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Mitotic recombination in the *paba 1* cistron of *Aspergillus nidulans*

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1. INTRODUCTION

In *Aspergillus nidulans* meiotic recombination between mutants within one cistron (Pritchard, 1955, 1960*a*; Siddiqi, 1962; Martin-Smith, 1961) is usually characterized by a prevalence of concomitant recombination of outside markers. Intra-cistron recombinants showing recombination of outside markers are supposed to be the result of single exchanges between the two mutant sites used in a cross. The results of testing two by two a number of mutants within one cistron are usually consistent with a linear order of the mutant sites. This feature of intragenic recombination has been taken to indicate that recombination between sites of a cistron—i.e. between extremely closely linked mutants—is essentially like recombination between loci further apart, i.e. each recombinational event should produce one wild-type and one double mutant strand.

Because of the rarity of meiotic intragenic recombination and the non-availability of techniques for *selecting* tetrads in which intragenic recombination has occurred, it is practically impossible to verify this deduction in *A. nidulans* by means of tetrad analysis. However, it is possible to carry out half-tetrad analysis by means of the technique of Roper & Pritchard (1955), using heteroallelic diploids and selecting diploid mitotic recombinants from them. The results obtained by Pritchard (1955, 1960*a*) showed that at least in some cases a diploid nucleus carrying the wild-type recombinant on one strand also carried the double mutant on the homologous strand, i.e. presumably both reciprocal products of the same recombinational event were recovered in one nucleus. But at the time of Pritchard's work the convenient technique of haploidization by the use of *p*-fluorophenylalanine (Morpurgo, 1961; Lhoas, 1961) was not available and, therefore, his analysis was based on a small number of recombinants. In the present work this new technique made it possible to obtain more adequate data.

The purpose of the present work was to find out whether mitotic recombination within the *paba1* cistron of *Aspergillus nidulans* is chiefly reciprocal or not, and to compare the process of mitotic recombination with that of meiotic recombination (Siddiqi, 1962) in the same cistron.

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2. MATERIALS AND METHODS

(i) *Markers and strains*

The sequence of the markers used in the present work on the right arm of chromosome I is as follows, the figures being in per cent recombination:

(Centromere)—*pro2*—8—*ad9*—0·5—*paba1*—16—*y*—6—*bi1*

In two of the diploids analysed an unlinked marker, *phen2* (chromosome 3), was also present. (For symbols, techniques and maps, see: Pontecorvo, Roper, Hemmons, Macdonald & Bufton, 1953; Pritchard, 1955, 1960*a*; Pontecorvo & Käfer, 1958; Käfer, 1958.)

The mutants of the *paba1* cistron used in the present work differ from wild-type in requiring for growth *p*-aminobenzoate (pABA). They were mapped by Siddiqi (1962) in the following order:

ad9—*paba5*—*paba2*—*paba15*—*paba18*—*paba19*

The total identified 'length' of the *paba1* cistron corresponds to a recombination fraction of some 5×10^{-4} and the recombination fractions measured were as follows:

paba5—*paba2* $0{\cdot}94 \times 10^{-5}$; *paba5*—*paba15* $3{\cdot}5 \times 10^{-5}$;

paba5—*paba18* 19×10^{-5}; and *paba2*—*paba19* 43×10^{-5}.

The following diploids were synthesized for the present work:

D15:	+ / *pro2*	*ad9* / +	*paba5* / +	+ / *paba2*	*y* / +	+ / *bi1*	+ / *phen2*
D14:	+ / *pro2*	*ad9* / +	+ / *paba5*	*paba2* / +	*y* / +	+ / *bi1*	
D7:	+ / *pro2*	*ad9* / +	*paba5* / +	+ / *paba15*	*y* / +	+ / *bi1*	+ / *phen2*
D5:	+ / *pro2*	*ad9* / +	+ / *paba5*	*paba15* / +	*y* / +	+ / *bi1*	
D3:	+ / *pro2*	*ad9* / +	*paba5* / +	+ / *paba18*	*y* / +	+ / *bi1*	
D6:	+ / *pro2*	*ad9* / +	+ / *paba5*	*paba18* / +	*y* / +	+ / *bi1*	
D20:	+ / *pro2*	*ad9* / +	+ / *paba2*	*paba19* / +	*y* / +	+ / *bi1*	

