Studies on Varietal Differences in Productivity and Related Characters between *japonica* and *indica* Rices and Their Genetic Behaviors

I. Plant characters related to varietal differences in productivity between *japonica* and *indica* varieties of rice plant

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Introduction

Since Kato¹⁴⁾ and his coworkers^{12,13)} classified the cultivated varieties of rice into two sub species i.e., *indica* and *japonica*, many workers came later to elaborate this concept or to widen it by characterizing the various properties of these groups.

Among the widely recognized characteristics of these two groups is the fact that *indica* varieties are low yielders as compared with *japonicas*. Grist⁹⁾ reported that the average yield of rice in countries where *japonica* varieties are grown is higher than that of countries growing *indica* varieties. The same was reported by Tanaka et al³³⁾, Nagai²⁸⁾, Yamada⁵⁰⁾ and Ghose et al⁸⁾.

In spite of this, the people in the regions cultivating *indica* varieties prefer this type of rices and their eating habit has been developed in favour of its typical qualities i.e. long and non-sticky grains which are in contrast to the short, round and mostly sticky grains of *japonica* type. The problem of low productivity in these regions, thus, cannot be solved by merely introducing high yielding *japonica* varieties, and any effort to improve rice condition and raise its productivity should be accompanied by the maintenance of quality characters of *indica* rices i.e. long and non-sticky grains.

To start a comprehensive project for the improvement of *indica* varieties through the hybridization between and *indica japonica* types, we

must first of all determine the plant characters contributing to higher productivity of *japonica* than *indica* varieties and then we initiate a breeding program with the objective to combine quality characters of *indica* with high yield-determining characters and other good agronomic characters of *japonica*.

With this idea in mind the author conducted a series of experiments. In the first he investigated the plant characters relating to yield in both *japonica* and *indica* varieties. Then he attempted to clarify and determine which of these characters were contributing to the varietal differences in yielding capacity between them.

One approach to yield analysis in cereal crops is that of Ball³⁾ and Engledow and Wadhan^{5,6,7)} which was developed by Matsushima¹⁹⁾. It is comprised of measuring the morphological characters as "yield determinants" such as number of plants per unit area, number of tillers per plant, number of ears per plant, number of grains per ear and weight per grain.

This technique, however, did not succeed in defining easily measured yield controlling characters that the cereal breeder can use as a basis for selection. The reason, as Watson⁴⁵⁾ pointed out, is that the different yield attributes are not independent expressions of growth. Some of them are inversely correlated. Circumstances that increase one tend to decrease another. Consequently, selection for one attribute, for example, ear number per plant, may involve counterselection for another such as number of

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grains per ear or grain size with little or no improvement in yield.

Moreover, the analysis of yield into components has the disadvantage of being static in nature. It gives only the pattern at the end and cannot say anything about the pathways by which the final pattern was reached. Without information on these pathways it becomes very difficult to interpret such quantities as genetic correlation coefficients, since the same final figure can arise from any of several distinct physiological causes. The other approach to yield analysis, therefore, should be more "substantial" than the above mentioned one which is more or less morphological in nature.

The yield (grains in case of rice plant) constitutes a part of the dry matter produced by the plant. Hence its magnitude is determined by the amount of dry matter produced by the plant and its distribution to the harvested part. Therefore, we should analyze the varietal differences in yielding capacity by investigating the characters related to dry matter production and distribution.

Watson and his coworkers^{46,47,48)} used the so-called "growth analysis" technique in their analysis of varietal differences in productivity of barley and wheat. Similar investigations were made by Lupton¹⁶⁾ on wheat. Their method of investigation consisted of analyzing the dry matter production in terms of leaf area and net assimilation rate (NAR). Formerly, it was thought that the leaf area and NAR were independent of each other¹⁰⁾. Afterward, however, it has been proved by Watson⁴⁶⁾ that, due to mutual shading of leaves, NAR is dependent on leaf area per unit area of land, that is, leaf area index (LAI).

