INHERITANCE MODES OF QUANTITATIVE TRAITS IN TWO RICE CROSSES[1]

—Genetical Studies on Rice Plant, XXXX.—

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Majority of the plant attributes directly related to plant growth, fertilizer response, or grain yield are believed to be so called quantitative rather than qualitative traits. Despite the relative abundance of the speculations and the analytical techniques based on the hypothetical models, the information based on actual plant data on the inheritance of these quantitative traits is rather scarce.

In previous studies, several plant attributes which have significant roles in yield and nitrogen response were pointed out (TANAKA, 1964; TANAKA and KAWANO, 1965; TANAKA *et al.* 1966; KAWANO and TANAKA, 1968 and in press). Many of these agronomically important attributes are greatly affected by the environmental condition under which the population is grown. How to separate an experimental error from the total variation or to minimize the experimental error is a key point in the genetic analysis of these attributes. If a study is made only on the comparisons between inbred lines or varieties, the proportion of variation associated with experimental error can be reduced by increasing the number of replication in each genotype. However, in an early generation of segregating population, it is impossible to have a number of replications in each genotype so that a precise comparison between genotypes on the basis of individual plant is needed. It would be required in this case that the variation due to experimental error be much smaller than that due to genotypic effect.

In an attempt to minimize the experimental error, water culture method is applied to two F_2 populations in this study. Analysis of inheritance mode in F_2 population will be made with respect to several agronomic attributes.

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1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo.

Materials and Methods

Two F_2 populations, *i.e.*, B 575 × Shen Li Sien and B 575 × Sakaemochi, and three parental varieties were prepared. B 575 is a low vegetative-vigor variety, Shen Li Sien is high in vegetative vigor with short growth duration, and Sakaemochi is a variety with very short growth duration. Each variety is distinctly different in plant type. In both F_2 populations, big variation is expected in many characters.

On May 1, 1968, fifteen-day old seedlings of F_2 plants were transplanted to 4-liter pots with four plants per pot under water culture condition in the green house, Faculty of Agriculture, Hokkaido University. Each F_2 population consisted of 204 individual plants in 51 pots. Forty seedlings each of the three parental varieties were transplanted to 10 pots each exactly in the same manner as F_2 plants.

The concentration and form of each nutritional element added in the culture solution were as follows:

N as NH_4NO_3	25 ppm
P as $NaH_2PO_4 \cdot 2H_2O$	10 ppm
K as K_2SO_4	40 ppm
Ca as $CaCl_2$	40 ppm
Mg as $MgSO_4 \cdot 7H_2O$	10 ppm
Fe as $FeCl_3 \cdot 6H_2O$	2 ppm
Mn as $MnCl_2 \cdot 4H_2O$	0.5 ppm
Si as SiO_2	a little

Ordinary tap water was used and the culture solution was renewed every week. The pH of the culture solution was adjusted at 4.6–4.8 at the time of every renewal. Two plants from each pot were sampled at 45 days after transplanting. The remaining two plants per pot were grown up to maturity. Mutual shading was negligible throughout the growing period.

Sampled plants were dried in an air-forced dry oven at 70°C for two days, weighed, ground, and analyzed for nitrogen by the micro-Kjeldahl method. Leaf on the main culm and tillers were counted every week. The number of leaf on the main culm at 6 weeks after transplanting was taken as a measurement for rate of leaf emergence at early stage of growth. Length and width of each leaf on the main culm were measured. The date on which the top tip of the panicle on the main culm appeared from the boot-leaf was recorded and regarded as heading date. Mean angle of outside tillers with the horizontal line at 8 weeks after transplanting was measured and regarded as a measurement for tiller angle.

TABLE 1. Total F_2 variance, error variance, and heritability in two F_2 populations.

Characters	F_2, B575 × S. L. S.			F_2, B575 × Sakaemochi		
	$\sigma^2_{F_2}$	σ^2_e	h^2	$\sigma^2_{F_2}$	σ^2_e	h^2
Plt. wt. at 6.5 weeks	1.339	0.113	91.95	0.798	0.104	87.07
N% of plant at 6.5 weeks	0.0245	0.0101	58.74	0.0292	0.0087	70.10
Total amt. of N in plt. at 6.5 weeks	306.9	42.4	86.19	253.9	41.8	83.52
Tiller number at 6 weeks	2.660	0.202	92.39	1.192	0.278	76.71
Rate of leaf emergence	0.1596	0.0073	95.37	0.1659	0.0109	93.43
Length of 7th leaf	14.18	2.12	85.07	11.57	2.93	74.56
Width of 7th leaf	0.01140	0.00106	90.68	0.01196	0.00129	89.24
Tiller angle at 8 weeks	41.85	3.94	90.59	14.03	3.51	72.13
Maximum tiller number	15.178	1.765	88.37	5.222	1.845	64.67
Number of days to flowering	281.13	0.73	99.74	67.76	1.78	97.37
Culm length	262.44	7.39	97.18	111.30	4.92	95.58
Length of panicle	10.543	0.336	96.81	1.381	0.288	79.15
Total no. of spikelets/plant	193715	10555	94.55	82460	7160	91.31
Number of panicle/plant	9.129	0.994	89.11	5.653	0.736	86.98
No. of spikelets/panicle	1422.5	38.2	97.31	708.6	33.5	95.27
Fertility	974.5	8.7	99.10	180.3	10.1	94.41

