Genet. Res., Camb. (1960), **1**, *pp.* 129–139
With 1 plate and 2 text figures
Printed in Great Britain

Migration of nuclei in *Coprinus lagopus*

By K. M. SWIEZYNSKI* and P. R. DAY
John Innes Horticultural Institution,
Bayfordbury, Hertford, Herts.

(*Received* 27 *July* 1959)

INTRODUCTION

The migration of nuclei in compatible matings between monokaryotic strains of a basidiomycete was established by Buller (1931) in *Coprinus lagopus*. Since then it has been observed in various other species and genera (Dickson, 1936; Fulton, 1950; Kimura, 1954; Snider & Raper, 1958). In *C. lagopus* when mycelium of a compatible strain is placed on one side of an established colony of a monokaryon the nuclei of the added mycelium spread within the mycelium of the monokaryon. Normally both strains in a compatible mating are able to accept and donate nuclei, but in some matings only one of the strains may accept nuclei, the other acting only as a donor. This behaviour has been called unilateral dikaryotization.

Migration of nuclei with the same allele at the *A* locus as the nuclei of the mycelium into which they pass has also been demonstrated in several basidiomycetes (Raper, 1953), but no migration of this kind has been found in *C. lagopus* (Papazian, 1958).

In another paper, Swiezynski & Day (1960) report the occurrence, and describe some of the properties of common *A*, common *B* and common *AB* heterokaryons in *C. lagopus*. This paper describes studies of nuclear migration during the establishment of these heterokaryons and the dikaryon.

MATERIALS AND METHODS

Strains derived from wild-type 68 (A_2B_1) (Day, 1959) and cultures and media described in our preceding paper (Swiezynski & Day, 1960) were used.

Matings and tests of migration were made in two ways. A plug 2 mm. in diameter, punched from a colony of one parent, was placed at the edge of an established colony, 20–40 mm. in diameter, of the other parent (Fig. 1). After given time intervals samples were taken from various parts of the established colony and tested for migrant nuclei. This method was used with reciprocal pairings for all measurements of the speed of nuclear migration. Alternatively, rectangular (1×15 mm.) inocula of the two mycelia to be mated were placed at an angle of about 45 degrees to each other, the nearest points being some 3 mm. apart (Fig. 2). Three such matings were made on a plate. After 3 or 4 days' incubation, two

* The senior author was supported by a Polish Academy of Sciences Scholarship while on leave of absence from the Institute of Genetics, Skierniewice, Poland.

samples from each parent, at points 10 and 20 mm. from the region of contact between the mycelia, were tested for migrant nuclei.

The samples were either small (*ca.* 1 mm. side) or large (*ca.* 3 mm. side). Several methods were used to detect migrant nuclei in them. When the mating was between compatible strains, dikaryotization was assumed to have taken place if clamp connexions were observed in the samples grown on fresh media. Samples from common *A* or common *B* matings were mated with a tester stock compatible with migrant nuclei but incompatible with resident nuclei. Abundant clamp formation was regarded as evidence of the presence of migrant nuclei. Samples