Two of the *paba* mutants used in the present work, namely, *paba5* and *paba19*, are leaky, i.e. they grow a little even without pABA; *paba5* is also temperature-sensitive; it is leaky at 37° C. (the standard temperature for *Aspergillus nidulans* cultures), while at 20°–25° C. it grows like the wild-type in the absence of pABA.

(ii) *Tests for reversion in homozygotes*

Siddiqi (1962) did not obtain any reversions of the mutants under discussion when 7×10^8 to 1×10^9 viable conidia were plated on medium lacking pABA.

In the present work conidia of diploids homozygous for either *paba2*, or *paba5*, or *paba15*, or *paba18* were stabbed at twenty-six points per dish on pABA-less agar medium. For each diploid not less than 200 such inocula were tested, and none produced pABA-independent sectors. From such numbers of colonies of diploids heteroallelic for two different mutants several sectors would have been obtained: thus, if spontaneous reversions of these mutants occur, they must be extremely infrequent.

(iii) *Isolation and analysis of mitotic recombinants*

As pointed out by Pritchard (1955), three operations are involved in the analysis of intragenic mitotic recombination in *Aspergillus nidulans*. First, a diploid heteroallelic for the two alleles studied is synthesized; second, phenotypically wild-type diploid recombinant colonies (in the present case pABA-independent) are isolated from the diploid; third, the genotypes of these wild-type colonies are determined by means of haploidization.

The seven diploids used in this work (p. 317) were all pABA-requiring because heteroallelic for non-complementing mutants of one cistron. The pABA-independent recombinants selected from each of these diploids (45 to 64, see Table 1) were obtained by stabbing conidia from individual colonies of each diploid in pABA-less medium and isolating only one diploid from each of the stabs which gave prototrophic growth. This minimized the danger of repeated isolation of the products of one recombinational event.

The techniques of haploidization used in the present work were as follows: 1·2–2 ml. of a 1% aqueous solution of DL-*p*-fluorophenylalanine (FPA) were added to 20 ml. of complete medium to give a final concentration of FPA of 0·00324 M to 0·0054 M, and the medium was poured into a Petri dish 10 cm. in diameter. The diploid to be haploidized was inoculated with a needle at ten to twenty-six well-spaced positions. After 5 to 7 days of incubation vigorously growing and abundantly conidiating sectors had developed from each of the stunted colonies arisen at the points of inoculation. As a rule the sectors were haploid; this was verified by determining the diameters of the conidia and the nutritional requirements and, in most cases, the colour of the sectors. Optimal FPA concentrations depended on the diploids to be haploidized, because strains vary in their FPA-sensitivity (Morpurgo, 1961).

Five to ten haploid sectors *of independent origin* were isolated from each diploid and tested for nutritional requirements. As anticipated, two types of haploids were obtained from each diploid; one was pABA-independent, and the other, usually, was pABA-requiring. The pABA-requiring haploid could carry either one or both *paba* mutants present in the original diploid and this had to be verified. For this purpose, all of the seventy pABA-requiring haploids which *did* show recombination between the markers outside the *paba* locus (Table 1, classes 2–5, 7, 9–11, 13–16, 19–21, 25, 27, 28, 30) were crossed to both parental *paba* mutants and by this means classified as single or double *paba* mutants.

For the same purpose, a sample of eighty, out of a total of 309, pABA-requiring

haploids which *did not* show recombination of outside markers, were tested in the same way. All eighty turned out to carry only either one or the other of the *paba* mutants present in the original diploid.

