Title	The Secondary Association of Meiotic Chromosomes in Oryza sativa L
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Citation	Journal of the Faculty of Science, Hokkaido Imperial University. Ser. 5, Botany, 5(3), 215-220
Issue Date	1942
Doc URL	https://hdl.handle.net/2115/26268
Type	departmental bulletin paper
File Information	5(3)_P215-220.pdf

The Secondary Association of Meiotic Chromosomes in *Oryza sativa* L.

By

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(With 13 Text-figures)

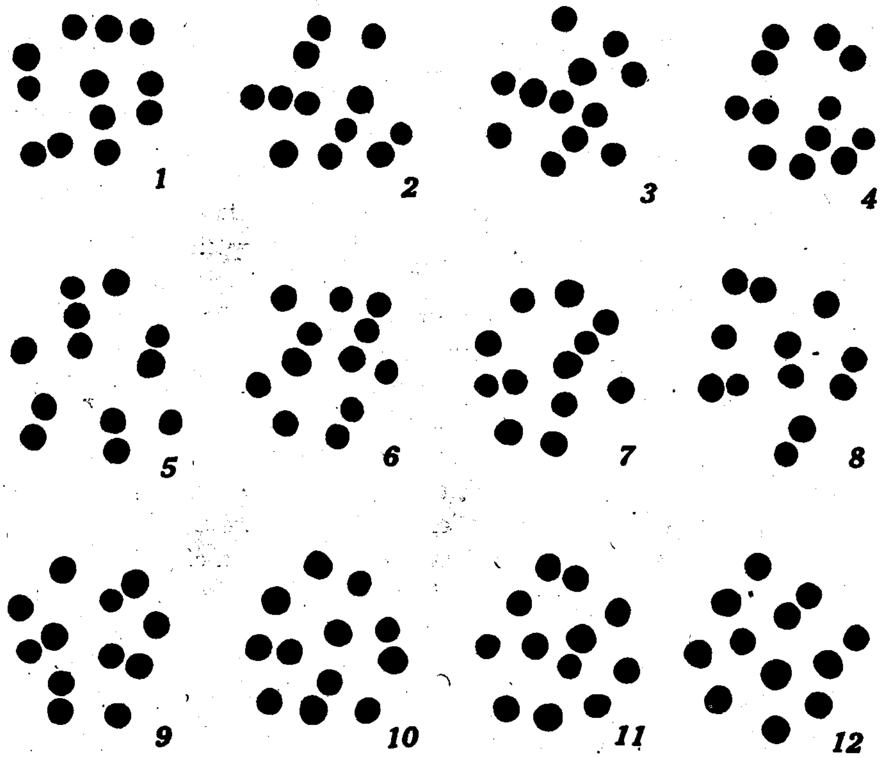
Since the hypothesis of secondary association was first advanced by DARLINGTON ('28), it has attracted much notice from cytologists and the existence of secondary association in meiotic chromosomes has been generally elucidated by many investigators (cf. LAWRENCE '31), although it was yet denied by some cytologists. It has been generally accepted that the secondary association of meiotic chromosomes manifests the chromosome homology in hybrids which are secondary balanced polyploids derived from ancestral forms.

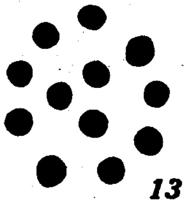
The cytology of *Oryza sativa*, especially the secondary association of meiotic-chromosomes, has been studied by KUWADA ('10), SAKAI ('35) and NANDI ('36). SAKAI suggested that 12 is not the basic number in *O. sativa* but 5 is the primary basic chromosome number and that 12 is secondary balanced number. And he concluded that *O. sativa* is a doubly hexasomic tetraploid plant. NANDI similary subscribes to the same facts, but the types and frequencies of secondary association tested by him, differ from SAKAI's results and he lacks sincerity with regard to the quotation of SAKAI's literature. On the other hand, LAWRENCE ('31) concluded from KUWADA's data that *O. sativa* is one derived from a secondary polyploid with 7 as basic chromosome number. The present study has, accordingly, been carried out with the aim to ascertain these different points of view.

The varieties used for the present observation were *Oibe* and *Genbōzu*. These seeds were sown in pots in the greenhouse of our laboratory. The PMCs were fixed in CARNOY's fixative with good results. After the procedure of the paraffin method, the microtome sections were cut 10 micra in thickness and stained partly with NEWTON's ioden gentian-violet, but mainly with HEIDENHAIN's iron-alum haematoxylin technique.

Observations

The observations presented here have been made mainly on the stages from prometaphase to metaphase and no attempt was made to study the early prophasic stages. From early prometaphase to metaphase the secondary association of meiotic chromosomes was very distinct and the following 13 types of secondary associations in the total 12 bivalents were acertained; (i) 2(3)+3(2), (ii) 2(3)+2(2)+2(1), (iii) 2(3)+1(2)+4(1), (iv) 1(3)+4(2)+1(1), (v) 1(3)+3(2)+3(1), (vi) 1(3)+2(2)+5(1), (vii) 1(3)+1(2)+7(1), (viii) 5(2)+2(1), (ix) 4(2)+4(1), (x) 3(2)+6(1), (xi) 2(2)+8(1), (xii) 1(2)+10(1), (xiii) 12(1) (Figs. 1–13). The





Figs. 1–13. MIs in PMCs showing the various secondary associations in *Oryza sativa* L.