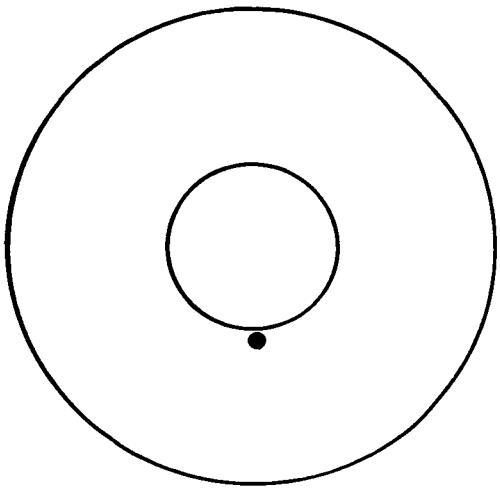


Fig. 1

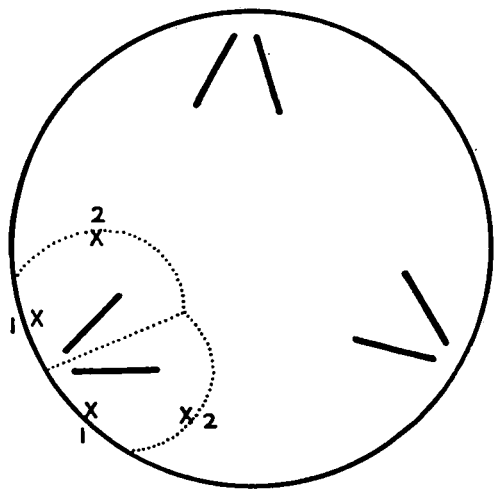
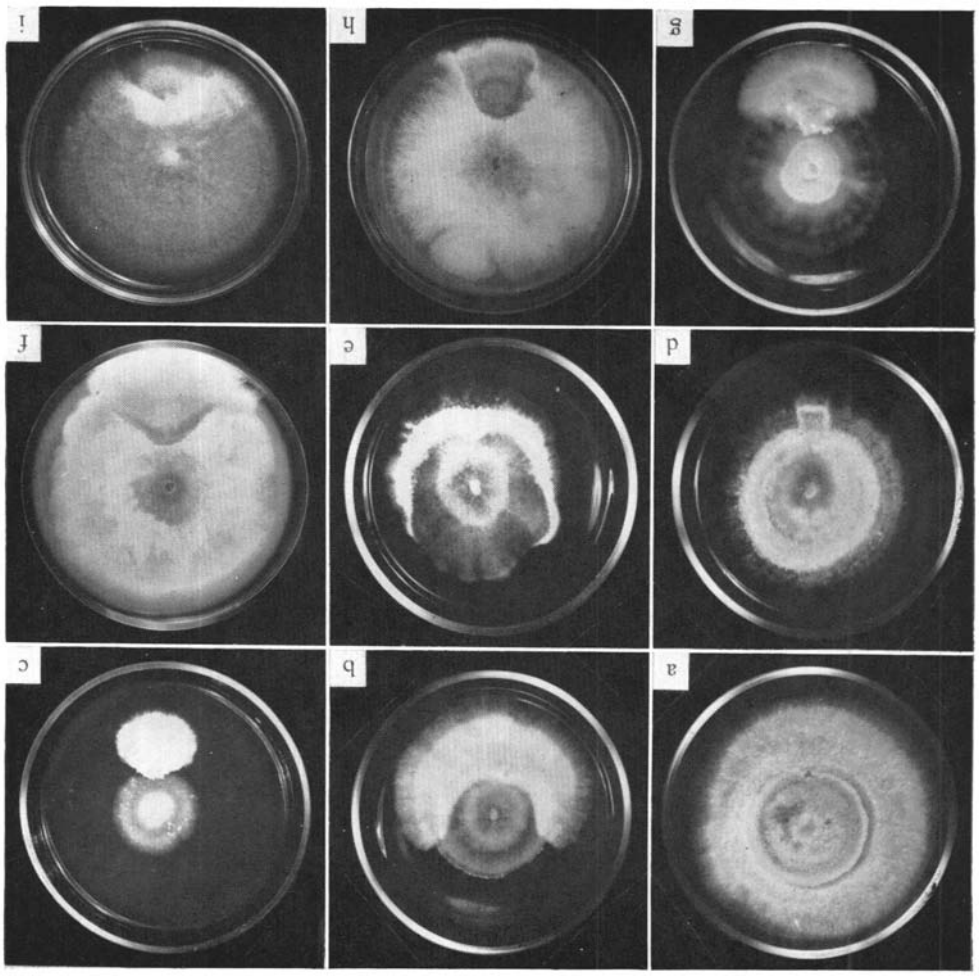


Fig. 2

Figs. 1 and 2. Methods of mating mycelia: Fig. 1: 2-mm. plug at edge of colony 20–40 mm. in diameter. Fig. 2: rectangular inocula (1 × 15 mm.) placed at an angle of about 45 degrees to each other. X, sampling points: 1, 10 mm., and 2, 20 mm. from region of contact between mycelia.

from matings between complementary auxotrophic strains were tested for prototrophy on minimal medium or on minimal medium supplemented with the requirement of the migrant nucleus only. Prototrophic growth on either medium was regarded as proof of the presence of migrant nuclei.