Because of hybrid partial-sterility, the data on grain yield seemed to have no sense. Instead, the total number of spikelets per plant, filled or unfilled, may serve as an indication of yield potential under the condition free from mutual shading. In highly sterile plants, tillering did not stop even at very late stage of growth so that the tillers which flowered more than 4 weeks later than the flowering of the main culm was disregarded from the observation. The number of spikelets per panicle was given as total number of spikelets divided by panicle number. Per cent of filled spikelets on representative two panicles was measured and regarded as a measurement for sterility. The mean of variances, each calculated in each parental variety, in each character was regarded as a measurement for error variation.

Results

1. Relative size of experimental error:

Experimental error seemed to be satisfactorily small in many characters.

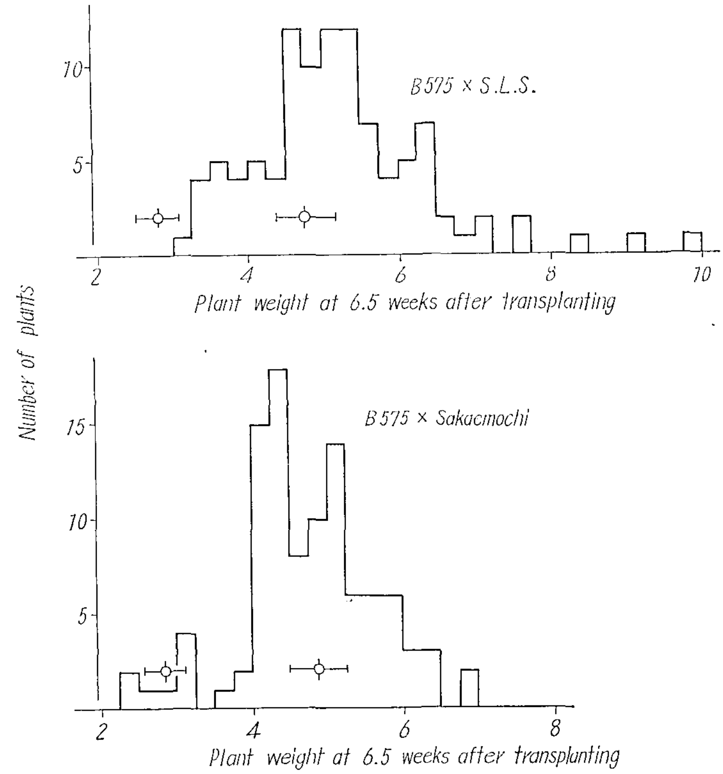

Fig. 1. F_2 distributions of plant weight at early stage of growth (cross figures indicate the parental mean with σ_e).

Heritability, simply given as (total F_2 variance—error variance)/(total F_2 variance), was higher than 90% in many characters (Table 1). It may be assumed that the phenotypic values of F_2 plants are made up almost only of genotypic effects. Thus, the genetic analysis of F_2 variation through the phenotypic values would be possible in many characters.

2. Plant weight at 6.5 weeks after transplanting (Fig. 1):

In both populations, F_2 distribution was somewhat far from normal but the variation was more or less continuous. The range of variation was greatly bigger than the parental difference. F_2 mean overwhelmingly exceeded the parental mean. In the population of B 575 × Shen Li Sien, more than half of

