ANALYSIS OF THE MATING TYPES OF *SCHIZOPHYLLUM COMMUNE* IN THE NATURAL POPULATION OF HONG KONG[1][2]

SHU-TING CHANG and WING-SHEUNG LUI[3]

(Received April 7, 1969)

Schizophyllum commune is a common wood-rotting mushroom and belongs to the family Schizophyllaceae of Basidiomycetes. It is world-wide in distribution. The fungus is tetrapolar where the heterothallism or self-incompatibility is genetically controlled by two incompatibility factors, A and B.

The first indication of differential control of the mating reaction by these two factors in this fungus was found by Papazian (1950). He recognized four distinct reactions by inter-mating of monosporous progeny from single fruit body. The four interactions may be designated as follows:

"+", differet-AB ($A \neq B \neq$) heterokaryon, the dikaryon leading to fruitification.

"F", common-A ($A = B \neq$) heterokaryon leading to formation of "flat" reaction which is a reduced development of aerial hyphae.

"B", common-B ($A \neq B =$) heterokaryon leading to formation of "barrage" mycelial reaction which is limited to the line of confrontation.

"−", common-AB ($A = B =$) heterokaryon showing no gross morphologically distinct reaction.

Review of the available data (Kniep 1922, 1923; Miles *et al.*, 1966) revealed that the frequencies of parental (A_xB_x, A_yB_y) and non-parental (A_xB_y, A_yB_x) progenies derived from a single fruit body ($A_xB_x + A_yB_y$) were almost the same and that the segregation of A and B factors insignificantly deviated from 1:1 ratio. This means that the A and B factors assort and segregate independently.

The occurrence of new incompatibility factors in low frequency in addition

(1) This study was supported in part by funds provided by the Institute of Science and Technology of the Chinese University of Hong Kong.

(2) The present article is a somewhat expanded and revised treatment of a paper "Incompatibility factors of *Schizophyllum commune*—The mating type analysis" read before the "Modern Genetics" held at the University of Hong Kong 28th-31st August, 1968.

(3) Department of Biology, Chung Chi College, The Chinese University of Hong Kong, Shatin, N. T., Hong Kong.

to those four mating types among the progenies of fruit bodies collected from nature or grown in the laboratory was first observed by Kniep (1923), who attributed the new factors to mutations at the loci of the "sex factors". However, Whitehouse (1949) found that the mutations of incompatibility factors were rare events which generally occurred at frequencies comparable to spontaneous mutations. Furthermore, Papazian (1950, 1951) found that two new factors appeared in crosses between the two parental strains. These two new factors were then mated with each other, and both the parental factors as well as the two new factors in the same tetrads were recovered. The recovery of the two original factors in a cross between the two new factors constituted conclusive evidence that recombination by crossing over between components of a compound locus rather than mutation appeared to be the most reasonable explanation for the occurrence of the new incompatibility factors. Based on the fact that the two new factors simultaneously resulted in a single cross, Papazian (1951) presented a two-locus model for the A factor and concluded that "The A incompatibility factor which functions as a unit physiologically is controlled by at least two closely linked genes". Owing to the large number of different A factors in natural population, he suggested that each distinct A factor is characterized by a specific combination of the multiple allelic series of the two loci. All of these were subsequently confirmed (Raper and Baxter *et al.*, 1958, 1960) and the two loci were designated as Aα and Aβ.

The B factor was once postulated as a three-locus factor (Raper and Baxter *et al.*, 1958, Raper 1966), and has subsequently been shown to exist in two types, "recombining" and "non-recombining" (Koltin and Raper 1967; Koltin *et al.*, 1967). The "recombining" factors were designated to be a two-locus model, Bα and Bβ, similar to that of A factor for the fact that only two types of recombinants were recovered in a single cross. The "non-recombining" factors were not due to a general supression of recombination in both A and B factors nor to the effect of temperature (Koltin and Raper 1967). The explanation based on chromosomal aberration was also discounted by Koltin and Raper (1967) due to the faet of high viability of the progeney in all the crosses involving non-recombining factors. Therefore, it is likely that the B factor can be distinguished into two major groups because of the physical relation between the loci comprising the factor. The non-recombining group might have its two loci so tightly linked as to be inseparable.