The occurrence of nuclear migration was not confirmed by other methods. It could be argued that what we accept as migration may be explained as enhanced growth of one mycelium through another. We think that this explanation is untenable for the following reasons: the parent mycelia in common *A* and common *AB* matings do not grow through each other. It is difficult to conceive how mycelia may grow through a dense, established, mass of hyphae in media nearly exhausted of nutrients. The most rapid nuclear migration occurs round the margins of the mated colonies (Buller, 1931), but in these areas there is no obvious invasion of hyphae.



a – c Compatible matings: *a*, Type I; *b*, Type II; *c*, Type IV.
d – f Common *A* matings: *d*, Type I; *e*, Type II; *f*, Type IV.
g – h Common *B* matings: *g*, Type III; *h*, Type IV.
i Common *AB* mating: Type III.

https://doi.org/10.1017/S0016672300000124 Published online by Cambridge University Press

All matings were made on complete medium in Petri dishes 100 mm. in diameter and incubated at 28° C. unless otherwise stated.

The influence of mating type on the migration of nuclei

To test the migration of nuclei, compatible, common A and common B matings were made of the four wild-type strains H_1 (A_5B_5), H_2 (A_6B_5), H_5 (A_5B_6) and H_9 (A_6B_6). No common AB matings were made because the heterokaryons cannot be recognized unless marked strains are used. At the same time, two mutants with choline (*chol*-1), and methionine (*me*-5) requirements, each represented by the four mating-type strains A_5B_5, A_5B_6, A_6B_5 and A_6B_6, were tested in all complementary combinations (i.e. choline- and methionine-requiring strains only were crossed). The choline- and methionine-requiring strains tend to be unilateral in compatible matings and they were selected to see if they would also only donate nuclei in incompatible matings. Certain matings with other mutant strains were also tested.

The reactions observed could be divided into the following types:

Type I: Nuclei from the added strain migrate rapidly and may be found in all parts of the established colony. Before migration is complete no margin is visible between the invaded and uninvaded areas.

Type II: The added nuclei migrate more slowly than in Type I. The migration proceeds most quickly in the young mycelium and eventually extends to the whole of the established colony. There is a visible margin between the invaded and uninvaded areas. This margin does not always correspond exactly with the extent of migration, and migrating nuclei may be found beyond this limit.

Type III: A slow spread of nuclei across the region of contact which perhaps might be due to limited hyphal growth of the added strain. The extent of invasion is often greater in the older parts of the colonies than in the periphery. Differences between the invaded and uninvaded area may or may not be visible.

Type IV: No migration of nuclei occurs. Nuclei of one strain only can be detected at a distance of 5 mm. from the region of contact.

Photographs illustrating these reaction types from matings made by the method shown in Fig. 1 are shown in Plate 1.

The results obtained from matings incubated for 4 days are presented in Table 1 and may be summarized as follows:

1. In compatible matings all types of reaction (I, II, III and IV) were observed. Type III or IV reactions were found when the established colony was formed by a unilateral stock.

2. In each common A mating nuclear migration could be observed, but in two combinations ($A_5B_5 \times A_5B_6$ and $A_2B_5 \times A_2B_6$) it was not observed in every test. In 27 out of 46 matings migration of Type I occurred. Nuclei containing either of the three A alleles tested (A_2, A_5 and A_6) were able to migrate in common A mycelia.