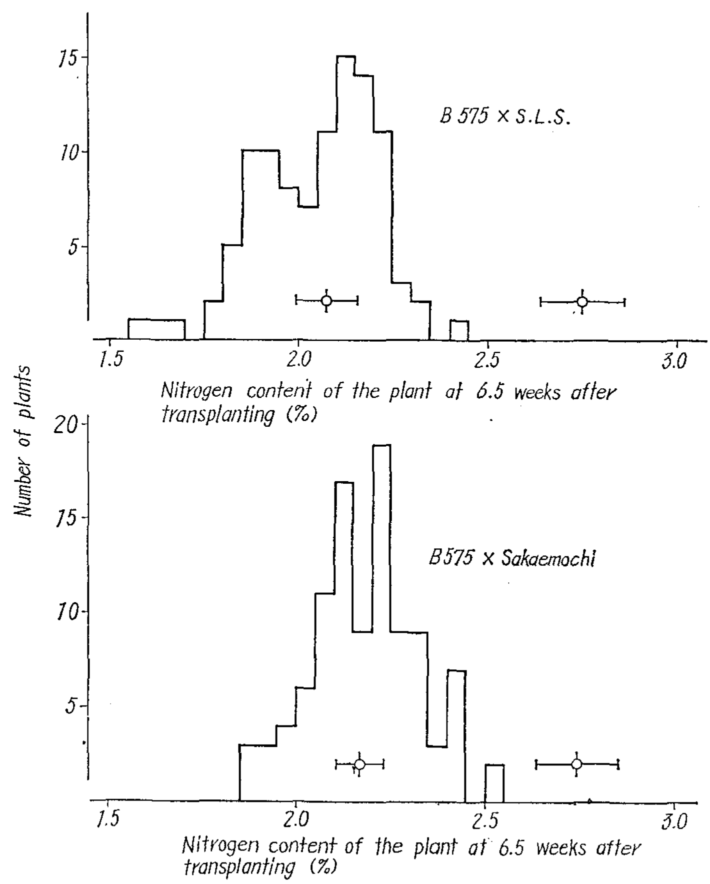

Fig. 2. F_2 distribution of nitrogen content of the plant at early stage of growth (cross figures indicate the parental mean with σ_e).

the plants exceeded the value of higher parent and not even one plant had a value lower than the value of the lower parent.

3. Nitrogen content of the plant at 6.5 weeks after transplanting (Fig. 2):

F_2 distribution was near normal and the range of variation was more or less equal to the parental difference. F_2 mean was much lower than the parental mean in both populations.

4. Total amount of nitrogen in the plant at 6.5 weeks after transplanting:

Measurement of this character is given merely as an arithmetic product between weight and nitrogen content of the plant. F_2 distribution followed more or less the same pattern as plant weight.

5. Tiller number at 6 weeks after transplanting (Fig. 3):

The mode of F_2 distribution was near normal. The range of F_2 variation was apparently wider than the parental difference in both populations. There was not big difference between F_2 means and the parental means.

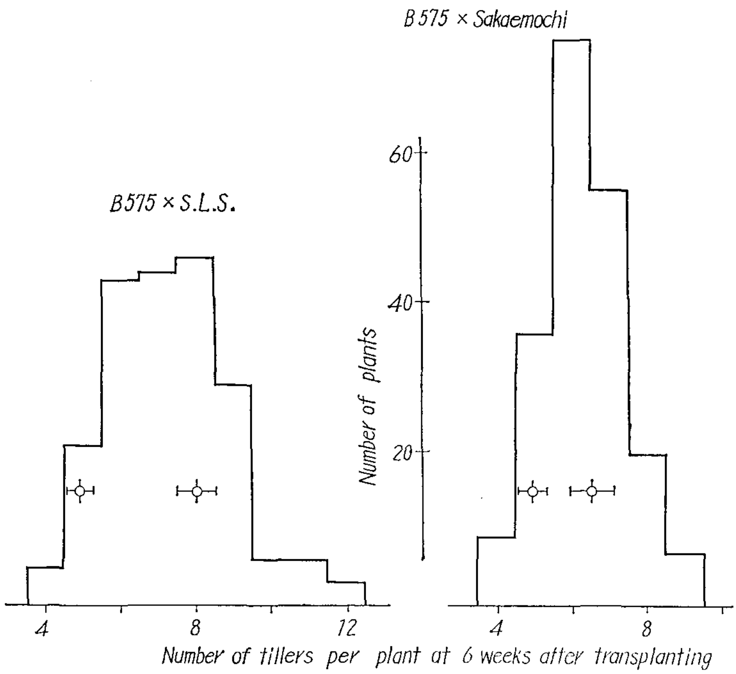

Fig. 3. F_2 distributions of tiller number at early stage of growth. (cross figures indicate the parental mean with σ_e).

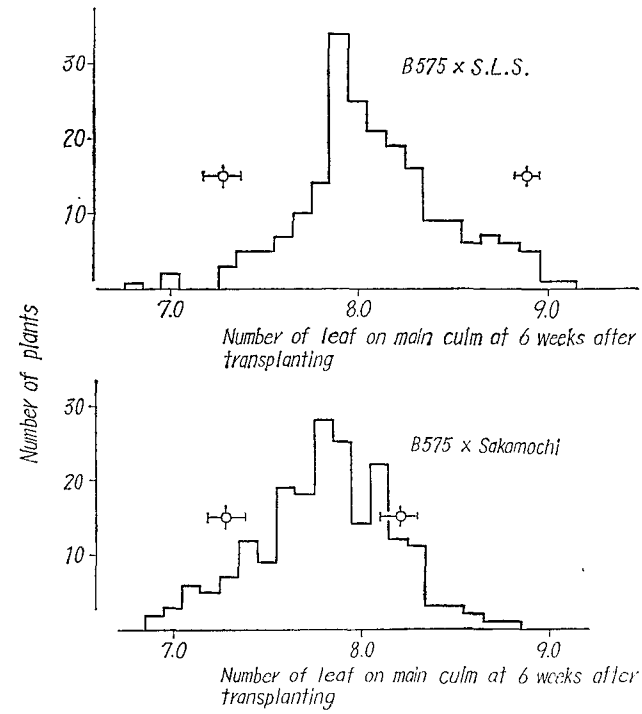

Fig. 4. F_2 distributions of rate of leaf emergence at early stage of growth (cross figures indicate the parental mean with σ_e).