Furthermore, the "net assimilation rate" has a very complex nature. As pointed out by Watson⁴⁵⁾ it does not correspond to a single physiological function. This growth attribute relates not only to photosynthetic efficiency of leaves, but also respiratory activity of leaves

and other parts of plant. It depends also on the proportional amount of leaves and other parts. Such complexity makes it too difficult to study the genetic behavior of this character. Therefore the use of growth analysis technique is not suitable to determine plant characters which contribute to varietal differences in grain production for the purpose of using them in a breeding program designed to improve the productivity of cereal crops.

Since the dry matter accumulated by the plant is determined by the difference of its photosynthesis and respiration, it appears more suitable, simple and practicable to analyze the dry matter production by directly measuring photosynthesis and respiration.

Several Japanese workers investigated the varietal differences in productivity among *japonica* varieties^{11,21,26,31,40-44)}. All of them placed more emphasis on the importance of the characters related to the utilization of light such as spacial arrangement of leaves, inclination of leaves etc.. The author, however, limited his investigation to the intrinsic characters related to productivity because he thought the characters related to the utilization of light are not of primary importance to the difference in productivity between *japonica* and *indica* varieties.

Keeping such objective in mind, the author conducted two pot experiments in which a number of varieties from *indica* and *japonica* types of rice were compared by studying the characters related to dry matter production during ripening period such as photosynthetic system, its efficiency, respiration etc... in an attempt to determine which of these characters are responsible for the higher yield in *japonica* than *indica* varieties.

MATERIALS AND METHODS

Two pot experiments were conducted in 1962 (experiment I) and in 1963 (experiment II), on a site in the experimental field of the University of Tokyo.

Varieties

Experiment I involved six varieties of rice plant two from *japonica* and four from *indica*. Their names, characteristics and symbols are given in Table 1. Experiment II also involved six varieties of rice plant three from *japonica* and three from *indica* groups. Their names, characteristics and symbols are listed in Table 2.

Method of culture

In experiment I, Wagner pots (1/2000 a) were used, each containing a rich, well pulverized soil. Each of them was supplied with equal amount of fertilizer, i.e. 5.0 g Ammonium sulphate, 12.0 g Super phosphate and 3.0 g Potassium chloride. In all, 96 pots were prepared i.e. 16 pots for each variety.

Seeds were sown in nursery bed on May 23, and seedlings were transplanted in the pots on June 27.

Two hills per pot with two seedlings per hill were maintained.

In experiment II, seeds were sown in nursery bed on May 15, and seedlings were transplanted into Wagner pots on June 25. Pot preparation was done in the same manner described for experiment I.

Sampling occasions

In experiment I, sampling was made after heading on four occasions with fortnightly intervals (see Table 3).

In experiment II, sampling was made on four occasions one of them was about 2 weeks before heading and the remaining three were made at heading and, 2 and 5 weeks after heading res-

pectively as shown in Table 4.

Procedure of various measurements

1) Dry weight

In experiment I, three pots were sampled for dry weight measurements at every sampling occasion. The plants were washed as free from soil as possible, then separated into their components, root, green leaf blade, withered leaf blade, leaf sheath + stem and panicle, on the day they were sampled and immediately dried in an electric oven maintained at a temperature of 65°C.

After drying the dry weight of each part was obtained.

Various ratios such as leaf blade/leaf sheath + stem ratio (LB/LS ratio) and top/root ratio (T/R ratio) were calculated from the dry weight data.

In experiment II, dry weight measurements were made at every sampling occasion in a similar manner to experiment I.

2) Starch determination

In experiment I, for starch analysis, dried samples of leaf sheath + stem obtained at heading were pulverized by milling machine and a part of them was boiled with water for an hour. After that an aliquot of the supernatant was analysed by iodine method.

In experiment II, starch determination was made by using photometric method as described by Nielsen²⁴⁾ and, Nielsen and Gleson²⁵⁾.

