STUDIES ON COMPETITION IN PLANTS

VIII. CHROMOSOME NUMBER, HYBRIDITY AND COMPETITIVE ABILITY IN *ORYZA SATIVA* L.*

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(With Two Text-figures)

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In the second and sixth reports of the present series, we reported that the autotetraploid plants of *Hordeum sativum* L. or *Nicotiana tabacum* L. were definitely inferior in competition to their diploid prototypes (Sakai & Suzuki, 1955*a*; Sakai, 1956). In the fifth report, however, the competitive superiority of amphidiploid hybrids to one or both of their parents in *Abelmoschus*, *Nicotiana* and *Triticum* × *Secale* was described (Sakai & Suzuki, 1955*b*). In addition, in another paper the results of another experiment were described in which the competitive ability of F_1 barley hybrids was found to be distinctly inferior to that of their parental varieties in spite of their very vigorous growth due to heterosis (Sakai & Gotoh, 1955).

Findings from these experiments suggest that while mere doubling of chromosome sets in diploid plants seems to decrease their competitive ability, doubling of different chromosome sets in species or genus hybrids rather appears to increase it. The high competitive ability of the amphidiploids, however, is not likely to be ascribable to hybrid vigour, if any. Thus, it remains to be investigated what is the mechanism that makes allopolyploidy very advantageous and autopolyploidy very disadvantageous in terms of competition.

Rice, *Oryza sativa* L., involves two subgroups, *Indica* and *Japonica*, which differ from each other in some respects so distinctly that it might not be impossible to consider them even as different species. For example, *Indica* and *Japonica* groups differ from each other with regard to grain shape, habit, and various other physiological, morphological and ecological properties, and the F_1 hybrids between them tend to show high sterility, though the chromosome number of both groups is the same, and the conjugation of chromosomes in the meiotic division looks quite normal.

Taking this situation into account, we have been interested in inquiring into the relation between competitive ability and polyploidy *v.* hybridity using varieties of the *Indica* and *Japonica* groups. The present paper reports the results of the experiment dealing with the problem.

MATERIALS AND METHODS

Four varieties of the *Japonica* and two of the *Indica* group were used. The former were Sensho, Sen-ichi, Sinriki-mochi and Sekitori, and they are called in the following description, for the sake of brevity, S_1, S_2, S_3 and S_4, respectively. The latter two varieties

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were Kuan-Yin-Sen and Karalath, called K_1 and K_2, respectively. Artificially induced autotetraploids of each *Japonica* variety, and the diploid and tetraploid F_1 hybrids between S_1 and S_2, S_3 and S_4, S_3 and K_1, and S_1 and K_2 were raised and used in the present experiment.

Seedlings of all the strains were raised in the nursery bed and were transplanted to the paddy field. The distance between adjacent rows was 30 cm., and the spacing between the adjacent plants in a row was 12 cm.

In 1953, an experiment comparing competitive ability between diploids and their autotetraploids was conducted with four *Japonica* varieties. In this case, the two chromosome races of each variety were compared with each other with regard to competitive ability by being grown separately and in mixtures. Plants were grown individually in pure-stand plots and in mixed plots, in which plants of both chromosome races were planted alternately in the row. Data on an individual plant basis were taken on top weight, number of panicles and weight of panicles. The experiment was conducted by the split-plot experimental design.

In 1954, another experiment was conducted in which diploid and tetraploid chromosome races of four *Japonica* and diploid races of two *Indica* varieties together with the diploid and tetraploid F_1 hybrids of four kinds were planted. To the writers' regret, attempts to get autotetraploids of the two *Indica* varieties did not succeed.

Competitive ability of various races was tested in this experiment by the aid of a diploid tester variety, Norin no. 29, one of the most popular commercial varieties in our country. Plants of the tester variety were grown alternating with plants of each of the races mentioned above. The experiment was conducted by the split-plot method with four replications. The data, however, were analysed according to the method of randomized blocks. Measurements were taken on the tester variety, and top weight and number of panicles on an individual plant basis were recorded.

Experimental results

(i) *Competition experiment with diploids and autotetraploids of four* Japonica *varieties*

Analysis of variance of data obtained in this experiment is presented in Table 1.

Mean values of four replications of diploid and autotetraploid plants of the four varieties in pure-stands and in mixtures are presented in Table 2.