Since the materials studied by other workers (Raper and Krongelb *et al.*, 1958; Miles *et al.*, 1966) so far were mostly obtained from temperate zone, it was thought of interest to analyze the incompatibility factors concerning the mating types, frequencies of recombination, distribution and the number of the factors of this fungus collected in nature of this subtropic area (Hong Kong).

Materials and Methods

Collection of Fruit Bodies:

The fruit bodies (Fig. 1) used in this study were collected from three locations (Table 1). For convenience, we employed a system of classification as follow.

Table 1. *The fruit bodies collected in nature from three different locations at various dates.*

Location	Date of Collection	Code number of fruit body
A) New Territories:		
Chung Chi Campus	June 1968	HK_1 ($A_9B_9+A_{10}B_{10}$)
Chung Chi Campus	June 1968	HK_7 ($A_{69}B_{69}+A_{70}B_{70}$)
Lam Tsung	Aug. 1968	HK_{21} ($A_{209}B_{209}+A_{210}B_{210}$)
Lam Tsung	Aug. 1968	HK_{24} ($A_{239}B_{239}+A_{240}B_{240}$)
Tai Po	Aug. 1968	HK_{26} ($A_{259}B_{259}+A_{260}B_{260}$)
Tai Po	Aug. 1968	HK_{27} ($A_{269}B_{269}+A_{270}B_{270}$)
Tai Po	Aug. 1968	HK_{28} ($A_{279}B_{279}+A_{280}B_{280}$)
B) Hong Kong Isalnd:		
H. K. University Campus	Aug. 1968	KH_{30} ($A_{299}B_{299}+A_{300}B_{300}$)
H. K. University Campus	Aug. 1968	HK_{31} ($A_{309}B_{309}+A_{310}B_{310}$)
H. K. University Campus	Aug. 1968	HK_{33} ($A_{329}B_{329}+A_{330}B_{330}$)
Tsai Wan Area	Sept. 1968	HK_{34} ($A_{339}B_{339}+A_{340}B_{340}$)
Tsai Tam Took Rd.	Sept. 1968	HK_{35} ($A_{349}B_{349}+A_{350}B_{350}$)
Tsai Wan Area	Sept. 1968	HK_{36} ($A_{359}B_{359}+A_{360}B_{360}$)
Tsai Wan Area	Sept. 1968	HK_{37} ($A_{369}B_{369}+A_{370}B_{370}$)
Tai Tam Took Reservoir	Sept. 1968	HK_{40} ($A_{399}B_{399}+A_{400}B_{400}$)
Repulse Bay Road	Sept. 1968	HK_{42} ($A_{419}B_{419}+A_{420}B_{420}$)
Repulse Bay Road	Sept. 1968	HK_{43} ($A_{429}B_{429}+A_{430}B_{430}$)
C) Kowloon Peninsula		
Kau Lung Peak	Oct. 1968	HK_{44} ($A_{439}B_{439}+A_{440}B_{440}$)
Kau Lung Peak	Oct. 1968	HK_{45} ($A_{449}B_{449}+A_{450}B_{450}$)
Kau Lung Peak	Oct. 1968	HK_{46} ($A_{459}B_{459}+A_{460}B_{460}$)
Kau Lung Peak	Oct. 1968	HK_{47} ($A_{469}B_{469}+A_{470}B_{470}$)
Kau Lung Peak	Oct. 1968	HK_{48} ($A_{479}B_{479}+A_{480}B_{480}$)
Kau Lung Peak	Oct. 1968	HK_{49} ($A_{489}B_{489}+A_{490}B_{490}$)

The first fruit body was given a code number HK_1 and the mating type designation 9–10 ($A_9B_9+A_{10}B_{10}$); the second one HK_2, the mating type designation 19–20 ($A_{19}B_{19}+A_{20}B_{20}$), etc. Each of them would produce four parental types; A_9B_9, $A_{10}B_{10}$, A_9B_{10} and $A_{10}B_9$ for HK_1 and $A_{19}B_{19}$, $A_{20}B_{20}$, $A_{19}B_{20}$ and A_{20}

B_{19} for HK_2. The codings like A_{11}, A_{12}...., B_{11}, B_{12}...., and A_{21}, A_{22}...., B_{21}, B_{22}.... are their non-parental types which are the results produced by recombination in A factor and B factor respectively.