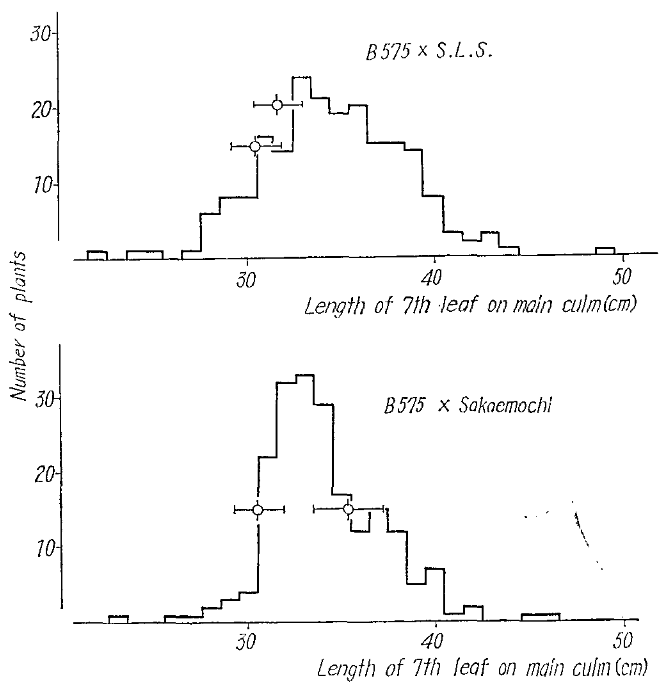

Fig. 5. F_2 distributions of leaf length at early stage of growth (cross figures indicate the parental mean with σ_e).

6. Rate of leaf emergence at early stage of growth (Fig. 4):

In both populations, F_2 distribution was typically normal and the range of F_2 variation accorded rather exactly with the parental difference. The parental mean, F_2 mean, and the peak of F_2 distribution took almost equal value.

7. Length of the 7th leaf on the main culm (Fig. 5):

In both populations, the mode of F_2 distribution was near normal. The range of F_2 variation was greatly bigger than the parental difference. F_2 mean significantly exceeded the parental mean. F_2 variation of the length of the longest leaf on the main culm followed more or less similar pattern to that of the 7th leaf.

8. Width of the 7th leaf on the main culm (Fig. 6)

F_2 distribution was near normal. The parental mean, F_2 mean, and the peak of F_2 distribution took more or less equal value in both populations.

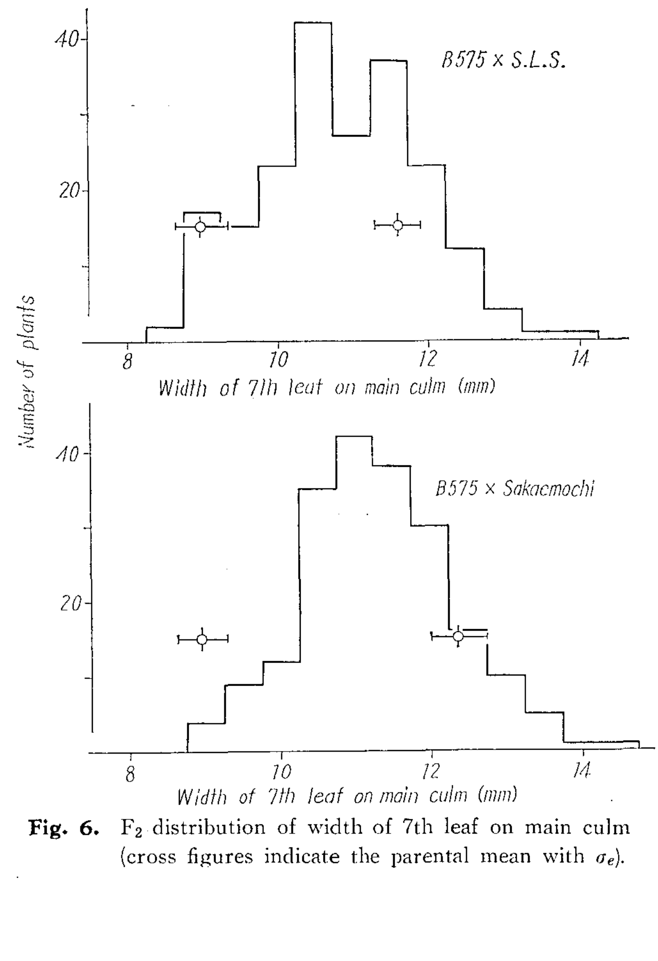

Fig. 6. F_2 distribution of width of 7th leaf on main culm (cross figures indicate the parental mean with σ_e).