On Table 1 these eighty haploids—tested by crossing—are indicated with one asterisk: 12 from Class 1; 44 from Class 8 (all D5 and D3, and 2 from D7); 15 from Class 12; 4 from Class 18; 2 from Class 23; 1 from Class 24; 1 from Class 26, and 1 from Class 29. These very laborious tests were performed mainly early in our work and this is why they are mainly confined to recombinants from diploids D3 and D5.

In all of the seven diploids analysed in the present work one of the *paba* mutants was leaky: *paba19* in D20 and *paba5* in the other diploids (the former indicated as $paba_y$ in the case of D20 and the latter as $paba_x$ in all other cases in Table 1). All pABA-requiring haploids in which the outside markers arrangement was like that of the leaky parental strain were leaky. There were 123 such leaky haploids with unchanged marker arrangement (Table 1: Classes 1, 6, 8, 12, 22, 23, 24, 26 and 29), thirty of which were test-crossed as mentioned above (leaky haploids with parental marker arrangement which were *not* tested by back-crossing are indicated with two asterisks in Table 1) and proved to carry a single *paba* mutant, i.e. the leaky mutant present in the original parental diploid. It is to be noted that all double *paba* mutants identified in the present work were non-leaky. In other words a haploid with two *paba* mutants, one of them non-leaky, has a non-leaky phenotype (cf. Pritchard, 1955, 1960). It is therefore legitimate to conclude from the above sample that most, possibly all, the haploids having a leaky *paba* phenotype and no change in the outside markers arrangement carried the corresponding parental strand.

3. RESULTS

(i) *Genotypes of the selected diploids*

Three hundred and ninety-three pABA-independent diploids were isolated from the seven parental pABA-requiring diploids. In Table 1 they are divided into thirty-three classes on the basis of the patterns of exchanges which would be required to produce them on the assumption of a classical model of recombination, i.e. reciprocal recombination involving in each exchange any two of the four strands. For each class, the exchange or exchanges required to produce the strand which does not carry one or both *paba* alleles (for short, the $paba^+$ strand) are indicated in Table 1; those required to produce the other strand will be described below. In Classes 31–33 both strands are $paba^+$.

(ii) *Reliability of the results*

There are some factors which could confuse the results. Mutational reversions from $paba^-$ to $paba^+$ can be ignored for the reasons given under 'Materials and Methods'.

A source of error which cannot be excluded without a special investigation, is the possibility that FPA, used for haploidization of recombinant diploids, induces intrachromosomal recombination. This would occur *after* the recombinational event

Table 1. *Genotypes of pABA independent diploids derived from diploids D15, D14, D7, D5, D3, D6 and D20. A proximal* paba *mutant in coupling with* ad9. *B distal* paba *mutant in coupling with* ad9