Table 1. *Analysis of variance of top weight, number of panicles and weight of panicles of diploid and autotetraploid plants for four rice varieties, both chromosome races of each variety being grown in pure-stand and in mixture*

Source	D.F.	Mean squares: Top weight	No. panicles	Wt. panicles
Replication	3	76·62	1·83	6·78
Variety	3	110·77	29·69**	16·55
Error (*a*)	9	52·90	1·42	10·04
Chromosome no.	1	2725·75**	230·85**	2688·29**
Chromosome no. × variety	3	126·33**	16·10**	22·22
Error (*b*)	12	16·21	1·27	6·50
Competition	1	85·53*	0·27	36·65**
Competition × chromosome no.	1	324·67**	16·70**	75·89**
Competition × variety	3	22·99	2·79*	2·06
Competition × variety × chromosome no.	3	5·41	3·43*	1·42
Error (*c*)	24	13·93	0·75	3·04

* Exceeds the 5% point. ** Exceeds the 1% point.

From Table 2 we can see that either top weight, number of panicles or weight of panicles per plant of diploids generally increases by being mix-planted with the tetraploids and that of tetraploids decreases by being grown among the diploids. These results are in general in good agreement with those obtained earlier with barley and tobacco.

Table 2. *Mean values of top weight, number of panicles and weight of panicles of diploid and autotetraploid plants of four* Japonica *varieties, each in pure-stand and in mixture with plants of* $2n$ *and* $4n$ *chromosome number of the same variety. On individual plant basis*

		S_1		S_2		S_3		S_4	
		$2x$	$4x$	$2x$	$4x$	$2x$	$4x$	$2x$	$4x$
Top weight (g.)	Pure-stand	29·84	25·02	27·85	19·75	35·55	22·11	30·45	22·62
	Mixture	32·35	24·88	34·32	15·15	45·57	19·27	38·73	21·45
No. of panicles	Pure-stand	6·94	4·57	8·59	8·36	10·90	6·67	8·94	4·59
	Mixture	7·37	5·11	9·12	5·63	13·29	5·80	10·12	4·07
Weight of panicles (g.)	Pure-stand	16·12	7·92	14·52	4·72	17·02	3·87	15·73	4·24
	Mixture	18·72	7·27	18·85	3·70	22·03	3·71	19·06	3·41

(ii) *Competition experiment with diploid and tetraploid plants of* F_1 *hybrids and their parents*

While this experiment was designed according to the split-plot method, statistical analysis of data was conducted as if it were planted by the method of complete randomized blocks. The statistical analysis was tried in two ways: one was testing the statistical significance of the effect of chromosome number, and the other was testing that of the effect of the diploid parents and diploid and tetraploid F_1 hybrids. In the former case, two *Indica* varieties were excluded from the analysis on account of their not having tetraploid races, and in the latter, tetraploids of four *Japonica* varieties were excluded from the analysis.

Analyses of variance of data proved that variation due to chromosome number as well as that due to parents *v.* hybrids was highly significant.

Mean values of four replicated plots of top weight and number of panicles on an individual plant basis in the tester variety mix-planted with various strains are presented in Table 3. Figs. 1 and 2 represent the average values diagrammatically.

It must be understood in these tables and diagrams that strains allowing the tester variety to have a larger number or higher bars are weaker in competition than those allowing the tester to have a smaller number or lower bars.

Table 3. *Mean values of top weight and number of panicles of the tester variety mix-planted with diploid and tetraploid plants of four* Japonica *varieties, diploid plants of two* Indica *varieties, and diploid and tetraploid plants of* F_1 *hybrids between pairs of* Japonica *or one* Japonica *and one* Indica *variety of rice plants*

S, *Japonica* varieties; K, *Indica* varieties.

			$S_1 \times S_2$			$S_3 \times S_4$			$S_3 \times K_1$			$S_1 \times K_2$		
			S_1	S_2	F_1	S_3	S_4	F_1	S_3	K_1	F_1	S_1	K_2	F_1
Tester variety (Norin no. 29)	Top wt. (g.)	$2x$	38·45	36·31	28·93	37·79	33·71	33·19	35·04	27·91	17·34	42·15	34·47	26·68
		$4x$	42·41	39·70	36·59	43·74	51·35	46·06	41·64	—	34·13	46·06	—	41·63
	No. of panicles	$2x$	8·84	8·97	7·14	9·22	7·93	8·11	8·76	7·25	5·11	9·05	8·45	7·66
		$4x$	9·67	9·04	8·40	9·78	10·68	10·36	9·29	—	8·64	10·14	—	9·07