3) Leaf measurements

In experiment I, the amount of leaves produced up to headings was estimated by summing up the dry weight of green and withered leaf

Table 1. Variety names, characteristics and symbols (Experiment I)

Subspecies Variety	Characteristics		Symbol
	Maturity	Plant Type	
<i>Japonica</i> : Norin 17	Early	Panicle Type	N 17
Norin 29	Medium Late	Medium Type	N 29
<i>Indica</i> : Kaladumai	Medium Early	Tillering Type	Ka
Kumari	Medium	Panicle Type	Ku
Dular	Early	Medium Type	Du
Dalashaita	Medium	Panicle Type	Da

Table 2. Variety names, characteristics and symbols (Experiment II)

Subspecies variety	Characteristics		Symbol
	Maturity	Plant Type	
<i>Japonica</i> : Norin 17	Early	Panicle Type	N 17
Gimmasari	Medium Early	Panicle Type	G
Norin 29	Medium Late	Medium Type	N 29
<i>Indica</i> : Pusur	Medium	Tillering Type	P
Dular	Early	Medium Type	Du
Kumari	Late	Panicle Type	Ku

Table 3 Heading and sampling dates in Experiment I

Variety	Heading Date	Sampling Date			
		1	2	3	4
N17	25 Aug.	29 Aug.	12 Sep.	26 Sep.	10 Oct.
N29	4 Sep.	8 Sep.	22 Sep.	6 Oct.	17 Oct.
Ka	28 Aug.	1 Sep.	13 Sep.	27 Sep.	11 Oct.
Ku	30 Aug.	3 Sep.	17 Sep.	1 Oct.	15 Oct.
Du	25 Aug.	29 Aug.	12 Sep.	26 Sep.	11 Oct.
Da	31 Aug.	4 Sep.	19 Sep.	2 Oct.	15 Oct.

Table 4. Heading and Sampling Dates in Experiment II

Variety	Heading Date	Sampling Date			
		1	2	3	4
N17	28 Aug.	15 Aug.	1 Sep.	15 Sep.	6 Oct.
G	31 Aug.	◇	4 Sep.	18 Sep.	9 Oct.
N29	5 Sep.	◇	9 Sep.	23 Sep.	14 Oct.
P	3 Sep.	◇	6 Sep.	20 Sep.	11 Oct.
Du	29 Aug.	◇	2 Sep.	16 Sep.	7 Oct.
Ku	10 Sep.	◇	13 Sep.	27 Sep.	18 Sep.

blades at the first sampling.

Degree of senescence was calculated as follows:

$$\frac{\text{Dry weight of withered leaf blade at sampling 3}}{\text{Dry weight of leaf blade produced up to heading}} \times 100$$

Leaf area estimation was followed by taking random samples of leaves from each plot, their area measured by printing on paper, cutting out print and weighing it. The total leaf weight was calculated from the dry weight ratio of total to sample leaves. When leaves began to yellow only the green fractions were measured.

In experiment II, leaf measurements have been carried out in the same way as in experiment I.

4) Photosynthesis and respiration

In experiment I, one pot from each variety

was used for the measurement of photosynthesis and respiration at every sampling occasion. Since the leaves of *indica* varieties withered completely at the last sampling occasion, the measurement of photosynthesis and respiration for these varieties was excluded. The apparatus used for measurement of photosynthesis and respiration consisted of plant chamber, blower, flow meter and a negative filter type infrared CO₂ analyzer, the operation principles of which have been described by Togari et al³²⁾. The pot was set in the assimilation chamber under isolated condition and the rate of apparent photosynthesis of the plant was measured from the absorption of CO₂ by the plant under light saturation condition. Rates of the respiration in

the light were estimated by correcting respiration measured in darkened chamber, assuming $Q_{10}=1.8$. These were added to apparent photosynthesis to give estimates of true photosynthesis. Since this value represents the full photosynthetic capacity possessed by the plant, we prefer to call it the "photosynthetic capacity".

Dividing the photosynthetic capacity by leaf area, the amount of photosynthesis per unit leaf area is obtained. It has been shown by Matsu-shima¹⁹⁾ that the photosynthetic activity of the parts other than leaf blade is very low compared with that of the leaf blade itself. Therefore the quotient obtained represents the mean of photosynthetic efficiency of the whole leaves, so, the author named it as "photosynthetic efficiency",

After the measurement of photosynthesis the respiration rate was measured on the same pot immediately from CO_2 out-put in darkened chamber. To make respiration rate comparable to each other, the values corrected into a respiration rate under the standard temperature of $30^\circ C$, assuming $Q_{10}=1.8$ and named "respiratory capacity". "Respiratory activity" was calculated by dividing the "respiratory capacity" by the dry weight of the living tissues (total dry weight of the plant minus dry weight of withered leaves).