Collection of Spores:

The mature fruit bodies obtained from tissue culture technique reported by Yanal (1968) as well as those collected directly in nature were inverted over an agar plate for a desired period of time under room temperature (ca 25°C). The agar plate was prepared by dissolving $MgSO_4$, 0.5 g, KH_2PO_4 0.46 g, K_2HPO_4 1 g, peptone 2 g, destrose 20 g, agar 20 g, yeast extract 2 g, and thiamin-HCl in one liter of distilled water. The spores where spread over the medium surface with a bent glass rod. After about 18 hours, the spores usually germinated and each of them was cut out from the medium under a microscope by a spore-cutter described by Raper (1963). Isolation of the spores was accomplished by a needle with its point blunted but sharpened uniformly on opposite sides by rubbing it against an oilstone. A small cylindrical block of agar containing a germinating spore could then be moved out. Four such small agar blocks were then placed on a plate for further growth.

Selection of Testers:

Any one of the isolates (monosporous progenies) could be chosen as the preliminary tester and used as a standardized one and mated with about 40 others. Those having different A and B factors crossed with the chosen one would show a "+" reaction; those with different A factor but with same B factor would show "B" reaction; those with same A but different B factors would only show "F" reaction; and those carrying the same A and B factors would show "—" reaction. The mycelial appearances as well as the hyphal features of the mating reactions are shown in Figures 2 and 3 respectively. One from each of the four reaction groups was then chosen as the four testers for mating type analysis.

Occassionally the original isolate selected was a recombinant at a mating type locus. This would be detected by showing the relative frequencies of mating reactions that were "F", "+" and "—". HK_{27} ($A_{269}B_{269}+A_{270}B_{270}$) for example:

Tested isolates	$A_{269}B_{269}$	$A_{270}B_{270}$	$A_{269}B_{270}$	$A_{270}B_{269}$
Mating reactions with selected isolate, $A_{269}B_{269}$	—	+	F	B
Frequencies	10	14	1	4

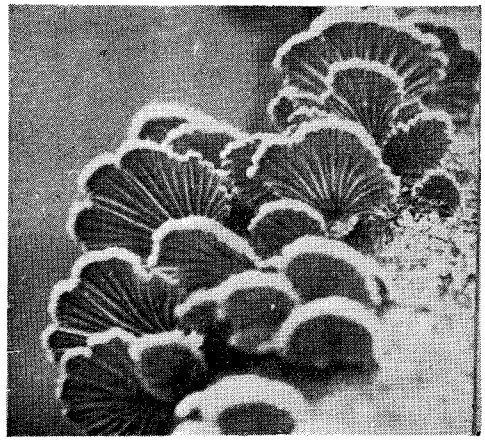

Figure 1. The mature fruit bodies of *Schizophyllum commune* are shown growing naturally on the dead twig. X ca 20.

The high proportion of "+" and "−" compared to a low proportion of "F" would indicate that a recombinant in A factor had been selected and that further testing would be required. If the distribution of the four mating types is quite close to 1:1:1:1 ratio, this is good evidence that one of the parental types has been chosen and those selected from this cross is of significant value on mating type analysis. Take stock HK_{28} ($A_{279}B_{279}+A_{280}B_{280}$) for example:

Tested isolates	$A_{279}B_{279}$	$A_{280}B_{280}$	$A_{279}B_{280}$	$A_{280}B_{279}$
	−	+	F	B
Mating reactions with selected isolate $A_{279}B_{279}{}^{(28-1)}$	28-90	28-89	28-85	28-13
	28-86	28-43	28-87	28-14
	28-5	28-92	28-88	28-91
	(**28-1**)	28-2	28-11	28-17
	28-3	(**28-96**)	(**28-4**)	28-7
	28-93	28-78		(**28-10**)
	28-94	28-8		28-12
	28-15			28-95
	28-9			
Frequencies	9	7	5	8

The circulated isolates, **21-1, 28-96, 28-4** and **28-10** were chosen as the four testers for futher analysis.