1, 2(3)+3(2). 2, 2(3)+2(2). 3, 2(3)+1(2)+4(1). 4, 2(3)+6(1). 5, 1(3)+4(2)+1(1). 6, 1(3)+3(2)+5(1). 7, 1(3)+1(2)+7(1). 8, 5(2)+2(1). 9, 4(2)+4(1). 10, 3(2)+6(1). 11, 2(2)+8(1). 12, 1(2)+10(1). 13, 12(1). ×3500.

maximum association was type (i), namely two groups of three bivalents and three groups of two bivalents. The type of six groups of two bivalents secondarily associated was never observed in the present study. These results are in agreement with the observations by SAKAI ('35) and NANDI ('36) and their frequencies of various associational types observed by the writer are also mostly the same as SAKAI's results, but they somewhat differ from the results reported by NANDI. The table shows the types and frequencies of secondary associations in the first meiotic metaphase in *O. sativa* represented by SAKAI, NANDI and the writer.

Table 1. Types and frequencies of secondary associations of M1 in *Oryza sativa* L. observed by three investigators.

Types of secondary association	Their frequencies		
	SAKAI	NANDI	OKUNO
(i) 2(3)+3(2)	8	3	3
(ii) 2(3)+2(2)+2(1)	9	6	3
(iii) 2(3)+1(1)+4(1)	0	4	1
(iv) 2(3)+6(1)	1	2	0
(v) 1(3)+4(2)+1(1)	7	—	6
(vi) 1(3)+3(2)+3(1)	13	—	12
(vii) 1(3)+2(2)+5(1)	7	2	6
(viii) 1(3)+1(2)+7(1)	0	—	1
(ix) 1(3)+9(1)	0	2	0
(x) 5(2)+2(1)	6	9	4
(xi) 4(2)+4(1)	8	3	6
(xii) 3(2)+6(1)	3	8	6
(xiii) 2(2)+8(1)	3	6	4
(xiv) 1(2)+10(1)	1	4	3
(xv) 12(1)	0	—	5
Total	66	49	60

It is anticipated that the bivalents thus associated secondarily are formed to be of similar size and configuration, but often the associated bivalents which differed from their size were observed in the present study (Figs. 1–13). The present finding is an interesting fact as compared with one which has been hitherto reported, but only two parallel cases were reported on *Populus nigra* and *Toisusu cardiophlla* by SUTÔ ('40) and DILLEWIJN ('40).

Discussion

Although some cytologists have a tendency to deny the secondary association, supposing that such a phenomenon may be arised from the artificial effect, there is in reality no definite fundation to deny it. Recently, it has been generally proved that the theory of secondary association in meiotic chromosomes implies that paired bivalent chromosomes, which descended from originally homologous chromosomes, even though they are too altered to pair primarily, reveal their affinity by pairing secondarily into definite groups. And the secondary association is a phenomenon intimately connected with allopolyploidy which is secondarily balanced. Such cases are reported on *Tricyrtis latifolia* (MATSUURA '31), *Brassica* (HAGA '38), *Dahlia Merckii* (LAWRENCE '31), *Digitalis* species (BUXTON and NEWTON '28), *Pomoideae* (MOFFETT '31) etc. Similarly, SAKAI ('35) and NANDI ('36) observed a strong secondary association at the meiosis of *O. sativa,* and from the genetical and cytological data, the former suggests that *O. sativa* is a double hexasomic tetraploid plant and that 5 is the primary basic number from which 12 was derived. On the other hand, the latter concluded that *O. sativa* is probably an allo-hexaploid plant based on $n=5$. The genom formulae of haploid set are represented by them as follows;

SAKAI				NANDI		
A_1	A_2		A	A_1	A_1	
B_1	B_2			B	B_1	B
C_1	C_2	C_3		C	C_1	
D_1	D_2	D_3		D	D_1	
E_1	E_2			E	E_1	
$(n=12)$				$(n=12)$		

Concerning the genom formula of *O. sativa,* the writer cannot determine which formula may be good or not, but as far as it's basic number and allopolyploidy is concerned, the writer's opinion is parallel with those advocated by them, namely *O. sativa* may be an allopolyploid derived from two original basic species, having 5 as the basic chromosome number, belonging to two different ancestral genomes in which two chromosomes were duplicated.

This work was carried out under the guidance of Prof. H. MATSUURA, to whom the writer wishes to express his sincere thanks for his valuable suggestions and criticisms.

The present work was aided by a grant from the Imperial Academy of Science, from the Scientific Research Fund of the Department of Education to which the writer wishes to express his sincere thanks.

Summary

1) The secondary association of meiotic chromosomes in *Oryza sativa* L. has been described.

2) The following 13 various types of secondary association were acertained; (i) 2(3)+3(2), (ii) 2(3)+2(2)+2(1), (iii) 2(3)+1(2)+4(1), (iv) 1(3)+4(2)+1(1), (v) 1(3)+3(2)+3(1), (vi) 1(3)+2(2)+5(1), (vii) 1(3)+1(2)+7(1), (viii) 5(2)+2(1), (ix) 4(2)+4(1), (x) 3(2)+6(1), (xi) 2(2)+8(1), (xii) 1(2)+10(1), (xiii) 12(1).

3) Two groups of three bivalents and three groups of two bivalents was the maximum type.

4) As already suggested by SAKAI ('35) and NANDI ('36), *O. sativa* may be a secondary balanced allopolyploid based on $n=5$ which is the primary basic number.

5) Associations of different sized bivalents were often observed.

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