Recombinant class no.	Parental diploids of type A: a	b	c	d	e	Parental diploids of type B: a	b	c	d	e	Exchanges required to produce the selected (*paba*⁺) strand	Numbers of recombinants obtained from parental diploids of type: A D15	B D14	A D7	B D5	A D3	B D6	B D20	Total
1	+ / *pro2*	*ad9*	$paba_x$	+	*y* / +	+ / *pro2*	*ad9*	+	$paba_x$	+ / *y*	*bi1* / +	c	2**	10**	4**	6*	6*	2**	11	41
2	+ / *pro2*	*ad9*	$paba_x$	$paba_y$	+ / +	+ / *pro2*	*ad9*	+	$paba_x$	+ / *y*	*bi1* / +	c	1*	–	2*	2*	5*	3*	1*	14
3	+ / *pro2*	*ad9*	+	$paba_y$	+ / +	+ / *pro2*	*ad9*	+	+	+ / $paba_y$	*bi1* / +	c	2*	2*	1*	1*	1*	–	1*	8
4	None					+ / *pro2*	*ad9*	+	+	+ / *y*	*bi1* / +	c	–	3*	–	1*	–	1*	5*	10
5	+ / *pro2*	+	+	$paba_y$	+ / +	None						c	–	–	–	–	1*	–	–	1
6	None					+ / +	*ad9*	+	+	+ / $paba_y$	*bi1* / +	c	–	–	–	–	–	–	4**	4
7	None					+ / +	*ad9*	+	+	+ / +	*bi1* / *bi1*	c	–	–	–	–	–	–	1*	1
8	+ / *pro2*	*ad9*	+	+	*y* / +	+ / *pro2*	*ad9*	+	$paba_y$	*y* / +	+ / *bi1*	bc	31	17	26*	24*	18*	8	11**	135
9	None					+ / *pro2*	*ad9*	$paba_x$	+	+ / +	*bi1* / *bi1*	bc	–	–	–	–	–	–	1*	1
10	+ / *pro2*	*ad9*	+	+	*y* / +	+ / *pro2*	*ad9*	+	$paba_y$	+ / +	*bi1* / *bi1*	bc	–	3*	–	–	2*	–	–	5
11	None					*pro2* / *pro2*	+	$paba_x$	+	*y* / +	+ / *bi1*	bc	–	1*	–	–	–	–	–	1
12	+ / *pro2*	*ad9*	$paba_x$	+	*y* / +	+ / *pro2*	*ad9*	+	+	*y* / +	+ / *bi1*	cd	14**	9**	17**	11*	4*	15**	26	96
13	+ / *pro2*	*ad9*	$paba_x$	$paba_y$	+ / +	None						cd	–	–	1*	–	1*	–	–	2
14	None					+ / *pro2*	*ad9*	+	+	*y* / +	+ / +	cd	–	–	–	1*	–	–	–	1

15	+	*ad9*	$paba_x$	+	+	*bi1*	+	*ad9*	+	+	*y*	+	cd	1*	1*	–	1*	–	2*	–	5
	pro2	+	+	+	+	*bi1*	*pro2*		$paba_x$	+	*y*	+									
16	None						+	*ad9*	+	+	*y*	+	cd	–	–	–	–	–	1*	–	1
							pro2	*ad9*	+	$paba_y$	*y*	+									
17	None						+	*ad9*	+	+	*y*	+	cd	–	1	–	–	–	–	–	1
