

ALLELISM TESTS AMONG VARIOUS HOMOTHALLISM-CONTROLLING GENES AND GENE SYSTEMS IN SACCHAROMYCES

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IN general, fertile *Saccharomyces* yeasts are divisible into heterothallic and homothallic strains. In a heterothallic strain, a stable haploid culture with a or α mating type is obtained from cultivation of each ascospore and diploidization occurs only by fusion of cells having opposite mating types. A single pair of alleles, i.e., a and α , on chromosome III (HAWTHORNE and MORTIMER 1968) determines mating types; all individuals of each haploid strain, therefore, belong to one or the other of two mating types. In a homothallic strain, on the other hand, diploidization takes place in a single spore culture and haplophase is limited to the ascospore or to a few haploid cells originating from ascospore germination.

The genetic system controlling homothallism *versus* heterothallism in *Saccharomyces* yeasts has been independently reported by several authors. WINGE and ROBERTS (1949) demonstrated in *S. chevalieri*, an epistatic gene for diploidization, D , which was independent of the mating-type locus and which was equally effective on the a and α mating-type alleles. OESER (1962) and HAWTHORNE (1963) suggested that the D gene produces homothallism by accelerating the mutation of a mating-type allele to the alternative form in a certain portion of the cells and forming zygotes between a and α cells within a culture. In *S. cerevisiae*, complementary gene systems consisting of HM_1 , HM_2 and HM_3 were reported (TAKAHASHI 1958), in which the HM_1 , HM_2 , hm_3 and hm_1 , HM_2 , HM_3 genotypes gave homothallic character to a culture. The D gene from *S. chevalieri* was considered to be different from the *S. cerevisiae* complementary HM gene system since the D gene and HM genes segregated independently (TAKAHASHI and IKEDA 1959). In general, homothallic strains of *Saccharomyces* yeasts are not incompatible with others. However, TAKAHASHI, SAITO and IKEDA (1958) described that the homothallic yeasts are equipped with a mating-type character but in a concealed form which, though it is not so strong as in heterothallic strains, is still detectable by special techniques such as "the minimal plate mating technique". It was found by TAKAHASHI and IKEDA (1959) that the homothallic strains carrying the D gene have the concealed mating potency for both a and α haploid strains, i.e., they are bisexual, while the homothallic strains carrying the HM genes are unisexual, i.e., they mate only with either a or α . In *S. lactis*, HERMAN and ROMAN (1966) found two unlinked, independent homothallic genes, H_a and H_α , which have specific effects on the mating-type allele, i.e., one locus is effective in changing the mating type from a to α , and the other from α to a . *S. lactis*, however, does not hybridize with *S. cerevisiae* and related strains.