In experiment II, two pots from each variety were used for the measurement of photosynthesis and respiration. The measurements were made in the same way and on the same principles of experiment I.

5) Measurement of 1000 grain weight

In experiment I, random samples of grains from each variety were taken for the four sampling occasions, dried in an electric oven, weighed, counted and their 1000 grain weight was calculated. In experiment II, the measurement was made in the same way.

RESULTS

Pattern of dry matter production and its distribution to various parts of plant

1) Total dry weight

The main feature of total dry weight change after heading are presented in Fig. 1. In experiment I, total dry weight increased in all varieties, but the rate of increment declined with the advancement of plant age. There was no consistent varietal differences in the time trend of dry matter accumulation but one of *indica* varieties Dalashaita decreased sharply in dry weight at the final stage of ripening period due to grain shattering (see Fig. 1A).

In experiment II, total dry weight in pre-heading stage increased almost on the same rate for both *indica* and *japonica* varieties, but after heading *indica* varieties increased very little while the increment was remarkable for *japonica*. In this experiment the variety Pusur decreased in dry weight at the final harvest because of the loss of withered leaves and grain shattering (See Fig. 1B).

The total dry weight at heading represents the amount of dry matter produced by each variety during the pre-heading stage. In experiment I (Fig. 2A), it is evident that *japonica* varieties produced more dry matter up to heading than *indicas*. It was clear from Table 3 that the heading date was not the same in all varieties, which implies that there were varietal differences in the duration of dry matter accumulation, yet the earliest variety Norin 17 and the latest one Norin 19 both from *japonica* type, accumulated the greatest amount of dry matter. Thus we may conclude that in pre-heading stage the productivity of *japonica* is higher than *indica*.

The results of experiment II is in full agreement with that of experiment I (Fig. 2B).

The amounts of dry matter produced during ripening period are presented in Fig. 3. In experiment I (Fig. 3A), it is evident that dry matter production during this period was higher in *japonica* varieties.

This tendency was more clear in experiment II (Fig. 3B), However variety Pusur from *indica* group has negative value as a result of withered leaf loss and grain shattering. Thus it

is clear that *japonica* varieties are more capable to accumulate great amount of dry matter especially in post heading stage.

2) Changes in dry weight of each organ during ripening period.

Time trend of dry weight of each organ is given separately in Fig. 4.

i) Panicle (Fig. 4-1)

In experiment I (Fig. 4-1A), the dry weight of panicles increased rapidly then the increment slowed down as the plants approached maturity but *indica* varieties were slower than *japonica*. Weight of panicles was greater for *japonica* group especially at the later stage of ripening period.

In experiment II (Fig. 4-1B), *japonica* varie-

ties surpassed *indicas* in panicle dry weight and the rate of dry weight increment was sharper.

ii) Leaf blade (Fig. 4-2)

In experiment I (Fig. 4-2A), the weight of total leaf blade decreased gradually with no detectable differences between the two groups. Weight of green leaf blade however, declined rapidly in both *indica* and *japonica* varieties due to senescence with the latter having a greater amount of green leaves particularly at the end of experiment. As to the dry weight of withered leaf blade there was a remarkable increase in the two groups with *indica* having greater weight than *japonica*.

The same tendency was obtained in experiment

Fig. 1 Changes in total dry weight.
Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

Fig. 2. Weight of dry matter produced up to heading.

Note: For symbols see Tables 1 and 2.

Fig. 3. Weight of dry matter produced in ripening period.

Note: For symbols see Table 1 and 2.

II as it is clear from Fig. 4-2B.

iii) Leaf sheath and stem (Fig. 4-3)

In experiment I (Fig. 4-3A), the dry weight of leaf sheath and stem decreased soon after heading, thereafter remained almost constant up to maturity. The degree of depression in dry weight of leaf sheath and stem was considerably higher for *japoica* than *indica*. *Japonica* varieties always had a greater leaf sheath and stem weight than *indica* ones. In experiment II (Fig. 4-3B), almost the same tendency was shown with the exception of variety Gimmasari from *japonica* which had increased in weight after heading then decreased. Thus we may conclude that the dry weight of leaf sheath and stem at the time of heading is greater for *japonica* than that of *indica*

Fig. 4-1. Changes in dry weight of panicle during ripening period.

Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

varieties and the fall in dry weight of leaf sheath and stem after heading is more for *japoica* than *indica* varieties.

iv) Root (Fig. 4-4)

In experiment I (Fig. 4-4A), the dry weight of roots decreased progressively after heading with the advancement of plant age. The degree of depression in dry weight of root was evidently less in *japonica* varieties.

In experiment II (Fig. 4-4B), the dry weight of roots also decreased after heading for all varieties.

3) Panicle yield (Fig. 5)

In experiment I, a part of the grains was lost by shattering at the end of the experiment. Therefore data of sampling 3 was taken for the comparison of the yield of all varieties. Fig. 5A shows that *japonica* varieties had markedly greater panicle yield than *indica*.

These differences between the two groups were strikingly exhibited in the results of experiment II (Fig. 5B).

4) Proportional dry weights of various parts of the plant

i) LB/LS ratio (Fig. 6)

In experiment I, the dry weight of leaf sheath + stem at heading stage was greater for *japonica* than *indica* groups while dry weight of leaf blade was nearly identical for both of them. Therefore the ratio of leaf blade

Fig. 4-2. Changes in dry weight of leaf blade during ripening period.

Fig. 4-3. Changes in dry weight of leaf sheath + stem during ripening period.

Fig. 4-4. Changes in dry weight of root during ripening period.

weight to leaf sheath + stem weight, that is LB/LS ratio, was lower in *japonica* varieties (Fig. 6A).

The results of experiment II (Fig. 6B) were in coincidence with that of experiment I.

ii) T/R ratio (Fig. 7)

Fig. 5. Panicle yield

Note: For symbols see Tables 1 and 2.

In experiment I, the weight of root at the time of heading was slightly less for *japonica* but the weight of top was greater in this group.

This brought the top/root ratio (T/R ratio) to a higher value for *japonica* (Fig. 7A).

In experiment II (Fig. 7B), a similar tendency was observed with the exception of Kumari variety from *indica*, where the greater top weight and relatively small root weight made it the highest in T/P ratio among the two groups.

iii) P/S ratio (Fig. 8)

In experiment I, the ratio of panicle weight to straw weight (P/S ratio) at sampling 3 was higher for *japonica* than *indica* (Fig. 8A). The difference in P/S ratio in experiment II was more remarkable (Fig. 8B). These data support the

Note: Leaf blade, Leaf sheath, LB/LS ratio.

Fig. 6. LB/LS ratio at heading.

For symbols see Tables 1 and 2.

conclusions obtained by Matsuo¹⁷⁾ and Tanaka et al¹³⁾.

5) Amount of reserve starch in leaf sheath + stem at the time of heading.

In both experiments (Fig. 9) the amount of starch stored in leaf sheath and stem was considerably greater in *japonica* than in *indica* varieties which implies that *japonica* varieties tend to accumulate more reserve carbohydrate during pre-heading stage than *indicas*.

photosynthetic system

1) Amount of leaf blade produced up to heading

As we have seen in the previous section, *japonica* and *indica* in both experiments produced almost equal amounts of leaf blade in pre-heading stage (Fig. 6).

2) Leaf area and leaf senescence

In both experiments, the leaf area declined in

all varieties with the advancement of growth after heading because of leaf senescence. However, the rate of reduction in leaf area was proportional to the degree of senescence, therefore the reduction was more remarkable in *indica* varieties than in *japonicas*, because of the high degree of senescence in the former as shown in Fig. 10 and 11.

In order to make the leaf area of all varieties comparable more easily, the means of leaf area of the first three samplings after heading are given in Fig. 12. Here we find more clearly that the leaf area during the ripening period was greater for *japonica* than *indica* varieties.

Photosynthetic capacity and efficiency

1) Changes in photosynthetic capacity during ripening period

In experiment I, the photosynthetic capacity of the plants after heading declined with the

Fig. 7. T/R ratio at heading. For symbols see Tables 1 and 2.

Fig. 8. P/S ratio at Sampling 3 (A) and 4 (B). For symbols see Tables 1 and 2.