Determination of Mating Types:

Matings were made by placing two small agar blocks containing mycelia of the appropriate mating types about 2–3 mm apart on agar plates. Four

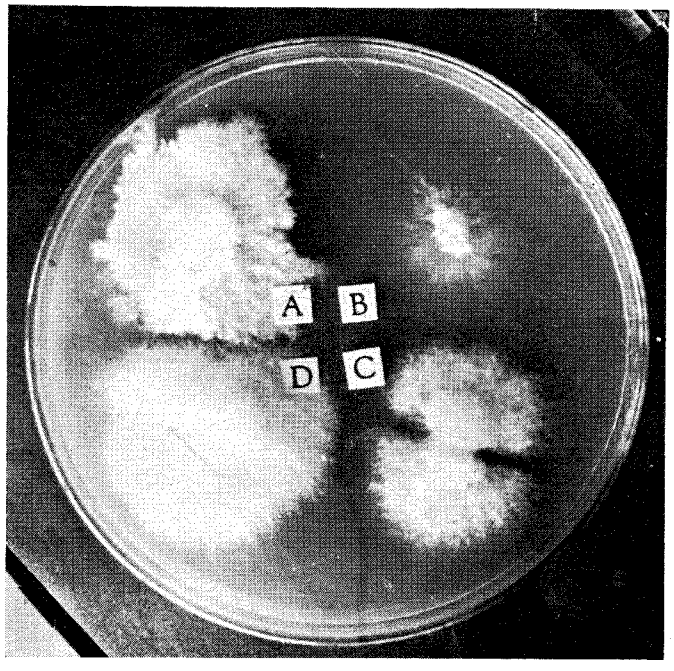

Figure 2. Mycelial appearences of the four mating reactions: A) different-AB, B) common-A; C) commom-B; and D) common-AB. X ca 4/5.

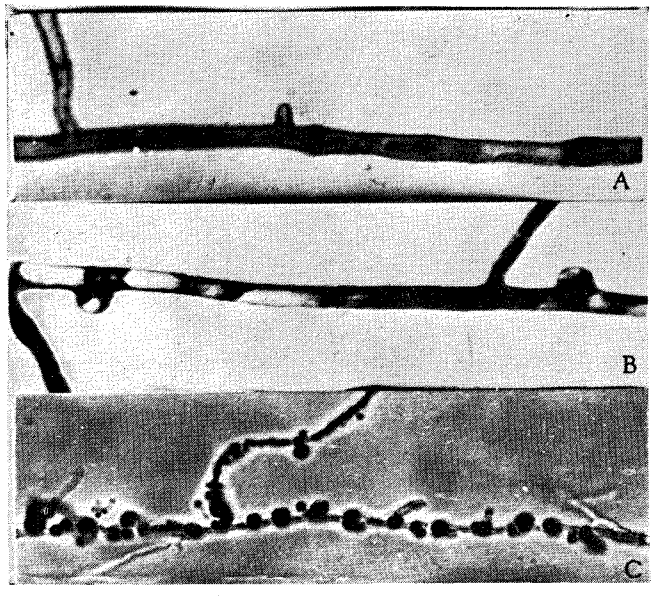

Figure 3. Hyphal features of the mating reactions between two homokaryotic strains: A) simple septa characteristics for both common-AB and common-B reactions; B) the presence of clamp connections for different-AB interaction; C) the presence of short branches and blobs of protoplasm for common-A reaction. X ca 800

matings were made per plate. The mating type of each strain can be determined by the four basic reactions between different A and B factors. Since the mating types of the four testers have been determined when mated with the preliminary tester designated as A_xB_x, those isolates giving no reactions with any one of these four testers would have similar mating type as that of the particular tester because only the mating types with identical incompatibility factors would give a "−" reaction in a crossing. In this way, the other three parental types can easily be sorted out if the pattern of interactions of mating type analysis (Table 2) is followed. Those isolates showing two "+" reactions in the testing sequence indicate that a recombination has taken place in either of the two factors A and B. If only "+" and "B" reactions appeared in crosses between isolates and the four selected testers, this means that a recombination in A factor must have taken place. Those isolates with only "+" and "F" reactions would indicate that crossing over has taken place in the B factor. If all four mating tests showed "+" reactions, this means that the crossing over might have occurred in both A and B factors.