							+	*ad9*	+	$paba_y$	*y*	+									
18	+	*ad9*	+	+	+	*bi1*	+	*ad9*	+	$paba_y$	*y*	+	bcd	7	6	2	3*	1*	7	–	26
	pro2	+	+	$paba_y$	+	*bi1*	*pro2*	+	+	+	*y*	+									
19	+	*ad9*	+	+	+	*bi1*	+	*ad9*	$paba_x$	+	+	*bi1*	bcd	2*	–	–	–	1*	1*	–	4
	pro2	+	$paba_x$	+	*y*	+	*pro2*	+	+	+	*y*	+									
20	+	*ad9*	+	+	+	*bi1*	+	*ad9*	+	$paba_y$	+	*bi1*	bcd	2*	2*	–	–	2*	–	–	6
	pro2	+	+	$paba_y$	*y*	+	*pro2*	+	+	+	*y*	+									
21	None						+	*ad9*	$paba_x$	$paba_y$	+	*bi1*	bcd	–	3*	–	–	–	–	1*	4
							pro2	+	+	+	*y*	+									
22	+	*ad9*	+	+	+	*bi1*	None						bcd	–	–	–	–	1**	–	–	1
	+	*ad9*	$paba_x$	+	*y*	+															
23	+	+	+	+	*y*	+	+	*ad9*	+	$paba_y$	*y*	+	ac	1	–	–	1*	1*	1	1**	5
	pro2	+	+	$paba_y$	+	*bi1*	*pro2*	*ad9*	+	+	+	*bi1*									
24	+	*ad9*	$paba_x$	+	*y*	+	+	+	+	+	+	*bi1*	abc	–	–	–	–	1*	1	–	2
	pro2	*ad9*	+	+	*y*	+	*pro2*	+	$paba_x$	+	+	*bi1*									
25	None						+	+	+	+	+	*bi1*	abc	–	1*	–	–	–	–	1*	2
							pro2	+	+	$paba_y$	*y*	+									
26	+	*ad9*	$paba_x$	+	*y*	+	None						acd	–	–	–	–	1*	–	–	1
	+	+	+	+	+	*bi1*															
27	None						+	*ad9*	$paba_x$	+	+	*bi1*	acd	–	1*	–	–	–	–	–	1
							pro2	*ad9*	+	+	*y*	+									
28	None						+	+	$paba_x$	+	+	*bi1*	acd	–	1*	–	–	–	1*	–	2
							pro2	*ad9*	+	+	*y*	+									
29	+	*ad9*	$paba_x$	+	*y*	+	+	+	+	+	*y*	+	abcd	–	2**	1**	–	1*	–	–	4
	pro2	*ad9*	+	+	+	*bi1*	*pro2*	+	$paba_x$	+	+	*bi1*									
30	+	*ad9*	$paba_x$	+	+	*bi1*	None						abcd	1*	–	–	–	–	–	–	1
	pro2	*ad9*	+	+	+	*bi1*															
31	*pro2*	+	+	+	*y*	+	+	*ad9*	+	+	+	*bi1*	c	–	–	–	–	1	1	–	2
	+	*ad9*	+	+	*y*	+	*pro2*	+	+	+	+	*bi1*	bc								
32	None						+	*ad9*	+	+	*y*	+	cd	–	1	–	–	–	–	1	2
							pro2	+	+	+	+	*bi1*	bc								
33	+	*ad9*	+	+	+	*bi1*	None						bcd	–	–	1	–	2	–	–	3
	pro2	+	+	+	*y*	+							c								
													Total	64	64	55	51	50	44	65	393