Fig. 9. Starch content in leaf sheath + stem at heading.

Note: For symbols see Tables 1 and 2.

Fig. 10. Leaf production and degree of senescence.

advance of age in all varieties (Fig. 13A), as already observed by Togari et al³⁶⁾ with *japonica* varieties. *Japonica* plants continued their photosynthetic activity up to sampling 4, while *indicas* ceased photosynthesizing after sampling 3. At heading, there were no detectable differences between varieties of the two groups, but later on, *japonica* varieties had a higher photosynthetic capacity than that of *indicas*.

In experiment II, (Fig. 13B), time trend of photosynthetic capacity was more distinct and clear. The photosynthetic capacity, from heading through maturity was higher for *japonica* group.

Fig. 11. Changes in leaf area during ripening period.

Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

It is evident from Fig. 13B, that in *indica* varieties the photosynthetic capacity attained its maximum value earlier than in *japonica* varieties. But, the photosynthetic capacity of *indica* varieties declined more rapidly than that of *japonica* varieties.

To make the photosynthetic capacity of different varieties more easily comparable, the means of the three samplings after heading were calculated and illustrated in Fig. 14. This chart shows that in both experiments, *japonica* varieties were superior in photosynthetic capacity to *indica* varieties during ripening period.

2) Changes in photosynthetic efficiency of leaf blade during ripening period

In experiment I, the photosynthetic efficiency of all varieties after heading diminished progressively as the plants advanced in age (Fig. 15A). The same was reported by Takeda³²⁾ and Murata²⁰⁾. Similar results have been obtained from experiment II (Fig. 15B). Since it was difficult from Fig. 15. to compare *indica* and

japonica varieties in photosynthetic efficiency due to the fluctuation in their curves, the means of the first three samplings were taken and represented in bargraphs in Fig. 16. The figure indicates that in experiment I, there was no detectable difference in photosynthetic efficiency between *japonica* and *indica* groups (Fig. 16A).

In experiment II, however, there was an indication that the leaves of *japonica* varieties were slightly more efficient in photosynthesis than that of *indica* varieties (Fig. 16B).

Respiratory capacity and activity

1) Changes in respiratory capacity during ripening period

In experiment 1, the respiratory capacity of plants, after panicle emergence, generally decreased steadily for all varieties (Fig. 17A).

This was in accord with the results obtained with *japonica* varieties by Yamada et al.⁴⁸⁾, Murata²⁰⁾, Togari et al.³⁶⁾, and Takeda³²⁾. The same tendency was observed in experiment II (Fig. 17B). Time trend of respiratory capacity shows no detectable variation between *indica* and *japonica* varieties and in order to make the varieties more easily comparable the means of the first three samplings after heading were calculated and presented in Fig. 18. It is evident from Fig. 18 that in both experiments there were no appreciable differences between the varieties of *japonica* and *indica* in respiratory capacity.

2) Changes in respiratory activity during ripening period

In experiment I, the respiratory activity after heading declined with the advancement of plant

Fig. 12. Mean leaf area in ripening period. Note: A Mean of samplings 1-3. B Mean of samplings 2-4. For symbols see Tables 1 and 2.

Fig. 13. Changes in photosynthetic capacity during ripening period.

Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4

Fig. 14. Mean photosynthetic capacity in ripening period.

Note: A Mean of samplings 1-3.

B Mean of samplings 2-4.

For symbols see Tables 1 and 2.

age (Fig. 19A). Here also it was difficult to compare *indica* and *japonica* varieties due to fluctuation in the curves, therefore the means of the first 3 samplings after heading were taken and illustrated in Fig. 20A. From this figure it is clear that *indica* varieties in general, had a higher respiratory activity than *jaonicas*.

As to the results of experiment II, it is evident from both Fig. 19B and Fig. 20B, that *indica* varieties had always a higher respiratory

Fig. 15. Changes in photosynthetic efficiency during ripening period.

Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

activity than *japonica* varieties.

3) Photosynthesis to respiration ratio (P/R ratio)

P/R ratio is considered to be an index of the plant efficiency in dry matter production, because, the accumulated dry matter is the difference between the gain from photosynthesis and loss by respiration.