In the previous publication (TAKANO and OSHIMA 1967a), the genetic con-

TABLE 1
Genotypes and sources of tested strains

Strain No.	Genotype			Source or reference	Thallism
	Homothallicism gene	Mating type	Genetic marker		
8256	HM_1, hm_2, hm_3	a	$ad_1 ga_1$	C. C. LINDEGREN	Hetero-
11163-3A	hm_1, HM_2, HM_3	Non-mater	ur_3	& T. TAKAHASHI	Homo-
1932-2A	D	Non-mater	ar_4, ly_2, met_4	T. TAKAHASHI	Homo-
C-1728a-6B	D	Non-mater	ur_3	D. C. HAWTHORNE	Homo-
C-1728b-4C	D	Non-mater	$ad_2 ga_4, le_1$	T. TAKAHASHI	Homo-
T-794-5B	$HO_\alpha HM$	Non-mater	$ga_1 ga_4, hi_4$	T. TAKAHASHI	Homo-
T-805-19B	$HO_\alpha HM$	Non-mater	$ad_1 ga_4, hi_4, met_2$	Constructed	Homo-
T-1030-5A	$ho_\alpha hm$	a	$ad_1 ga_1, hi_4, ly_2, thr_4, tr_1$	Constructed	Hetero-
787-3D	$ho_\alpha hm$	α	$ad_1 ga_1, hi_4, ly_2$	Constructed	Hetero-
T-1023-36B	$ho_\alpha hm$	α	$ar_4 ga_1, hi_4, le_2, thr_4, tr_1$	Y. OSHIMA	Hetero-
T-1068-34B	$ho_\alpha hm$	α	$ad_1 ar_4, hi_4, le_2, ly_2, met_2, thr_4$	Constructed	Hetero-
T-1068-43B	$ho_\alpha hm$	α	$ad_1 ar_4, hi_4, le_2, ly_2, met_2, thr_4, tr_1$	Constructed	Hetero-
787-2C	$ho_\alpha HM$	a	$ad_1 hi_3, ly_2, ur_3$	Y. OSHIMA	Hetero-
T-1010-7B	$ho_\alpha HM$	α	$ga_1 ga_4, hi_3, hi_4, le_2, thr_4$	Constructed	Hetero-
T-1014-15A*	$HO_\alpha hm$	Non-mater	$ad_1 ga_1, ga_4, hi_4, ly_2, thr_4, tr_1$	Constructed	Homo-
T-1023-2C*	$HO_\alpha hm$	Non-mater	$ga_1 hi_4, le_2, ly_2, thr_4, tr_1$	Constructed	Homo-
T-1023-2C-1A†	$HO_\alpha hm$	a'	$ga_1 hi_4, le_2, ly_2, thr_4, tr_1$	Constructed	Hetero-
T-1023-23B-1A†	$HO_\alpha hm$	a'	$ad_1 ar_4, ga_1, hi_4, le_2, ly_2, tr_1$	Constructed	Hetero-

The auxotrophic and fermentative traits are used as standard genetic markers for the tetrad analysis. The terminology follows the suggestion of the Carbondale Yeast Genetics Conference (VON BORSTEL 1963).

* Homothallic culture which gives a 2 homothallic : 2a (i.e., a') segregation in ascus.

† The a' segregants from the homothallic culture T-1023-2C and T-1023-23B, respectively.

trolling system for homothallism in *S. oviformis* was described. This system is composed of two unlinked genes. One of them, HO_α , is an allele-specific gene for the α mating-type allele and changes α to homothallism, and the other, HM , is not effective by itself alone, but is effective in changing the α mating-type culture to homothallism if combined with HO_α . Those two homothallic genes have no linkage with the mating-type locus or with each other. It was also revealed that the HO_α gene acts as a specific mutator for the α mating-type allele in converting it to an a mating-type allele (i.e., a'). The mutational event occurs at the mating-type locus on chromosome III, but probably at a different site from the site that determines the normal a mating-type allele, during the first few divisions of the haploid cells after spore germination (OSHIMA and TAKANO 1968).

This paper describes allelism tests among homothallic genes or gene systems of different origins, i.e., the D gene from *S. chevalieri*, TAKAHASHI's complementary HM gene system from *S. cerevisiae*, and the gene system consisting of HO_α and HM from *S. oviformis*. The results indicate that the D gene does not consist of a single gene but rather of two complementary genes which are allelic with HO_α and HM , and that the hm_1, HM_2, HM_3 genotype also corresponds to the HO_α, HM genotype. It is suggested that the HM_1 gene is identical to the α mating-type allele itself.

MATERIALS AND METHODS

Organisms: Homothallic strains having the hm_1, HM_2, HM_3 genotype or the D gene were kindly supplied by T. TAKAHASHI of the Brewing Science Research Institute, Suita. Another homothallic strain marked with the D gene was obtained by courtesy of D. C. HAWTHORNE of University of Washington, Seattle. These homothallic strains carrying the D or HM genes sporulated well and each single-spore culture from them consisted of diploid cells and each self-sporulated again. A haploid strain, 8256, originated from LINDEGREN's Carbondale breeding stocks was used as a heterothallic strain having the HM_1, hm_2, hm_3 genotype as suggested by TAKAHASHI (1958). Many homothallic or heterothallic strains containing several different combinations of the HO_α and HM genes were selected from the breeding stocks which had been produced in the previous studies (TAKANO and OSHIMA 1967a,b; OSHIMA and TAKANO 1968) as the tester strains for allelism tests. Genotypes and sources of these tester strains are listed in Table 1.

