A DELETION IN YEAST AND ITS BEARING ON THE STRUCTURE OF THE MATING TYPE LOCUS[1]

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THERE is growing evidence for the composite nature of the loci controlling mating types in yeasts as well as in the higher fungi (*Coprinus lagopus:* DAY 1963; *Collybia velutipes:* TAKEMARU 1961; *Pleurotus ostreatus:* TERAKAWA 1960; and *Schizophyllum commune:* RAPER, BAXTER, and ELLINGBOE 1960). In the yeast *Schizosaccharomyces pombe*, LEUPOLD (1958) has demonstrated recombination (0.4 percent) between the + and − alleles of the heterothallic strains to give a third phenotype for homothallism. The tetrads with a homothallic segregant also contain the reciprocal recombinant which although of the + phenotype is distinguished from the original + parent by its failure to give homothallic recombinants when backcrossed to the − parent. The results are consistent with the interpretation that there are separate cistrons determining the + and − activities, and when neither is defective, the strain is homothallic. In *Saccharomyces cerevisiae*, an investigation of mating type mutations has led to the following evidence for a similar complexity of the mating type locus.

METHODS AND EXPERIMENTAL RESULTS

To obtain mating-type mutants, haploid strains of like mating type, each with two nutritional requirements which were complementary to the others, were mixed in a complete natural medium and allowed to undergo several divisions before being plated on a minimal synthetic medium. Among the prototrophic diploid strains recovered, there was one in which a mutation of α to a was accompanied by the appearance of a recessive lethal completely linked to the new a gene. The analysis of 70 four-spored asci showed that only the two α spores in each ascus were able to grow. The a spores generally showed signs of germination and sometimes produced a single bud before dying. The germinating a spores were found to be capable of mating with α vegetative cells to form new hybrids heterozygous for the lethal.

The a spores carrying the lethal were first crossed to haploids with a marker, thr_4 (threonineless), linked to α. The diploid hybrids were threonine dependent and gave four-spored asci which showed the segregation of the lethal. The two viable spores were always of the genotype α thr_4. Since there had been no history of thr_4 in the pedigree of the original lethal heterozygote, it is postulated that the lethal phenotype is due to a deletion which includes the locus of thr_4.

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To verify and delimit the postulated deletion, spores with the lethal from a prototrophic hybrid were mated with cells from a haploid clone with the following linked markers: centromere–22 units–α–16 units–thr_4–20 units–MA_2 (maltose fermentation). The hybrid obtained was threonine dependent and fermented maltose. The dissection of 44 asci gave 20 tetrads with two viable spores and 21 tetrads with a single viable spore. All the surviving clones carried α thr_4 and 57 out of the 61 fermented maltose. Thus, if there is no interference with crossing over, the deletion extends from the mating type locus to within about six units of MA_2.

DISCUSSION

It seems probable that the change in mating type from α to a was due to the occurrence of the adjacent deletion rather than a second independent event. Given this, one can picture how this might have happened if the mating type locus is a complex with an operator and structural cistrons for both the α and a products. The deletion could include enough of the α cistron to render it inoperative while leaving the a portion functional. The presence of a functional a gene is indicated by the observation that the deletion heterozygote does not mate and is able to sporulate, the properties of an a/α diploid and not those of an α/α diploid or aneuploids monosomic for the chromosome carrying α (ROMAN and SANDS 1953, and personal communication).

If the mating response system in Saccharomyces is analogous to that found in the yeast *Hansenula wingei* (BROCK 1959), a mutation of the mating type alleles results in the substitution of distinctly different gene products. With a complex mating type locus instead of a simple structural gene, it is easier to envisage how a single mutation can bring about such a change. There is the possibility that the mating type gene is a regulator gene controlling the activity of structural genes located elsewhere. However, there are two arguments against this: (1) The two-gene segregation ratios that might occasionally be expected have not been found in the analysis of 640 hybrids of the heterothallic strains. (2) The gene *D* for homothallism (WINGE and ROBERTS 1949) would appear to have this very same role.

The concept of a complex mating type locus is compatible with the complicated interaction that occurs between the mating type genes and the gene *D* for diploidization or homothallism. Gene *D* acts as a "mutator gene" in causing the mating type gene to mutate to its allele during the first few divisions of the haploid cells from the homothallic spore (OESER 1962; HAWTHORNE 1963). Cells of opposite mating type then fuse and the clone may soon consist of only diploid cells. The products of both α and a in the diploid jointly act to block further action of gene *D*. This interaction suggests a mutually repressible system with operators and structural genes at both the mating type and *D* loci.

SUMMARY

A mutation of the mating type gene, in Saccharomyces, from α to a was appar-

ently brought about by the occurrence of a deletion which extended from the mating type locus for 30 units distally with respect to the centromere. To explain this, it is postulated that the mating type locus is a complex with α and α cistrons and that the deletion includes the latter.

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