P/R ratio was higher for *japonica* than *indica* varieties in both experiments (Fig. 21).

Pattern of dry matter accumulation in grain

In experiment I, the 1000 grain weight continued

Fig. 16. Mean photosynthetic efficiency in ripening period.
Note: A Mean of samplings 1-3. B Mean of samplings 2-4. For symbols see Tables 1 and 2.

Fig. 18. Mean respiratory capacity in ripening period.
Note: A Mean of samplings 1-3. B Mean of samplings 2-4. For symbols see Tables 1 and 2.

to increase as the plants advanced in age up to sampling 4 in case of Norin 17 from *japonica* (Fig. 22A). The varieties Norin 29 from *japonica*, Kumari and Dular from *indica* continued to increase in their 1000 grain weight up to sampling 3, there after remained nearly constant, while that of Kaladumai and Dalashaita varieties

Fig. 17. Changes in respiratory capacity during ripening period.
Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

Fig. 19 Changes in respiratory activity during ripening period.

Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

from *indica* increased until only sampling 2, and therefrom, remained almost unchanged. *Japonica* and *indica* groups showed no marked difference in their 1000 grain weight at sampling 1 and 2, but the differences were considerable at sampling 3 and 4, with *japonica* having greater weight.

The picture was more clear in experiment II (Fig. 22B). Here *japonica* varieties continued to accumulate dry matter in their grains 5 weeks after heading (sampling 3) while that of *indica* varieties ceased to have any increment only two weeks after heading (sampling 2) with the exception of the variety Kumari in which 1000 grain weight continued to increase up to sampling

Fig. 20. Mean respiratory activity in ripening period

Note: A Mean of samplings 1-3. B Mean of sampling 2-4. For symbols see Tables 1 and 2.

3, but on slower rate. In this experiment also, there were no varietal differences in 1000 grain weight at sampling 2 and 3 but at sampling 4, *japonica* surpassed *indica* remarkably. From the foregoing results, it may be concluded that in *japonica* varieties accumulation of matter in grains continued for a longer period than that of *indica* varieties. This might be due to the maintenance of activity of matter accumulation in grain over longer period in *japonica* varieties as reported by Tsunoda⁴⁴.

DISCUSSION

In the previous sections, the varietal differences in plant characters which are considered to be related to grain production have been described. From the results obtained, we will attempt to identify those characters which are responsible for the varietal differences in yielding capacity between *japonica* and *indica* varieties.

The dry matter which enters the grains of rice plant is derived from two sources, namely, (1) the reserve carbohydrates stored in the leaf sheath and stem in pre-heading stage and translocated later to the developing grains and (2) the assimilate produced by current photosynthesis^{1,2,15,22,38,39}.

It was evident that *japonica* varieties have built up a larger storage organs in pre-heading stage compared to *indica*. Fig. 4—3 shows that at the time of heading, *japonica* had larger weight of leaf sheath + stem than *indica* varieties. Moreover the relative

Fig. 21. P/R ratio in ripening period. Note: A Mean of samplings 1-3. B Mean of samplings 2-4. For symbols see Tables 1 and 2.

size of the storage organs is also larger in *japonica* varieties as it is clear from their low LB/LS ratio (Fig. 6). There is also an evidence that *japonica* varieties have transported more reserve carbohydrates to the developing grains, such evidence is derived from Fig. 4—3 where the leaf sheath + stems of *japonica* varieties decreased in weight more than *indica*.

The results of analysis of storage organs at the time of heading also show that *japonica* varieties contain much more reserve starch than *indica* varieties (Fig. 9). Hence as far as the first source of grain filling materials is concerned *japonica* varieties are richer than *indica* varieties.

Thus we may conclude that the characteristic of *japonica* varieties to store greater amount of

Fig. 22. Changes in 1000 grain weight during ripening period. Note: For symbols and sampling occasions see Tables 1, 2, 3 and 4.

reserve carbohydrates in their leaf sheath and stem during pre-heading stage account in part for the greater yielding capacity of this group.