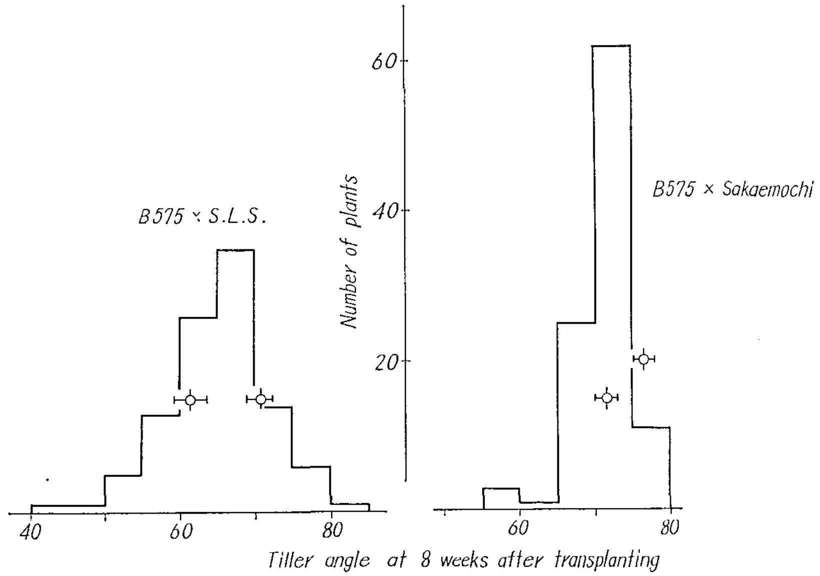

Fig. 7. F_2 distributions of tiller angle (cross figures indicate the parental mean with σ_e).

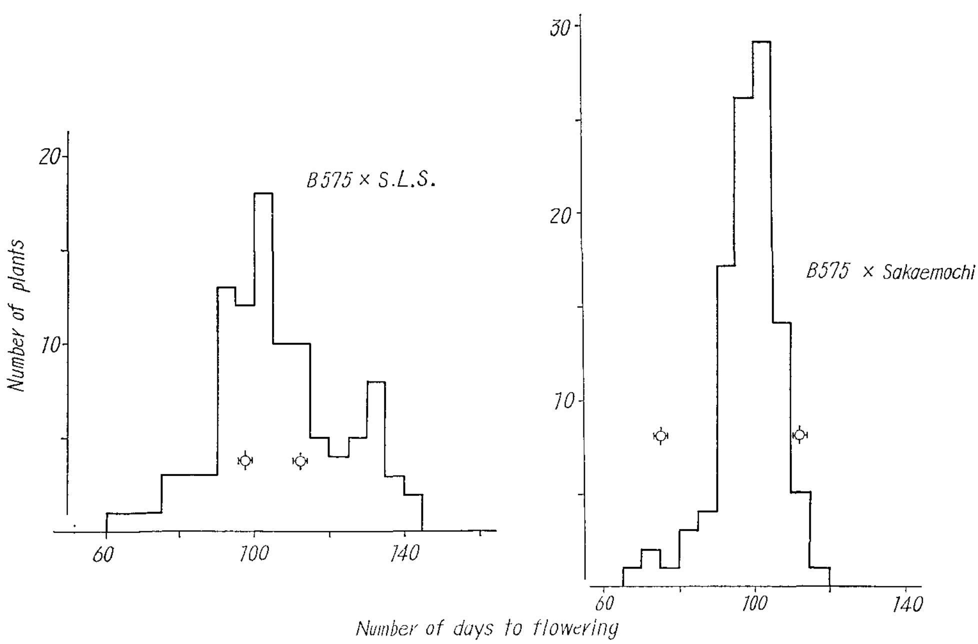

Fig. 8. F_2 distributions of growth duration (cross figures indicate the parental mean with σ_e).

9. Tiller angle (Fig. 7):

In the population of B 575 × Shen Li Sien, the range of F_2 variation was much wider than the parental difference and the mode of F_2 distribution was near noormal. In the population of B 575 × Sakaemochi, the variation was not very big.

10. Number of day to heading (Fig. 8):

All the plants flowered by the end of September. The period during which all the F_2 plants and their parental varieties had their flower bud initiations (June–August) may be regarded as long-day condition. This indicates that all the plants in this experiment were non-photosensitive.