3. In the crosses between choline- and methionine-requiring strains in which

Table 1. *Migration of nuclei in various mating-type combinations*

Established strain	Added strain	Compatible: Number of matings	Compatible: Type of reaction I	II	III	IV	Common *A*: Number of matings	Common *A*: Type of reaction I	II	III	IV	Common *B*: Number of matings	Common *B*: Type of reaction I	II	III	IV	Common *AB*: Number of matings	Common *AB*: Type of reaction I	II	III	IV
Wild-type-1*	Wild-type-1	12	12	—	—	—	12	8	—	4	—	8	—	—	—	8†	—	—	—	—	—
	Wild-type-2	—	—	—	—	—	6	5	—	—	1†	6	—	—	—	3†	—	—	—	—	—
Wild-type-2*	Wild-type-1	—	—	—	—	—	6	5	—	—	1†	6	—	—	—	3†	—	—	—	—	—
Wild-type-1	*me*-5 *ad*-5	1	—	1	—	—	1	—	1	—	—	1	—	—	—	1	—	—	—	—	—
,,	*ad*-5	1	1	—	—	—	1	—	—	—	1	1	—	—	—	1	—	—	—	—	—
me-5 *ad*-5	Wild-type-1	1	—	—	—	1	1	—	—	—	1	1	—	—	—	1	—	—	—	—	—
me-5	,,	—	—	—	—	—	1	1	—	—	—	1	—	—	—	1†	1	—	—	—	1†
chol-1	,,	—	—	—	—	—	2	1	1	—	—	2	—	—	—	2†	2	—	—	—	2†
ad-8	,,	—	—	—	—	—	4	2	2	—	—	4	—	—	2	2	3	—	—	1	2
chol-1	*me*-5	6	3	2	1	—	6	4	1	—	1	6	—	—	1	5	6	—	—	1	5
me-5	*chol*-1	6	1	2	3	—	6	1	2	2	1	6	—	—	2	4	6	—	—	3	3

* Wild-type-1 strains had A_5, A_6, B_5 or B_6 alleles
Wild-type-2 strains had either A_2 or B_1 alleles
† Scored after 3 days

all mating type combinations were tested, the migration of common *A* nuclei was about as frequent as the migration of compatible nuclei.

4. No extensive migration of common *B* or common *AB* nuclei was found. In a few matings the nuclei of the added strain were found a short distance from the region of contact (Type III). They were never found more than 10 mm. from it, although sometimes enhanced mycelial growth occurred more than 10 mm. on either side of the junction of mycelia (Plate I, *i*).

Comparison of the speed of migration of compatible and common A *nuclei*

The four wild-type strains A_5B_5, A_5B_6, A_6B_5 and A_6B_6 were each reciprocally mated with the compatible strains A_6B_6, A_6B_5, A_5B_6 and A_5B_5 respectively, and also with the common *A* strains A_5B_6, A_5B_5, A_6B_6 and A_6B_5 (see Fig. 1). The matings were made when the established colonies were about 40 mm. in diameter. Large samples were taken from the established colonies after 30 and 60 hours. Initially the matings were carried out on complete medium. Ten samples were taken from each colony at each time and the sampling was repeated after 80 and 100 hours. At each sampling time the radius of the colony formed by the added mycelium was also measured. This colony soon became either a dikaryon or a common *A* heterokaryon, according to the mating, forming a sector in the established colony. Nuclear migration was observed in every mating, and migrant nuclei were detected in the marginal and central parts of the invaded colonies. The rate of migration was much faster than the rate of growth of the mycelium. In samples taken from the margins of common *A* matings after 80 and 100 hours sometimes migrant nuclei were not found although they had been detected in earlier samples taken along the same radii. This behaviour suggests that there may be a secondary inhibition of common *A* nuclear migration (Swiezynski & Day, 1960).

All four combinations of compatible and common *A* matings were repeated on complete and on minimal medium. Eight small samples were taken each time, mainly from the colony margins. The growth-rates for the added mycelia and the nuclear migration rates were calculated. The results are given in Table 2.