Table 2. *The pattern of interactions of mating type analysis.*

Selected testers					
(1) A_xB_x	(2) A_yB_y	(3) A_xB_y	(4) A_yB_x	Mating types	
−	+	F	B	A_xB_x	parental types
+	−	B	F	A_yB_y	
F	B	−	+	A_xB_y	
B	F	+	−	A_yB_x	
B	+	+	B	aB_x	recombinant A types
+	B	B	+	aB_y	
F	+	F	+	A_xb	recombinant B types
+	F	+	F	A_yb	
+	+	+	+	ab	recombinant AB type
F/F*	+/F	F/F	+/F	A_xB_m	suspected B mutations
+/F	F/F	+/F	F/F	A_yB_m	

* Symbols to left and right of the diagonal indicate reactions of testers at above and mating types at right respectively.

Those isolates showing "−" reactions on only one side of all four mating tests would indicate that a modifier mutation (Raper and Raper 1966) might have occured because a strain carrying this kind of mutants would show unilateral reaction which means they only donate but not receive nuclei. There

is another type of isolates which reacted unilaterally and showed a "flat" appearance that was different from their parents. It is suspected that a primary mutation in B factors might have occurred in these "Flat" isolates (Raper *et al.*, 1965) or a heterokaryon resulted from a mixture of two strains which are common in A factors.

Results

21 samples out of 49 fruit bodies collected from various hosts in nature of Hong Kong (Table I) were examined in this study. Each sample consisted of approximately 100 isolates. The 28 missing fruit numbers (Table 3) were due either to contamination or to the failure of fruiting from tissue culture even after a few months. The deviation of the sample size was entirely due to contamination.

Table 3. *The mating type analysis and the percentage of recombination in the 21 stocks collected in Hong Kong*

Stock Name	Mating type designation		Sample size	Parents				Recombinants				Percentage of recombination	
				A_xB_x	A_yB_y	A_xB_y	A_yB_x	aB_x	aB_y	A_xb	A_yb		
	x	y										a	b
HK 1	9	10	80	18	18	17	22	0	3	2	1	3.8	3.8
HK 7	69	70	81	17	24	16	20	0	2	1	1	2.5	2.5
HK 21	209	210	85	25	10	18	27	3	2	0	0	5.9	0.0
HK 24	239	240	84	21	19	23	19	2	0	0	0	2.4	0.0
HK 26	259	260	84	19	19	24	24	4	1	0	0	6.0	0.0
HK 27	269	270	72	13	15	14	16	5	5	0	0	13.9	0.0
HK 28	279	280	98	24	23	21	19	4	4	2	1	8.2	3.1
HK 30	299	300	104	32	24	22	22	3	0	0	1	2.9	0.9
HK 33	329	330	80	13	21	26	16	3	1	0	0	5.0	0.0
HK 34	339	340	105	30	24	26	25	0	0	0	0	0.0	0.0
HK 35	349	350	60	12	13	11	19	1	3	0	0	6.6	0.0
HK 36	359	360	112	28	24	24	25	3	7	0	0	8.8	0.0
HK 37	369	370	127	38	22	25	37	4	1	0	0	3.9	0.0
HK 42	419	420	100	22	30	26	21	0	0	1	0	0.0	1.0
HK 43	429	430	105	30	32	29	21	0	0	2	1	0.0	2.9
HK 44	439	440	84	17	15	16	25	3	7	0	0	11.9	0.0
HK 45	449	450	66	13	14	10	19	3	4	3	0	10.6	4.6
HK 46	459	460	69	20	15	12	8	2	2	0	0	5.7	0.0
HK 47	469	470	50	13	13	8	16	2	0	0	0	4.0	0.0
HK 48	479	480	73	14	17	11	27	1	1	0	0	2.8	0.0
HK 49	489	490	55	11	15	10	14	1	4	0	0	9.1	0.0

The number of parental and non-parental types as well as the percentages of recombinations are listed in Table 3. The percentages of recombination within the two loci of A factor range from 2.4 to 13.9 with a mean equal to 6.3. These figures were calculated from 18 out of 21 crosses which had recombinant A factors while in the remaining 3 the recombinations were not obtained. The recombination percentages occurring whithin the B factor range from 0.9 to 4.6, with a mean value of 2.7. However out of 21 stocks 13 showed no recombination.