* *paba* strand tested by crossing back to both *paba* parents.

** *paba* strand leaky and therefore inferred to carry only one (the leaky one) *paba* mutant.

which gave rise to the selected pABA-independent diploid, and would therefore confuse the analysis. This effect, if it occurs at all, turns out to be negligible.

Consider a recombinant with the following genotype:

+	*ad9*	$paba_x$	$paba_y$	+	*bi1*
pro2	+	+	+	*y*	+

Any further recombination in the *pro–bi* interval occurring during haploidization would produce new types of recombinants: in addition to *ad paba bi* and *pro y* haploids there would be, for example, *ad paba y* and *pro bi* sectors and so on. Out of at least 2000 haploid sectors of independent origin tested from the 393 diploids analysed, only once three, instead of two, types of haploid sectors were obtained from one diploid recombinant. If FPA induced appreciable intrachromosomal recombination during the time of haploidization, some of the exchanges should have occurred in the *y–bi* interval, but none was observed.

Thus, the frequencies of both mutational reversions and additional recombinations during haploidization would not alter seriously the picture of intragenic mitotic recombination.

4. ANALYSIS OF THE RESULTS

(i) *Reciprocity of exchanges*

Out of 393 pABA-independent diploids (Table 1) obtained from seven diploids heteroallelic for *paba* mutants, thirty-five (Classes 3–5, 19, 20, 25, 27, 28 and 30) carried both $paba^+$ and $paba^-$ strands which were recombinant in respect of outside markers. In eighteen diploids (Classes 2 and 21) the $paba^+$ strand showed recombination of outside markers, and the $paba^-$ strand carried the two *paba* mutants and was recombinant in respect of the outside markers. In seventy-eight diploids (Classes 1, 18, 23, 24 and 29) the $paba^+$ strand showed recombination of outside markers and the $paba^-$ strand was fully parental. In thirteen diploids (Classes 9, 10 and 14–16) the $paba^+$ strand showed one or the other parental arrangement of outside markers, and the $paba^-$ strand showed recombination of outside markers. In two diploids (Class 13) the $paba^+$ strand showed one of the parental arrangements of outside markers, and the $paba^-$ strand was recombinant in respect of both the *paba* cistron and the outside markers. In the most numerous group, consisting of 231 diploids (Classes 8 and 12), the $paba^+$ strand showed a parental arrangement of outside markers, and the $paba^-$ strand was fully parental. Nine diploids (Classes 6, 7, 11, 17, 22 and 26) were either of non-disjunctional origin or arose by further exchanges in the centromere–*pro* interval; it is impossible to distinguish between these two alternatives. In seven diploids (Classes 31–33) both strands were $paba^+$, and these include a number of arrangements in respect of the outside markers of either or both strands.

The simplest interpretation for the origin of the large proportion (231 out of 393) of diploids in which the $paba^+$ strand showed a parental arrangement of outside markers is a process of non-reciprocal recombination. This interpretation is further supported by the fact that, even among the fifty-three diploids in which both

strands showed recombination of outside markers, only one-third (Classes 2 and 21) contained reciprocal recombinants in respect of the *paba* sites.

(ii) *Types of exchanges*

The types of exchanges observed in the half-tetrads analysed can be divided into three main groups.

In the first and most numerous group, only one strand was apparently recombinant (Table 1, Classes 8 and 12). Corresponding types have been observed in tetrad and half-tetrad analyses in yeast (Lindegren, 1953; Roman, 1956, 1958), *Neurospora crassa* (Case & Giles, 1958*a*,*b*; H. K. Mitchell, 1957; M. B. Mitchell, 1955*a*,*b*; Stadler, 1959; Suyama, Munkres & Woodward, 1959; Stadler & Towe, 1963), *Aspergillus nidulans* (Strickland, 1958), *Ascobolus immersus* (Lissouba, 1960; Lissouba & Rizet, 1960; Rizet, Lissouba & Mousseau, 1960; Lissouba, Mousseau, Rizet & Rossignol, 1962) and *Sordaria fimicola* (Olive, 1959; Kitani, Olive & El-Ani, 1961).

In the second group, two strands were recombinant as follows: (*a*) single, reciprocal exchanges (Class 2); (*b*) single, probably inexactly reciprocal exchanges (Classes 3, 4 and 5); similar exchanges have been observed in *Neurospora* tetrads (Case & Giles, 1958*a*; Stadler, 1959; Stadler & Towe, 1963); (*c*) multiple exchanges, both reciprocal and non-reciprocal (Classes 19, 20, 21, 25, 27, 28, 32 and 33); similar exchanges have been observed in *Neurospora* tetrads by M. B. Mitchell (1955*a*), by Case & Giles (1958*a*) and by Stadler & Towe (1963).

In the third group at least three strands were recombinant (Classes 7, 9, 10, 11, 13, 14, 15, 16, 30 and 31). Strickland (1961) and Stadler & Towe (1963) obtained similar recombination patterns in *Neurospora*, while one of the tetrads analysed by Giles, DeSerres & Barbour (1957) in *Neurospora* seems to indicate that three strands can be involved in exchanges within very short regions. Alternatively, this group of diploids could have arisen by non-reciprocal exchanges over the *paba–bi* interval, which is twenty-two meiotic map units long. This seems unlikely, since the data so far available seem to indicate that non-reciprocal exchanges as a rule occur over very short distances (however, cf. Strickland, 1958).

The distribution of exchanges among *paba*$^+$ strands is shown in Table 2, and the total frequencies of exchanges in the marked intervals are shown in Table 3.

The data for diploids heteroallelic for the same pairs of *paba* mutants but with reciprocal arrangements of the outside markers were tested for homogeneity. The data for diploids D7 and D5 (heteroallelic for *paba5* and *paba15*) and those for diploids D15 and D14 (heteroallelic for *paba2* and *paba5*) proved to be homogeneous and they have been pooled in Tables 2 and 3. Those for diploids D3 and D6 (heteroallelic for *paba5* and *paba18*) were not homogeneous, and are given separately in the two tables.