In the population of B 575 × Shen Li Sien, the mode of F_2 distribution

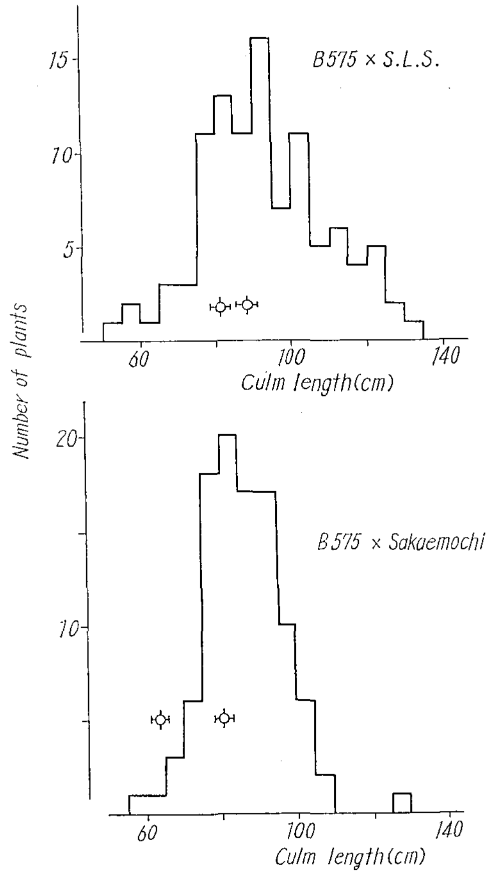

Fig. 9. F_2 distributions of culm length (cross figures indicate the parental mean with σ_e).

was somewhat far from normal but the variation was continuous. The range of variation greatly exceeded the parental difference. In the population of B 575 × Sakaemochi, the mode of F_2 distribution was near normal and the range of variation was more or less equal to the parental difference.

11. Culm length (Fig. 9):

F_2 distribution was near normal and the range of F_2 variation was wider than the parental difference in both populations. In the population of B 575 × Shen Li Sien especially, the range of F_2 variation exceeded the parental difference by about ten times. F_2 mean exceeded the parental mean in both populations.

12. Panicle length:

In the population of B 575 × Shen Li Sien, the range of F_2 variation

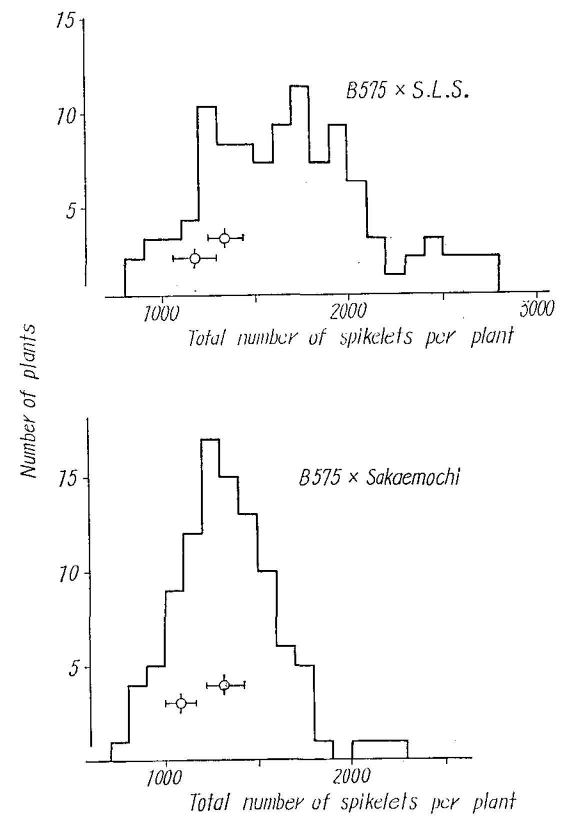

Fig. 10. F_2 distributions of total number of spikelets per plant (cross figures indicate the parental mean with σ_e).

exceeded the parental difference by more than ten times. The mode of distribution was near normal. In the population of B575 × Sakaemochi, the range of F_2 variation was more or less equal to the parental difference. The mode of F_2 distribution was also near normal. Generally speaking, the variation followed the same pattern of culm length of the same F_2 population.

13. Total number of spikelets per plant (Fig. 10):

The F_2 variation was so big that the plant with the biggest number of spikelets had more than three times as many spikelets as the one with the smallest number. F_2 distribution was somewhat far from normal but con-