Techniques: The general techniques, media and genetic terminology were described in the previous publication (TAKANO and OSHIMA 1967a).

RESULTS

Table 2 shows the expected segregations of the various phenotypes in tetrads from crosses between different combinations of the homothallic genes HO_α and HM , assuming that these genes segregate independently from each other and from the mating-type locus. Ten possible genotypes of diploid cells are listed. They are classified into seven categories according to the pattern of segregation of homothallism *versus* heterothallism in their asci. Segregation of Type I yields $2a : 2a$ in every ascus, i.e., the regular pattern for the mating-type alleles in heterothallic cultures. Type II shows the pattern of specific conversion of the α mating-type clone to homothallism. Type III shows the specific complementary controlling system. Type IV shows a 2 homothallic : $2a$ segregation in every ascus,

which is the typical segregation pattern for the $\alpha HO_\alpha hm$ homothallic spore culture. Type V shows a 2 homothallic : 2 heterothallic segregation, as if the homothallism was controlled by an epistatic gene for both mating-type alleles. In Type VI, more than two homothallic spore cultures can be expected in every ascus, and the α mating-type clones are never produced in the heterothallic progenies. Type VII shows the 4 homothallic : 0 heterothallic segregation in every ascus. Results of the following allelism tests are compared with these expected segregation patterns.

(A) *Allelism tests between an $hm_1 HM_2 HM_3$ homothallic culture (11163-3A) and the standard strains with the HO_α and HM gene system:* Single-spore cultures from 11163-3A are diploids. They sporulated well and were homozygously marked with ur_s . Results of tetrad analyses of the crosses between the homothallic spores from 11163-3A and the standard strains with various combinations of the HO_α and HM genes are shown in Table 3. It is evident that the homothallic system composed of $hm_1 HM_2 HM_3$ is allelic with the $HO_\alpha HM$ genotype from the tetrad data of T-1125, in which a 4 homothallic : 0 heterothallic segregation was observed in all of the 34 asci dissected. In other crosses, i.e., T-1101, T-1103, T-1104 and T-1105, it was likewise concluded that the $hm_1 HM_2 HM_3$ genotype must correspond to the $HO_\alpha HM$ genotype, although two aberrant asci were observed in T-1101 and T-1103. Further evidence supporting the existence of the HO_α gene in 11163-3A was shown from the tetrad analyses of the various homothallic clones segregated from T-1101 and T-1103. Those homothallic clones were self-sporulated and the four-spored asci were dissected. Some of these homothallic

TABLE 3

Tetrad segregations from hybrids between 11163-3A ($hm_1 HM_2 HM_3$; homothallic) and various standard strains for the HO_α and HM genes

Segregation in asci	Strains crossed with 11163-3A, their genotypes and cross numbers				
	T-1068-34B $\alpha ho_\alpha hm$	T-1030-5A $a ho_\alpha hm$	787-2C $a ho_\alpha HM$	T-1023-23B-1A $a' HO_\alpha hm$	T-805-19B $HO_\alpha HM$
Homothallic : α : α	T-1101	T-1103	T-1104	T-1105	T-1125
4 : 0 : 0	0	0	0	3	34
3 : 1 : 0	0	0	0	7	0
3 : 0 : 1	0	0	0	0	0
2 : 1 : 1	2	8	14	0	0
2 : 2 : 0	3	3	4	0	0
2 : 0 : 2	1	0	5	0	0
1 : 2 : 1	3	12	0	0	0
1 : 1 : 2	0	3	0	0	0
0 : 2 : 2	0	1	0	0	0
0 : 3 : 1	0	1*	0	0	0
1 : 3 : 0	1*	0	0	0	0

Possible type of segregation III III V VI VII

Each cross was made between a spore from 11163-3A and a heterothallic haploid vegetative cell except for T-1125 which was made by the spore-to-spore mating method (TAKANO and OSHIMA 1967a).