It is apparent from Table 3 and Figs. 1 and 2 that tetraploid plants are always weak competitors against the diploid plants having the same kind of genes, either in parental varieties or in the hybrids. Further information obtained from the table as well as from the diagrams is that in some cross combinations the competitive ability of the F_1 hybrids

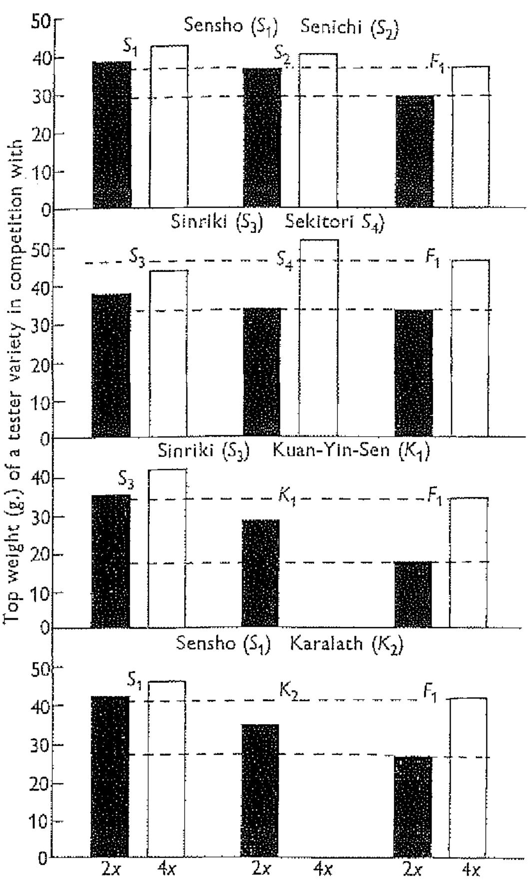

Fig. 1

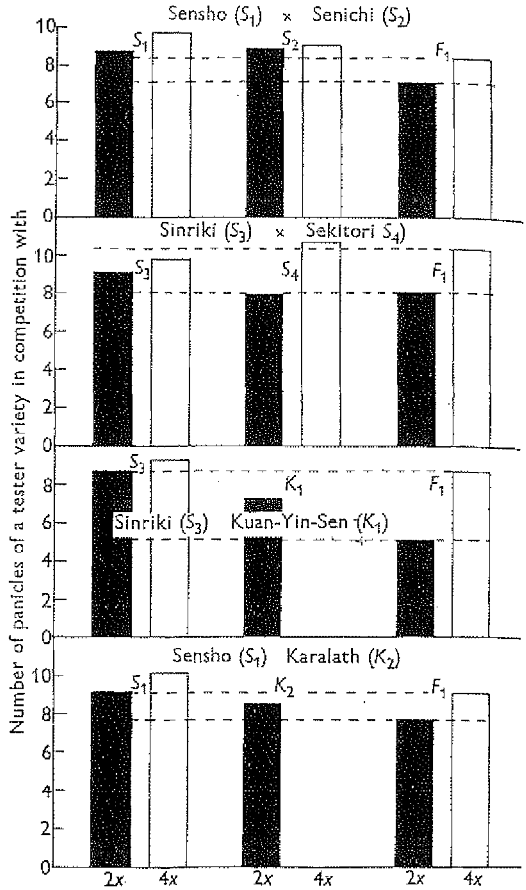

Fig. 2

Fig. 1. Diagrammatic illustration of comparative competitive ability of $2x$ and $4x$ plants of pure-line rice varieties and their $2x$ and $4x$ F_1 hybrids. Bars represent top weight of the $2x$ tester variety mix-planted with $2x$ (black bar) and $4x$ (white bar) parents and their F_1 hybrids.

Fig. 2. Diagrammatic illustration of competitive ability of $2x$ and $4x$ plants of pure-line rice varieties and their $2x$ and $4x$ F_1 hybrids. Bars represent panicle number of the $2x$ tester variety mix-planted with $2x$ (black bar) and $4x$ (white bar) parents and their F_1 hybrids.

is approximately the same or inferior to that of the stronger parent (e.g. $S_3 \times S_4$), while in others it is far superior to those of both parents. As a result of interaction between these two opposed tendencies, tetraploid plants of F_1 hybrids become rather stronger competitors than both parents in some cases (e.g., number of panicles in $S_1 \times S_2$), weaker in another case ($S_3 \times S_4$), and more or less stronger than the weaker parent in still other cases ($S_3 \times K_1$ and $S_1 \times K_2$).