Table 2. *Speed of migration of compatible and common* A *nuclei*

		After 30 hr.		After 60 hr.	
Type of mating	Number of colonies tested	Speed of growth (mm./hr.)	Speed of migration (mm./hr.)	Speed of growth (mm./hr.)	Speed of migration (mm./hr.)
			Complete medium		
Compatible	4	0·17–0·24	0·66–1·00	0·18–0·25	0·83–0·92
Common *A*	4	0·20–0·23	0	0·18–0·25	0·00–0·66
			Minimal medium		
Compatible	4	0·10–0·17	0·33–0·50	0·10–0·15	0·50–0·92
Common *A*	4	0·17–0·24	0	0·13–0·22	0·00–0·50

The rates given are the smallest and largest for each group of four plates

https://doi.org/10.1017/S0016672300000124 Published online by Cambridge University Press

The following conclusions may be drawn:

1. The rate of migration of nuclei exceeds the rate of growth of the mycelium. It should be pointed out that the calculated rate of nuclear migration is certainly too small, for reasons discussed in detail by Snider & Raper (1958).

2. The migration of common *A* nuclei is slower than the migration of compatible nuclei.

3. There was no significant difference between the speeds of nuclear migration on minimal and on complete medium when measured after 60 hours.

Heterokaryon-monokaryon matings

This section describes the results of two series of experiments to investigate the extent of nuclear migration, in either direction, between heterokaryons and monokaryons (het-mon matings).

In the first series a variety of het-mon matings were set up using wild-type strains. The method shown in Fig. 2 was used. Samples from both parents of each mating were tested for clamp formation. Samples from some matings were also mated with tester stocks to demonstrate the presence of migrant nuclei. To simplify presentation the suffixes x and y have been introduced to denote alleles 5 or 6 at either of the mating type loci, so that when x is 5, y is 6, and when x is 6, y is 5. The suffix z denotes the alleles A_2 or B_1. Thus the two formulae $(A_5B_5 \times A_6B_5)$ and $(A_5B_6 \times A_6B_6)$ can be represented by $A_xB_x \times A_yB_x$). The results from the het-mon matings are given in Table 3.

Several of the test matings are ambiguous. Thus the first line of Table 3 shows that clamps were formed on the monokaryon in 2 out of 4 het-mon matings: $(A_xB_x \times A_yB_y) \times A_xB_y$. Since such matings are incompatible, the finding of clamps on the monokaryon component in similar test matings (next 4 lines, column 6, Table 3) cannot be taken as evidence of migration of nuclei, compatible with the tester stock, into the dikaryon. The data in Table 4, which are based on a prototrophy test for migrant nuclei, show that such migration does not occur. The cause of this anomaly, which is part of the Buller phenomenon, is referred to in detail in the discussion.

In the second series of experiments, compatible, common *A* and common *B* heterokaryons were composed of auxotrophic mutants with the same growth requirements and were therefore unable to grow on minimal medium. Monokaryons were either wild type or complementary auxotrophic mutants. Common *AB* heterokaryons were always composed of complementary auxotrophic strains and het-mon matings with them were performed on minimal medium to ensure maximum stability of the heterokaryon.

The migration of nuclei was again established by tests for the presence of clamps, and tests of the compatibility of samples with appropriate tester stocks. In addition tests were made of the ability of samples to grow on minimal medium. The results are given in Table 4.