From the analysis in inter-stock matings, the identical mating type factors among the 42 parental strains of the 21 stocks were sorted out in Table 4. The frequency distribution of specific factors of the A and B series is stated in Table 5. There are 36 distinguishing A factors and 35 specific B factors. The results show that the majority of A and B factors appeared once while only a few of them showed a slightly higher number of repeats. The data reveal no significant departure from the expected frequency distribution of specific factors in a sample taken from a population which all factors of each series are equally frequent.

Table 4. *Identical mating type factors among the 42 parental strains collected in Hong Kong.*

A factors	B factors
$A_{70}=A_{359}=A_{370}$	$B_{9}=B_{360}=B_{369}$
$A_{279}=A_{270}$	$B_{10}=B_{280}=B_{269}$
$A_{360}=A_{369}$	$B_{89}=B_{499}$
$A_{420}=A_{430}$	$B_{420}=B_{430}$
$A_{479}=A_{490}$	$B_{460}=B_{490}$

Table 5. *The frequency distribution of specific factors of the A and B series in the samples.*

No. of strains	Factor	Times of occurrence of specific factors			Total
		1	2	3	
42	A	31	4	1	36
	B	30	3	2	35

The frequency of repeats of each factor A and B collected in different areas is visualized in Table 6. They did not show significant deviation from one another. Thus the specific factors of both incompatibility series are randomly distributed in respect to geographical locations (Raper and Krongelb *et al.*, 1958; Whitehouse 1949).

Table 6. *The frequency of factor repeats in different areas of Hong Kong.*

Areas where samples were collected	Strains	Crosses	A repeats		B repeats	
			no.	freq.	no.	freq.
Hong Kong	42	1,764	6	0.0034	7	0.0040
New Territories	14	196	1	0.0051	2	0.0102
Hong Kong Island	16	256	2	0.0079	2	0.0079
Kowloon Pennisula	12	144	1	0.0069	1	0.0069

Discussion

Schizophyllum commune is an obligative saprophytic fungus growing on dead twigs and barks of various kinds of tree hosts (Table 1). It can grow well and fruit in a chemically defined medium with an optimum pH of 6.8 at 32°C.

All of the 21 stocks from this investigation show no significant deviation from 1:1:1:1 ratio (Table 3) for the four mating types, indicating that the A and B factors of the parental fruit body segregate and assort independently during the formation of spores.

The results from this study are quite similar to those of Raper and Baxter *et al.* (1958), Raper *et al.* (1960), Miles *et al.* (1966) and Koltin and Raper (1967) in that the recombination percentage of the A factor is higher than that of the B factor. It was explained by Raper *et al.* (1960) and Koltin and Raper (1967) that the distance between the two loci in the B factor is so closely linked that crossing over could occur only infrequently. The recombination percentages between the two loci in both A and B factors obtained by different investigators at different temperatures are listed in Table 7 for comparison. As reported by Raper and Baxter *et al.* (1958 and 1960) that the temperature is an important factor in governing crossing over. The higher the temperature is, the higher the recombination percentage will be. However after making a comparison among the data, it seems that this statement holds true only for the A factor but not for the B factor. Because the mean percentage of recombination in B factor was about 2 regardless of the temperature level whereas in A factor 4.8 and 6.3 for temperatures at 23 and 25°C as well as 10.1 and 12.3 for temperatures at 33 and 34°C respectively. So further exploration on the effect of temperature on the recombination percentage of B factor is needed.