* These asci were considered aberrant.

clones produced a 2 homothallic : 2 α segregation in all the dissected asci, indicating the presence of HO_α in those cultures.

(B) *Genetic analyses of the heterothallic strain, 8256*: A heterothallic haploid strain, 8256, originated from LINDEGREN's Carbondale breeding stocks was thought to have the $\alpha HM_1 hm_2 hm_3$ genotype. The HM_1 gene, in combination with HM_2 , is effective in conversion of a heterothallic culture to homothallism and is closely linked to the mating-type locus (TAKAHASHI 1958). These facts suggest that the HM_1 gene should be complementary with either the HO_α or HM gene.

In order to test this prediction, various crosses were made between 8256 and the standard strains for the HO_α and HM gene system. Results of the tetrad analyses of those crosses are summarized in Table 4. The crosses between 8256 and the heterothallic haploid strains with the $\alpha ho_\alpha hm$ and $\alpha ho_\alpha HM$ genotype (i.e., T-1141 and T-1142) gave the normal 2 α : 2 α segregation in every ascus. The specific segregation pattern for the α mating-type allele—i.e., Type II segregation, was observed in the cross T-1143, which was a cross between 8256 and a spore from a $\alpha HO_\alpha hm$ homothallic culture. Type III segregation was observed in the crosses between 8256 and the $HO_\alpha HM$ homothallic strain. Furthermore, the cross between 8256 and 11163-3A—i.e., T-1148, demonstrated a pattern of segregation similar to Type III.

These results can be explained if (1) the HM_1 gene is not complementary to either HO_α or HM , or (2) the HM_1 gene was not present in 8256. The latter explanation is more likely, because it was shown that the HM_1 gene was complementary to HM_2 in the conversion of heterothallic cultures to homothallism and

TABLE 4

Tetrad segregations from hybrids between 8256 ($HM_1 hm_2 hm_3$; heterothallic α) and various standard strains for the HO_α and HM genes

Segregation in asci	Strains crossed with 8256, their genotypes and cross numbers				
	T-1023-36B $\alpha ho_\alpha hm$	T1010-7B $\alpha ho_\alpha HM$	T-1023-2C $\alpha HO_\alpha hm$	T-794-5B $HO_\alpha HM$	11163-3A $hm_1 HM_2 HM_3$
Homothallic : α : α	T-1141*	T-1142*	T-1143†	T-1145‡	T-1148‡
4 : 0 : 0	0	0	0	0	0
3 : 1 : 0	0	0	0	0	0
3 : 0 : 1	0	0	0	0	0
2 : 1 : 1	0	0	0	9	5
2 : 2 : 0	0	0	4	6	2
2 : 0 : 2	0	0	0	0	0
1 : 2 : 1	0	0	13	15	1
1 : 1 : 2	0	0	0	4	0
0 : 2 : 2	14	5	3	1	0
1 : 3 : 0	0	0	1‡	0	0

Possible type of segregation I I II III III

* Crosses were made by the mass-mating method (LINDEGREN and LINDEGREN 1943).

† Crosses were made by the cell-to-spore conjugation under the microscope with a micromanipulator.

‡ This ascus was considered aberrant.

that the HM_2 gene was identical to either HO_α or HM by the foregoing experiments in this paper.

(C) *Allelism tests between the D gene and the HO_α HM gene system*: The D gene has been thought to be a single dominant gene controlling the directed mutation of a mating-type allele to the alternative form in some of the cells within a culture. It has been shown that the HO_α gene causes the directed mutation of the α mating-type allele to a but not the a allele to α (OSHIMA and TAKANO 1968).