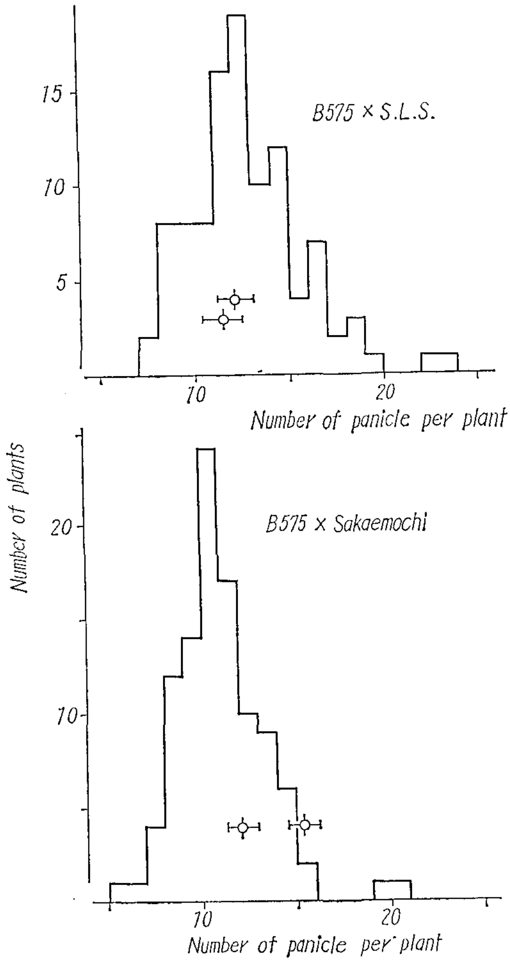

Fig. 11. F_2 distributions of panicle number per plant (cross figures indicate the parental mean with σ_e).

tinuous in the population of B 575 × Shen Li Sien while it was near normal in the population of B 575 × Sakaemochi. The range of F_2 variation was much wider than the parental difference in both populations. The F_2 mean exceeded the parental mean, especially in the population of B 575 × Shen Li Sien where the F_2 mean was 1681 and the parental mean 1238.

14. Number of panicle (Fig. 11):

F_2 variation was such that the plant with the biggest number of panicles had more than three times as many panicles as the one with the smallest number. F_2 distribution was more or less normal and the range of F_2 variation greatly exceeded the parental difference in both populations. F_2 variation of maximum tiller number took the pattern very similar to that of this character.

15. Number of spikelets per panicle (Fig. 12):

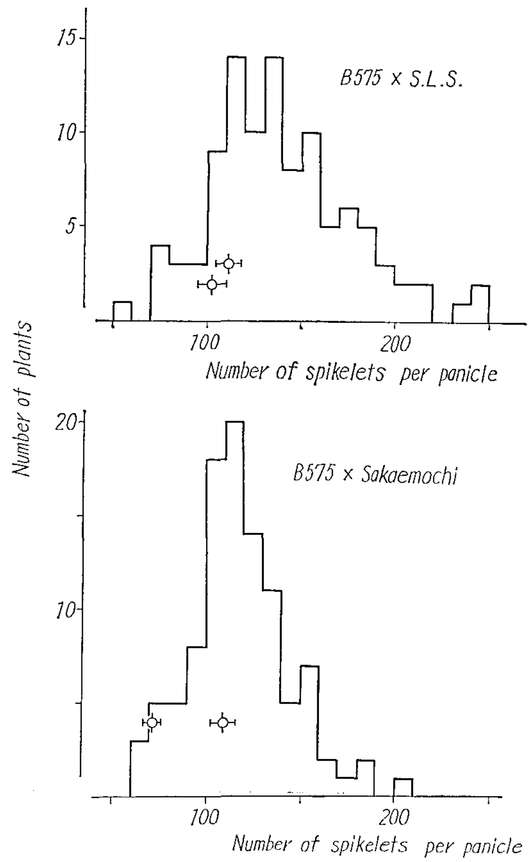

Fig. 12. F_2 distributions of spikelet number per panicle (cross figures indicate the parental mean with σ_e).

F_2 distribution was more or less normal, the range of F_2 variation was much wider than the parental difference, and the F_2 mean significantly exceeded the parental mean. The inheritance mode of this character was quite similar to that of the total number of spikelets per plant.

16. Sterility (Fig. 13):

The mode of F_2 distribution was distinctly different from all of the characters already mentioned. In the population of B575 × Shen Li Sien, there were two peaks of distribution; one was big and located at 0–5% and the other