Table 3. *Heterokaryon-monokaryon matings: wild-type strains*

Heterokaryon	Monokaryon	Number of matings	Clamps on		Number of compatible results from mating two samples of			
			Heterokaryon	Monokaryon	Heterokaryon with		Monokaryon with	
Compatible	A_xB_y	4*	4	2	—		—	
($A_xB_x \times A_yB_y$)	A_xB_z	2	2	2	A_yB_x*	1	—	
	A_yB_z	2	2	2	A_xB_y*	2	—	
	A_zB_y	2	2	2	A_xB_y*	1	—	
	A_zB_y	2	2	2	A_yB_x*	1	—	
Common *B*	A_yB_y	2	0†	2	A_xB_x	2	A_xB_y	2
($A_xB_x \times A_yB_x$)	A_xB_y	2	0†	2	A_yB_x	0	A_yB_y	2
	A_zB_x	2	0†	0	—		A_zB_y	0
	A_xB_z	2	0†	2	—		—	
	A_yB_z	2	0†	2	—		—	
Common *A*	A_yB_x	2	0	1	A_xB_y	0	A_yB_y	1
($A_xB_x \times A_xB_y$)	A_yB_y	2	0	2	A_xB_x	0	A_yB_x	2
	A_xB_z	2	0	0	—		A_yB_z	2
	A_zB_x	2	0	2	—		—	
	A_zB_y	2	0	2	—		—	

* Incompatible het-mon matings.

† Only typical common *B* heterokaryon clamps were found.

The following conclusions may be drawn from Tables 3 and 4:

1. All heterokaryons regularly donated nuclei to monokaryons which were compatible, or had only one *A* factor in common, with one or both of the heterokaryon nuclei. Appropriate matings showed that compatible, common *A* and common *B* heterokaryons were able to donate either nucleus.

Table 4. *Heterokaryon-monokaryon matings: auxotrophic strains*

Composition		Number of matings	Number of positive results				
			Heterokaryon		Monokaryon		
Heterokaryon	Monokaryon		On minimal medium	Clamps	Mated with		Clamps
Compatible							
$A_xB_x \times A_yB_y$	A_xB_x	4	0	+	A_yB_y	4	4
,,	A_xB_x	4	0	+	A_yB_y	3	4
,,	A_yB_x	4	0	+	A_xB_x	4	4
,,	A_xB_y	4	0	+	A_xB_x	4	4
,,	A_xB_x	4	0	+	—		4
Common *B*							
$A_xB_x \times A_yB_x$	A_yB_y	3	0	—	A_xB_y	2	3
,,	A_xB_y	3	0	—	A_yB_y	2	3
,,	A_xB_x	3	0	—	A_xB_y	—	—
,,	A_xB_x	3	0	—	—		3
,,	A_yB_x	3	0	—	—		3
,,	A_xB_x	3	0	—	—		3
Common *A*							
$A_xB_x \times A_xB_y$	A_yB_x	4	—	—	A_yB_y	—	4
,,	A_yB_y	4	—	—	A_xB_x	1	4
,,	A_xB_x	4	2	—	A_yB_x	4	—
,,	A_xB_x	4	4	3	—		4
,,	A_xB_y	4	2	2	—		4
,,	A_xB_x	4	3	3	—		4
Common *AB*							
$A_xB_x \times A_xB_x$*	A_xB_y	9	Mated with A_yB_y 5	—	—		—
,,	A_yB_y	7	—	7	—		7

* These heterokaryons were prototrophic

2. Compatible and common *B* heterokaryons never accepted nuclei from the monokaryon whether compatible or not. Common *A* heterokaryons frequently accept compatible and common *A* nuclei although in some matings no migration occurred. Common *AB* heterokaryons accept compatible and common *A* nuclei.

The data in Table 4 show that in matings of the type $(A_xB_x \times A_xB_y) \times A_yB_x$ there is no migration in the heterokaryon but that migration occurs when the

https://doi.org/10.1017/S0016672300000124 Published online by Cambridge University Press

monokaryon is A_zB_x. The A_zB_x monokaryon was prototrophic, and since the A_yB_x monokaryon was auxotrophic its nuclei may have had a lower potentiality for migration. To determine whether such a heterokaryon can accept an A_yB_x nucleus, four different matings were made between auxotrophic common *A* heterokaryons and prototrophic wild-type monokaryons using the two methods described above (Figs. 1 and 2). Samples were tested for clamp formation and prototrophy. Each monokaryon had nuclei compatible with one or other of the heterokaryon nuclei. The results, given in Table 5, show that migration of A_5 or A_6 nuclei in common *A* heterokaryons occurred in 7 out of 16 matings.