As to the dry matter produced during ripening period, it was greater for *japonica* than *indica* varieties (Figs. 3). The magnitude of dry matter produced by plant is determined by the relative amount of its photosynthesis and respiration as pointed out by Boysen Jensen⁴⁾. The varietal differences in plant characters relating to them during ripening period have been described with details in the former sections.

During ripening period, the photosynthetic capacity of *japonica* varieties was remarkably higher than that of *indicas*, therefore we may take it as a base for the higher dry matter productivity of *japonica* varieties. The varietal differences in photosynthetic capacity might be attributed to the differences in either the size of photosynthetic system or its efficiency. Figs. 15 and 16 show that in experiment I, the photosynthetic efficiency was nearly equal in both *japonica* and *indica* varieties and only slight differences were found in experiment II. This is in agreement with the findings of Osada²⁹⁾ in his studies on the photosynthesis of *indica* and *japonica* varieties where he found no differences between them in photosynthetic efficiency. However, leaf area was consistently and remarkably higher in *japonica* varieties than in *indica* varieties. From these results it may be concluded that the varietal differences in photosynthetic capacity were mainly caused by the larger photosynthetic system of *japonica* (see Fig. 11, 12).

As to the size of photosynthetic system during ripening period it is determined by two factors, namely, the magnitude of leaf blade produced up to heading and the degree of leaf senescence during ripening period. Fig. 10. indicated that at heading, there was no difference in leaf production between the two groups. The difference was in the degree of senescence, being lower for *japonica* than *indica* varieties (Fig. 10). Thus the higher photosynthetic capacity in *japonica*

varieties is mainly attributed to the slower senescence of their leaves in the later stage of growth.

It was also evident from Figs. 18 and 19 that no marked differences in respiratory capacity between the two groups were observed. The relative amount of respiration to photosynthesis, however, was smaller in *japonica* group, bringing its P/R ratio to a higher value than *indica* (Fig. 22). This implies that during ripening stage *japonica* varieties are more efficient in dry matter production.

The pattern of dry matter accumulation in grain was investigated and it was suggested that in *japonica* varieties the grains maintained their activity of dry matter accumulation over a longer period than *indicas*. This characteristic of *japonica* varieties may contribute to the greater accumulation of matter in their grains.

From the foregoing discussion we may conclude that the following four basic characters account for the higher yielding capacity of *japonica* over *indica* varieties.

- 1) Reserve carbohydrates: *japonica* varieties tend to accumulate greater amount of reserve carbohydrates in leaf sheath + stem in pre-heading stage.
- 2) Degree of senescence: *japonica* varieties have a slower leaf senescence during ripening period which results in greater leaf area and consequently larger photosynthetic capacity.
- 3) P/R ratio: *japonica* varieties have a higher P/R ratio which implies a higher efficiency in dry matter production.
- 4) Ripening period: *japonica* varieties have a longer ripening period which gives the grain more time to accumulate more dry matter.

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〔和 文 摘 要〕

日本稲とインド稲との間の生産力の差異とそれに関する
形質およびその遺伝関係について

第1報 日本稲とインド稲との間の生産力の差異とそれ
に関する形質について

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japonica および *indica* に属する水稻各数品種をポット栽培し、光合成・物質生産の面から両者の生産力の生理学的基礎を検討した。その結果、*japonica* 系品種の生産力の高さは、次の4つの点に基づくことを認めた。

(1) 出穂期における貯蔵炭水化物の量が多いこと：*japonica* 系の品種は、*indica* 系のそれに比べ、出穂期における稈、葉鞘中の貯蔵炭水化物の量が多い。このことは、穂への炭水化物の給源を豊富ならしめている。

(2) 稔実期における葉の老化の進行がおそいこと：*japonica* 系品種は、*indica* 系品種に比べ、稔実期における葉の老化枯死の進行がおそい。このことは、稔実期の葉面積を比較的大きく保ち、それを通じて個体の光合成能力を高く維持せしめている。

(3) 光合成・呼吸比が高いこと：稔実期において、*japonica* 系品種は、*indica* 系品種に比べ、より高い光合成/呼吸比を示す。これは、物質生産の効率を高からしめる。

(4) 稔実期間が長いこと：*japonica* 系品種は、*indica* 系品種に比べ稔実期間がより長い。したがって、それだけ多くの物質を穂に集積できる。

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