preparatory process for the birth of the new life of next generation. Indeed, this an interesting problem.

Therefore, the understanding of the physiological phenomena of ripening must be more deepened by the comprehension of germination physiology and the limitless beauty of nature could be, then appreciated more and more.