Table 5. *Nuclear migration into a common* A *heterokaryon from a monokaryon*

Mating types and requirements	Method used: 1 colony per plate (Fig. 1)	Method used: 3 colonies per plate (Fig. 2)
$(A_5B_5 \times A_5B_6)$ *chol* $\times A_6B_6$	+	+
,, $\times A_6B_5$	—	+
$(A_5B_5 \times A_5B_6)$ *ad* $\times A_6B_6$	—	—
,, $\times A_6B_5$	—	—
$(A_6B_5 \times A_6B_6)$ *chol* $\times A_5B_5$	+	+
,, $\times A_5B_6$	+	+
$(A_6B_5 \times A_6B_6)$ *ad* $\times A_5B_5$	—	—
,, $\times A_5B_6$	—	—

DISCUSSION

Migration of nuclei in compatible matings between monokaryotic strains of tetrapolar basidiomycetes has been found in many species since Buller's classical account of 'diploidization' in *Coprinus lagopus* published in 1931. Nuclear migration in common *A* matings has been observed in some species, notably *Schizophyllum commune* (Raper, 1953; Raper & San Antonio, 1954; Snider & Raper, 1958) and *Cyathus stercoreus* (Fulton, 1950). Our finding that common *A* migration also occurs in *C. lagopus* confirms the existence in this species of what may prove to be general behaviour. So far as we are aware, extensive nuclear migration in common *B* matings has never been recorded. It is not seen in *C. lagopus*.

We find that the dikaryon of *C. lagopus* is unable to accept compatible nuclei. Both dikaryons and common *B* heterokaryons produce clamp connexions which arise during synchronized mitotic divisions of the nuclei in the growing hyphal tips. It seems possible that the mechanism controlling this synchronized division which is called into play when nuclei having different *A* alleles are present in the same cell, may also restrict or even prevent nuclear migration.

Snider & Raper (1958) found that common *A* nuclei in *S. commune* migrate at the same rate as compatible nuclei, but are not as densely distributed. The data presented here and our results published elsewhere (Swiezynski & Day, 1960) show

that this is not the case in *C. lagopus*. In *Coprinus* the migration of common *A* nuclei is slower than the migration of compatible nuclei and there appears to be some secondary limitation of migration, perhaps connected with changes due to ageing in the recipient mycelium, which retards the movement of either nucleus into the new growth of the heterokaryon.

The first studies of dikaryon × monokaryon (di-mon) matings were made by Buller (1930, 1931). The migration of nuclei from a dikaryon to a monokaryon was termed the Buller phenomenon (Quintanilha, 1937). A great deal of interest has centred on the finding that incompatible di-mon matings of the type $(A_1B_1 \times A_2B_2) \times A_1B_2$ lead to dikaryotization of the monokaryon. Several authors (Papazian, 1950; Kimura, 1958; Crowe, 1958) have shown that the resulting dikaryon may contain both nuclei of the original dikaryon $(A_1B_1 \times A_2B_2)$ or a recombinant nucleus from this dikaryon (A_2B_1) which is compatible with the nucleus of the monokaryon. Interesting examples are cited by Kimura (1958), who found that in compatible and hemi-compatible di-mon matings with *C. macrorhizus* both nuclei of the dikaryon sometimes passed to the monokaryon, supplanting its own nucleus. An explanation of the migration of both nuclei of a dikaryon, to displace the nuclei of an established monokaryon, may be found in our studies. We have shown (Tables 1–5) that common *A* migration regularly occurs between monokaryons and from heterokaryons to monokaryons. It seems reasonable to suppose therefore that in a non-compatible mating—for example, $(A_1B_1 \times A_2B_2) \times A_1B_2$—the A_1B_1 nucleus would migrate into the A_1B_2 mycelium inoculated alongside. The common *A* heterokaryon $(A_1B_1 + A_1B_2)$ thus formed would then be able to accept the other nucleus of the dikaryon (A_2B_2), becoming dikaryotized as we have already shown may happen (Table 5). In this way the migration of both nuclei may be understood. To explain the migration of both nuclei in hemi-compatible di-mon matings—for example, $(A_1B_1 \times A_2B_2) \times A_2B_3$—we only need assume that the A_2B_2 nucleus of the dikaryon was the first to migrate and was then followed by the A_1B_1 nucleus, and the first of the two possible dikaryons to become established was $A_1B_1 \times A_2B_2$. It is to be expected that this would be a rare event since compatible nuclei tend to migrate more rapidly than common *A* nuclei. To explain the migration of both dikaryon nuclei in compatible di-mon matings (e.g. $(A_1B_1 \times A_2B_2) \times A_3B_3$), Kimura (1958) has suggested that there are different degrees of affinity between unlike alleles probably controlled by modifier genes. In our view this explanation is unnecessary.