In both A and B factors low frequency of recombination was found to be dominant (Stamber and Raper 1966; Simchen 1967; Koltin and Raper 1967). The genetic suppression of recombination can be expressed only in a dikaryon whether the reduced frequency of recombination was dominant or the interac-

Table 7. *Comparison of the percentage of recombinants for A and B factors incubated at different temperatures.*

Investigator and Date		Temp. of incubation	percentage of recombinants	
			A factor	B factor
Raper, Boxter and Middleton (1958)	average	23°C	4.8	—
		33°C	10.1	—
	range	23°C	0.9-14.5	—
		33°C	3.9-15.9	—
Miles, Takemanue and Kimura (1966)	average	34°C	12.3	2.0
	range	34°C	5.0-21.0	2.0-2.0
Koltin, Raper and Simchen (1967)	average	30°C	—	2.3
	range	30°C	—	0.1-8.0
Chang average and Lui (this report)	average	25°C	6.3	2.7
	range	25°C	2.4-13.9	0.9-4.6

ting strains possessed the gene for low recombination. The data cited in Table 7 were also revealed that the percentages of recombination of both A and B factors were not constant. Recently, it was reported by Koltin and Raper (1967) that the various frequencies of recombination are probably controlled by the different physical relation of the multiple series of the two loci in the recombining B factors. Those with two loci farther from each other would cross more readily than those which are combined in close linkage relationship. Furthermore, the 13 non-recombining B factor stocks in our samples also agree with the postulation of Koltin and Raper (1967) that half of the B factors are non-recombining. Those of non-recombining strains would have α and β closely linked together and inseparable by crossing over. Therefore this gives difficulties in mapping the α and β loci in reference with those of the A factors because no significant evidence has been reported that a non-recombining group exists in A factors.

The result of 36 A factors and 35 B factors out of 42 strains (Table 5) is expected because the number of alternate factors of each series was found to be quite large in the total natural population of the species (Kneip 1922; Whitehouse 1949). The data (Table 6) obtained from this study plus the results (Table 8) reported by other investigators for the frequency of factor repeats in regions with different climatic conditions indicate random distribution of the incompatibility factors with respect to climatic condition. Miles *et al.* (1966) collected the fruit bodies from the same trees within a small area; those collected by Raper and Krongelb *et al.* (1958) came from regions widely separate and even from different countries; those of ours were collected neither from the same trees nor from different countries. From the comparative results, it appears that the closer the distance between two districts, the higher is the possibility of factor repeats in the A factor but not so in B factor.

Conclusively, our data plus other available information, agree with the asumption that the number of alternate factors are equal in frequency and random in distribution among the natural population.

Summary

We analyzed the mating types of one of our local materials, *Schizophyllum commune*, and compared it with what had been done by other investigators who dealt mainly with the fungus collected in temperate zones. The results from our study resembled those of others in that the recombination percentage of A factor is higher than that of the B factor and that the non-recombining factor does exist in the B factor. Our data also showed that the number of both factors A and B is very large and that all the factors in each series occurred equally. They are also random in distribution with respect to geographical location and climatic condition.

Table 8. *Comparison of the frequency of factor repeats among the different climatic conditions*

Data	Climate	Strains	Crosses	A repeats		B repeats	
				no.	freq.	no.	freq.
Raper, Krongelb, & Baxter (1958)	temperate tropic	84 30	3,584 425	7 2	0.0019 0.0046	60 5	0.0167 0.0120
Miles, Takemaru, & K'mura (1966)	temperate	30	900	6	0.0066	5	0.0055
Chang & Lui (this report)	subtropic	42	1,764	6	0.0034	7	0.0040

As reported by other investigators that the temperature is an important factor governing the recombination, it was observed that the higher the temperature is, the higher the recombination percentage will be. However, after making a comparison of this study with the results obtained by other workers, an unpredictable information was found that increasing in temperature did increase the crossing over in A factor but not in B factor. It is suggested that the effect of temperature on the recombination in the B factor should be cleared up by further investigation.