Results of the tetrad analyses of the crosses between homothallic strains carrying the D gene and the standard strains for the HO_α and HM gene system are presented in Table 5. It is evident that the D cultures from different sources are homogeneous since they gave similar tetrad segregation patterns in crosses to strains of the same genotypic composition. The crosses between the D cultures and 787-2C ($a ho_\alpha HM$) showed a 2 homothallic : 2 heterothallic segregation in every ascus (Type V segregation) with two aberrant asci in T-1259 and T-1261. These results agree well with the observation by WINGE and ROBERTS (1949). However, the segregation pattern which indicates the presence of the complementary system in the D gene, i.e., Type III segregation, was observed in the crosses between D and $ho_\alpha hm$. This result clearly indicates that the D gene is not a single gene but a multiple-gene system. In the crosses between the D cultures and the $HO_\alpha HM$ culture, only the 4 homothallic : 0 heterothallic segregation was observed. Therefore, it is evident that the D culture contains both the HO_α and HM genes. These arguments are also supported by the tetrad data of crosses in the D and $HO_\alpha hm$ combination, which showed the unique segregation pattern, i.e., Type VI segregation, in which no heterothallic α mating-type segregants were observed. A comparatively high frequency (32.4%) of the 2 homothallic : 2 a asci was observed in cross T-1269, but it was proved by further genetic analyses of the segregants of T-1269 that this deviation is not attributable to the homothallic genes or another unknown homothallic gene but due to another unknown mechanism. In order to confirm the presence of the HO_α gene in these D strains, further tetrad analyses were made on homothallic segregants from T-1255 which showed Type III segregation. Some of these homothallic cultures gave the 2 homothallic : 2 a segregation in all dissected asci. The allelic identity between the D gene and the $hm_1 HM_2 HM_3$ genotype was also confirmed by the tetrad analysis of the cross between 1932-2A (D) and 11163-3A ($hm_1 HM_2 HM_3$), in which the 4 homothallic : 0 heterothallic segregation was observed in all of 9 asci dissected.

DISCUSSION

Genetic analyses of the crosses between the $hm_1 HM_2 HM_3$ homothallic clone and the strains with various combinations of the HO_α and HM genes clearly support the view that the homothallism due to the $hm_1 HM_2 HM_3$ genotype corresponds to the α (or a) $HO_\alpha HM$ genotype. Unfortunately, it was impossible to decide which one of the genes in the $hm_1 HM_2 HM_3$ genotype was allelic with the HO_α or HM gene, because the $hm_1 HM_2 hm_3$ or $hm_1 hm_2 HM_3$ strain was not available for the present study. The original report by TAKAHASHI (1958), how-

TABLE 5

Tetrad segregations from hybrids between homothallic strains carrying the D gene and strains with different genotypes for the HO_α and HM genes

Part 1: The D strains from T. TAKAHASHI

Segregation in asci Homothallic : a : α	Combination and cross numbers							
	C-1728a-6B D × T-1068-43B α ho _α hm	C-1728b-4C D × T-1068-43B α ho _α hm	C-1728a-6B D × 787-2C a ho _α HM	C-1728b-4C D × 787-2C a ho _α HM	C-1728b-4C D × T-1023-2C-1A a' HO _α hm	C-1728b-4C D × T-1023-2C α HO _α hm	C-1728a-6B D × T-794-5B HO _α HM	C-1728b-4C D × T-794-5B HO _α HM
	T-1251*	T-1255*	T-1259*	T-1263*	T-1271*	T-1274†	T-1275†	T-1279†
4 : 0 : 0	0	0	0	0	6	6	34	36
3 : 1 : 0	0	0	0	0	26	25	0	0
3 : 0 : 1	0	1‡	0	0	0	0	0	0
2 : 1 : 1	5	5	15	15	0	0	0	0
2 : 2 : 0	5	4	1	1	8	10	0	0
2 : 0 : 2	0	0	1	1	0	0	0	0
1 : 2 : 1	4	6	1‡	0	0	0	0	0
1 : 1 : 2	0	0	0	0	0	0	0	0
0 : 2 : 2	0	1	0	0	0	0	0	0
0 : 3 : 1	0	1‡	0	0	0	0	0	0