The great majority of non-selected exchanges occurred in intervals adjacent to *c*. Thus, in interval *a* there were further exchanges only in 4·8% of the *paba*$^+$ recombinants, in *b* in 52·9%, in *d* in 42·3% of recombinants, and in *e* no further exchanges were observed. This means that negative interference, in mitotic as in meiotic recombination, is strictly localized.

Table 2. *Types of exchanges in pABA-independent strands*

Diploid:	D14 + D15		D7 + D5		D3		D6		D20		Classes of diploids
Interval	No.	%	No.	%	No.	%	No.	%	No.	%	
c	20	15·50	18	16·82	16	30·19	7	15·56	23	34·84	1–7, 31, 33
bc	53	41·09	51	47·66	21	39·62	9	20·00	13	19·69	8–11, 31, 32
cd	27	20·93	30	28·05	5	9·42	18	40·00	27	40·91	12–17, 32
bcd	22	17·05	6	5·61	7	13·21	8	17·78	1	1·52	18–22
abc	1	0·78	—	—	1	1·89	1	2·22	1	1·52	23
ac	1	0·78	1	0·93	1	1·89	1	2·22	1	1·52	24–25
acb	3	1·55	—	—	1	1·89	1	2·22	—	—	26–28
abcd	3	2·32	1	0·93	1	1·89	—	—	—	—	29–30
Total	129		107		53		45		66		

Table 3. *Total frequencies of non-selected exchanges in pABA-independent strands*

Diploid:	D14+D15 No.	D14+D15 %	D7+D5 No.	D7+D5 %	D3 No.	D3 %	D6 No.	D6 %	D20 No.	D20 %	Total	Per cent of total
Interval												
a	7	5·00	2	1·87	4	7·55	3	6·67	2	3·03	18	4·76
b	79	56·43	58	54·20	30	56·60	18	40·00	15	22·73	200	52·91
d	54	38·57	37	34·58	14	26·41	27	60·00	28	42·42	160	42·33
Total no. of exchanges	140		97		48		48		45		378	
No. of strands	129		107		53		45		66		400	
Mean no. of non-selected exchanges per strand	1·09		0·91		0·90		1·07		0·68		0·95	

5. DISCUSSION

There are striking differences between the patterns of mitotic and meiotic recombination within the *paba1* region. The proportion of single exchanges (additional to that selected) to double and multiple exchanges is much greater in meiotic recombination than in mitotic recombination.

The total frequency of non-selected exchanges (i.e. other than in the interval *c* where the exchange is selected) falls rather sharply in meiotic recombination as the length of the interval of selection increases. In mitotic recombination this decrease is not so sharp (Table 2: D14 = *paba2/paba5*, D3 = *paba5/paba18*. From crosses where the *pro–ad* interval was marked (Siddiqi & Putrament, 1963), it appears that there is no increase in meiotic exchanges in this interval among pABA-independent recombinants. In mitotic recombination, on the contrary, exchanges in the *pro–ad* interval *a* are observed in 4·8% of pABA-independent recombinants (Table 3). One can suppose that in mitotic recombination effective pairing segments are longer than in meiotic recombination.

SUMMARY

The results of the analysis of 393 mitotic recombinants within the *paba1* region of *Aspergillus nidulans* can be summarized as follows:

1. Reciprocal, non-reciprocal and probably inexactly reciprocal exchanges occur in intra-cistron mitotic recombination.

2. Negative interference observed in intracistron mitotic recombination in the *paba1* region of *Aspergillus nidulans* is more intense than that observed in meiotic recombination in the same cistron.

3. In intragenic mitotic recombination multiple exchanges can involve three or even four chromatids within one effective pairing segment.

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