香港裂褶菌交配型之遺傳分析

張樹庭 呂詠裳

本試驗之目的在研討香港裂褶菌交配型的遺傳分析。以前瑞帕爾氏等（1958）及邁爾斯氏等（1966）曾做過類似的研究，但其材料多取於溫帶地區而香港即位於亞熱帶區。同時並欲藉此種遺傳分析，探悉香港地區有關該菌A和B兩不親和因子之分佈與數目情形。

試驗結果證明A因子之互換比率顯著高於B因子者。更證明B因子約有半數爲不互換因子。此兩點與高登氏等（1967）的報告相符合。A和B兩不親和因子內所含等位基因之數目甚大。所有等位基因在每一系列中出現之機率大約是相等。至於等位基因的分佈情形似與地理分區及氣候狀況無關。

從多方面的實驗結果，均證明溫度對互換率有關。即溫度增高互換率也增大。然而經研討比較各溫度下之互換率時却發現一不尋常之現象，即溫度祇影響因子A之互換頻率而對B因子却無作用。因此溫度對B因子之互換作用究竟影響如何？有待更深入一層之探討也。

Literature Cited

KNIEP. H., 1922 Uber geschlechtsbestimmung und redktionsteilung. Verh. Phy. Med. Ges. Wurzb. 47:1-28. 1923 Uber erbliche Anderunger von geschlechtsfaktor en bei pilzen. Z. Indukt. Abstamm. u.-Vererblehre 31: 170-183.

KOLTIN. Y. and J. R. RAPER, 1967 The genetic structure of the incompatibility factors of *Schizophyllum commune:* three functionally distinct classes of B factors. Proc. Nat. Acad. Sci. U. S. 58: 1220-1226.

_____, _____, and G. SIMCHEN, 1967 The genetic structure of the incompatibility factors of *Schizophyllum commune:* the B factor. Proc. Nat. Acad. Sci. U. S. 57: 55-62.

MILES, P. G., T. TAKEMARU and K. KIMURA, 1966 Incompatibility factors in the natural population of *Schizophyllum commune.* (I) Analysis of the incompatibility factors present in fruit bodies collected within a small area. Bot. Mag, (Tokyo) 79: 693-705.

PAPAZIAN, H. P., 1950 Physiology of the incompatibility factors in *Schizophyllum commune.* Hull Botanical Gazette 112: 143-163.

_____, 1951 The incompatibility factors and a related gene in *Schizophyllum commune.* Genetics 36: 441-459.

RAPER, C. A. and J. R. RAPER, 1966 Mutations modifying sexual morphogenesis in *Schizophyllum.* Genetics 54: 1151-1168.

RAPER, J. R., 1963 Device for the isolation of spores. J. Bacteriol. 85: 342-344.

_____, 1966 Genetics of sexuality in higher fungi. The Ronald Press Company, New York.

_____, D. H. BOYD, and C. A. RAPER, 1965 Primary and secondary mutations at the incompatibility loci in *Schizophyllum.* Proc. Nat. Acad. Sci. U. S. 63: 1324-1332.

_____, G. S. KRONGELB and M. G. BAXTER, 1958 The number and distribution of incompatibility factors in *Schizophyllum.* The Amer. Nat. 92: 221-232.

_____, M. G. BAXTER and R. B. MIDDLETON, 1958 The genetic structure of the incompatibility factors in *Schizophyllum commune.* Proc. Nat. Acad. Sci. U.S. 44: 889-900.

_____, _____, and A. H. ELLINGBOE, 1960 The Genetic structure of the incompatibility factors of *Schizophyllum commune.* The A factor. Proc. Nat, Acad. Sci. U. S. 46: 833-864.

_____, and P. G. MILES, 1958 The genetics of *Schizophyllum commune.* Genetics 43: 530-546.

STAMBERG, J. and J. R. RAPER, 1966 Genetic recombination in *Schizophyllum commune.* Amer. J. Bot. 53: 626.

SIMCHEN, G., 1967 Genetic control of recombination and the incompatibility system in *Schizophyllum commune.* Genet. Res. Camb., 9: 195-210.

WHITEHOUSE, H. L. K., 1949 Multiple allelomorph heterothallism in the fungi. New Phytol. 48: 212-244.

Yanal, J., 1968 Isolating dikaryons of *Schizophyllum commune* from fruit bodies collected in the wild. Incompatibility Items (Edited by P. G. Miles. Department of Biology State University of New York at Buffalo).