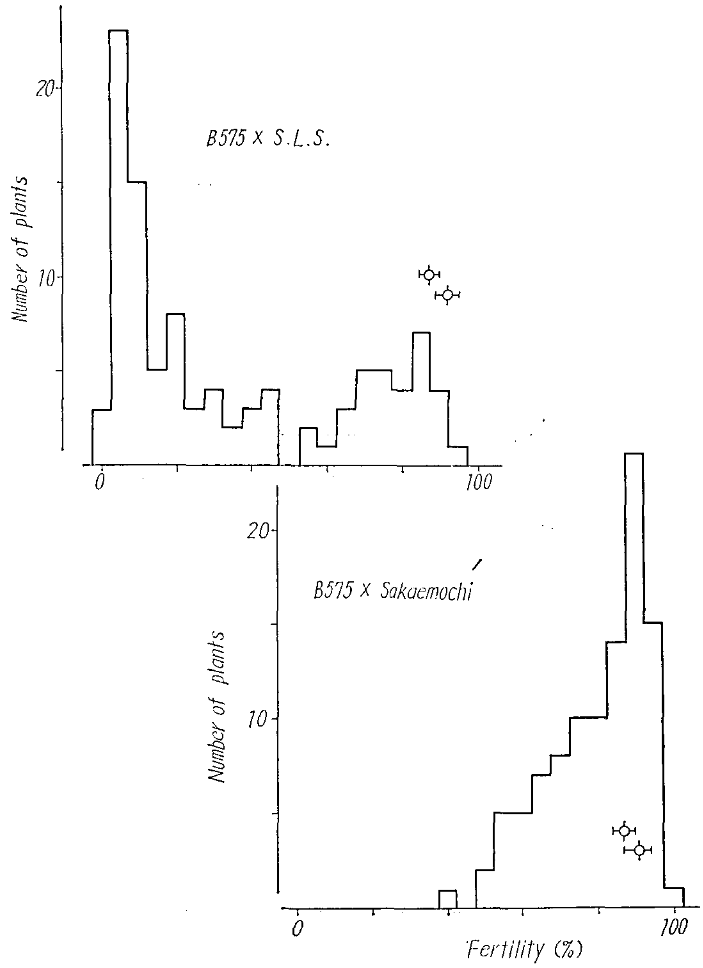

Fig. 13. F_2 distribution of seed fertility (cross figures indicate the parental mean with σ_e).

was small located at 70–80%. In the population of B 575 × Sakaemochi, the mode of distribution was a highly skewed one.

Discussion

The analysis on F_2 variations apparently shows that in cross hybrids of this study, no character is conditioned monogenically. The general indication is that many of the agronomic traits are under the control of relatively big number of genetic factors, each having relatively small effect.

Rate of leaf emergene is the only exceptional character whose variation seems to accord well with a simple variation model of poli-genic effects without intra- and inter-allelic interaction and heterosis. In many characters, big interaction among genetic factors seems to be significant. Thus, explaining the inheritance by a simple variation model would be impossible in many of the agronomic traits.

Distinctly dissimilar variation mode of F_2 seed sterility suggests that the genetic system responsible for hybrid partial sterility is fundamentally different from that for any other agronomic character.

It was indicated in the study of rice F_1 hybrids that F_1 heterosis existed in plant weight, total amount of nitrogen in the plant, tiller number, leaf length, leaf width, total number of spikelets per plant, number of spikelets per panicle, clum length and panicle length, whereas negative heterosis existed in nitrogen content of the plant and panicle number, and further no heterosis was observed in rate of leaf emergence (KAWANO *et al.*, in press). Should the difference between F_2 mean and the parental mean be taken as a general measurement for F_2 heterosis in each character, the data in this paper would strongly support the view that F_2 heterosis exists in the character of which F_1 heterosis exists and the degree of F_2 heterosis follows the degree of F_1 heterosis in the same character.

A more precise analysis of inheritance in each character may be possible by increasing the number of plants in a segregating population or having a further analysis in later generations. However, the continuity of variation in segregating population suggests that the next problem would be the analysis of genetic interrelationship among characters rather than the more precise analysis of a single character. In the following paper, discussion will be made on this subject.

Summary

F_2 populations of two rice crosses and their parental varieties were grown under water culture condition to observe the variation exhibited by F_2 plants

in many agronomic traits. The variation due to experimental error, estimated through the variation of each parental variety, was small so satisfactorily that the genetic analysis was possible through the phenotypic variation in F_2 population.

With one exception, the modes of F_2 distributions were more or less normal in all the characters examined, i. e., plant weight, nitrogen content of the plant, total amount of nitrogen in the plant, tiller number, rate of leaf emergence, length and width of leaf, tiller angle, culm length, panicle length, number of days to heading, panicle number, number of spikelets per panicle, and total number of spikelets per plant. This leads to a possible conclusion that these characters are under the control of relatively big number of genetic factors, each having relatively small effect. One exception was F_2 sterility. F_2 distribution of this character was distinctly different from that of any other character. It is highly possible that the genetic system responsible for hybrid partial sterility is fundamentally different from those for other agronomic traits.

Rate of leaf emergence was the only exceptional character whose variation seems to accord well with a model of simple additive poli-genic variation. In many characters, big interactions possibly exist among the genetic factors corresponding to each character.

The F_2 mean significantly exceeded the parental mean in plant weight, total amount of nitrogen in the plant, leaf length, culm length, panicle length, number of spikelets per panicle, and total number of spikelets per plant. The existence of F_2 heterosis is highly possible in these characters. The F_2 mean of nitrogen content of the plant at early stage of growth was much lower than the parental mean. In this character, negative F_2 heterosis is also highly possible.

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