DISCUSSION

As described at the beginning of this paper, the senior writer and Suzuki have found that doubling of chromosome number in a pure-line variety decreases the competitive ability, while allopolyploid plants artificially induced from species or genus hybrids are superior to one or both parents as competitors. In still another experiment it has been found that F_1 hybrids of barley varieties are generally inferior to their parents in competitive ability in spite of their very vigorous growth due to heterosis. Then what would make allopolyploid plants good competitors against their parents?

Oryza sativa L. includes numerous varieties belonging to *Indica* or *Japonica* subgroups. It is generally accepted by rice geneticists that these two groups are rather remotely related to each other, and some tend to consider tetraploids of F_1 hybrids between them as something like segmental allopolyploids in the sense of Stebbins's definition (Stebbins, 1950). It seemed to be interesting, therefore, to investigate the relation between competitive ability and chromosome number in combination with hybridity, using hybrids among rice varieties.

It has been found, as described above, that the competitive ability of tetraploid plants is always inferior to that of their diploid prototypes regardless of whether they are derived from pure lines or hybrids. It has been also found that the F_1 hybrids often possess very strong competitive ability, in some cases far stronger than both parents. Thus, it will be quite reasonable to assume that some hybrids, possessing very strong competitive ability in the diploid condition, may still in the tetraploid condition remain stronger than the weaker diploid parent or stronger even than the stronger parent. In this connexion, the findings in barley should be borne in mind (Sakai & Suzuki, 1955*a*). It was concluded that 'a diploid variety with higher competitive ability tends to produce a tetraploid race with relatively higher competitive ability, and a diploid with lower competitive ability a tetraploid race with relatively low competitive ability' and 'the autotetraploid race of Bohemia no. 1 (a barley variety) tended to approximate or even exceed the diploid tester variety in competitive ability'.

At the present time, I have no material for experimenting with immediate interspecific or intergeneric hybrids in *Abelmoschus*, *Nicotiana*, or between *Triticum* and *Secale*. The supposition may be made, however, that they would be very strong competitors against their parental species.

Lastly it should be mentioned that F_1 hybrids among rice varieties are in general better competitors than both parents. Admitting the fact that the competitive ability is independent of vigorous growth due to heterosis, we could advance the hypothesis that the genes controlling competitive ability might show over-dominance in the heterozygous condition. This hypothesis, if proved, would explain why an amphidiploid can be superior to one or both parents with regard to competitive ability.

CONCLUSION

Doubling of chromosomes in rice either in pure varieties or hybrids has been found to bring about an apparent decrease in competitive ability. The F_1 hybrids, however, have been found generally to be good competitors against their parents, the superiority of the hybrid in competitive ability in some cases appearing extremely high. Thus it is concluded that some hybrids can be stronger than their parents with which they compete, even in the tetraploid condition if the competitive ability of the hybrid in the diploid condition was very high. The high competitive ability of F_1 hybrids should not be understood as a result of vigorous growth due to heterosis of the hybrids. It has been assumed in this respect that genes controlling competitive ability can exhibit over-dominance in the heterozygous condition.

Summary

In 1953, four varieties of the *Japonica* rice group were compared for their competitive ability with their respective tetraploid plants. It was found that tetraploids were always inferior to their diploid prototypes in this respect. In 1954, these diploid and tetraploid races of *Japonica* varieties, two diploid varieties of *Indica* group and diploid and tetraploid F_1 hybrids between two of the four *Japonica* varieties or between *Japonica* and *Indica* varieties were compared for their competitive ability by the use of a standard tester. It was found that the F_1 hybrids often show very notable superiority to both parents. Doubling of the chromosome number in hybrids always decreases their competitive ability just as doubling of chromosomes in pure-line varieties does. It may be possible to find a tetraploid hybrid with higher competitive ability than its parental varieties if the original hybrid possesses a very high competitive ability. This possibility may probably explain the competitive superiority of amphidiploids to their parental species. The very high competitive ability of hybrids is assumed to be due to over-dominance of competitive ability genes in heterozygous condition.

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