Possible type of segregation

Part 2: The D strain 1932-2A from D. C. HAWTHORNE

Segregation in asci Homothallic : a : α	Strains crossed with 1932-2A, their genotypes and cross numbers				
	787-3D α ho _α hm T-1253*	787-2C a ho _α HM T-1261*	T-1014-15A α HO _α hm T-1269†	T-1023-2C-1A a' HO _α hm T-1295*	T-794-5B HO _α HM T-1277†
	4 : 0 : 0	0	0	6	6
3 : 1 : 0	0	0	42	24	0
3 : 0 : 1	0	0	0	0	0
2 : 1 : 1	12	14	0	0	0
2 : 2 : 0	3	3	23	8	0
2 : 0 : 2	0	4	0	0	0
1 : 2 : 1	9	1‡	0	0	0
1 : 1 : 2	4	0	0	0	0
0 : 2 : 2	0	0	0	0	0

Possible type of segregation

* Crosses were made by the spore-to-cell mating method.

† Crosses were made by the spore-to-spore mating method.

‡ These asci were considered aberrant.

ever, showed that HM_2 is indispensable for homothallism. Thus, one may suppose that HM_2 corresponds to HO_α and that HM_3 corresponds to HM . Another complementary homothallic gene in the HM system, HM_1 , which was supposed to be closely linked to the mating-type locus by TAKAHASHI (1958), has not been found in strain 8256. This evidence strongly suggests that the HM_1 gene is the α mating-type allele itself and that one of the homothallic genotypes, $HM_1 HM_2 hm_s$, probably corresponds to the $\alpha HO_\alpha hm$ genotype.

Genetic analyses of the epistatic homothallic gene, D , obviously support the

conclusion that the *D* gene is not a single gene but consists of the HO_α and *HM* genes. On the basis of above arguments, the genetic data of other authors (WINGE and ROBERTS 1949; TAKAHASHI 1958; TAKAHASHI and IKEDA 1959) are explained consistently, except for the observation (TAKAHASHI and IKEDA 1959) that two heterothallic α mating type haploid clones were found in imperfect tetrads (containing one ungerminated spore) from crosses between *D* and the homothallic strain with the $HM_1 HM_2 hm_3$ genotype (i.e., $\alpha HO_\alpha hm$); α mating-type clones are not expected from these tetrads.

TAKAHASHI and IKEDA (1959) reported that homothallic strains containing the *D* gene have the bisexual concealed mating potency while homothallic strains with the complementary *HM* gene system are unisexual. Present authors (TAKANO and OSHIMA 1967b) also tested the concealed mating potency of several homothallic strains having the α (or *a*) $HO_\alpha HM$ or $\alpha HO_\alpha hm$ genotype and could not observe any particular relationship between these two homothallic genotypes and the unisexuality or bisexuality of concealed mating type.

In conclusion, the genetic systems controlling homothallism *versus* heterothallism in *S. cerevisiae*, *S. chevalieri*, *S. oviformis* and *Saccharomyces* breeding stocks related to these original strains are composed of two genes; the HO_α gene, a specific mutator for the α mating-type allele, and the *HM* gene, which in combination with HO_α can convert the *a* mating-type allele to homothallism.

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SUMMARY

Allelism tests were made among the homothallic genes and gene systems in *Saccharomyces*, i.e., the *D* gene from *S. chevalieri*, the complementary *HM* gene system from *S. cerevisiae* and the system comprised of the HO_α and *HM* genes isolated from *S. oviformis*. It is evident that the *D* gene and the $hm_1 HM_2 HM_3$ genotype, one of the homothallic gene combinations in the *S. cerevisiae* *HM* system, correspond to the α (or *a*) $HO_\alpha HM$ genotype. However, no evidence was observed that supports the existence of another complementary *HM* gene, HM_1 , except for the suggestion that HM_1 is the α mating-type allele itself.

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