SUMMARY

1. Four main types of interaction between paired mycelia of *Coprinus lagopus* have been defined in terms of the extent of nuclear migration.

2. Nuclear migration was demonstrated in matings between monokaryotic mycelia with common *A* alleles. No extensive migration of nuclei was found in common *B* or common *AB* matings.

3. The speed of nuclear migration in common *A* matings was slower than in

compatible matings. Migration occurred to approximately the same extent in both kinds of matings.

4. In heterokaryon-monokaryon matings compatible and common *B* heterokaryons acted only as donors. Common *AB* heterokaryons acted as donors and as acceptors of compatible or common *A* nuclei. Common *A* heterokaryons always acted as donors and frequently acted as acceptors of compatible or common *A* nuclei.

5. A simple explanation is suggested for the frequently observed fact that in an incompatible di-mon mating both nuclei of the dikaryon may migrate and eventually eliminate the nuclei of the established monokaryon.

REFERENCES

Buller, A. H. R. (1931). *Researches on Fungi*, **4.** Longmans, Green & Co., London.

Crowe, L. K. (1958). (Abstract.) The exchange of genes between nuclei of a dicaryon. *Proc. X Int. Congr. Genet., Montreal*, **2**, 61–62.

Day, P. R. (1959). A cytoplasmically controlled abnormality of the tetrads of *Coprinus lagopus*. *Heredity*, **13**, 81–87.

Dickson, H. (1936). Observations on inheritance in *Coprinus macrorhizus*. *Ann. Bot.*, **50**, 719–733.

Fulton, I. W. (1950). Unilateral nuclear migration and the interactions of haploid mycelia in the fungus *Cyathus stercoreus*. *Proc. nat. Acad. Sci., Wash.*, **36**, 306–312.

Kimura, K. (1954). Diploidisation in the Hymenomycetes. I. Preliminary experiments. *Biol. J. Okayama Univ.*, **1**, 226–233.

Kimura, K. (1958). Diploidisation in the Hymenomycetes. II. Nuclear behaviour in the Buller phenomenon. *Biol. J. Okayama Univ.*, **4**, 1–59.

Papazian, H. P. (1950). Physiology of the incompatibility factors in *Schizophyllum commune*. *Bot. Gaz.*, **112**, 143–163.

Papazian, H. P. (1958). The genetics of basidiomycetes. *Advanc. Genet.*, **9**, 41–69.

Quintanilha, A. (1937). Contribution à l'étude génétique du phénomène de Buller. *C. R. Acad. Sci., Paris*, **205**, 745–747.

Raper, J. R. (1953). Tetrapolar sexuality. *Quart. Rev. Biol.*, **28**, 233–259.

Raper, J. R. & San Antonio, J. P. (1954). Heterokaryotic mutagenesis in *Schizophyllum commune*. *Amer. J. Bot.*, **41**, 69–86.

Snider, P. J. & Raper, J. R. (1958). Nuclear migration in the basidiomycete *Schizophyllum commune*. *Amer. J. Bot.*, **45**, 538–546.

Swiezynski, K. M. & Day, P. R. (1960). Heterokaryon formation in *Coprinus lagopus*. *Genet. Res.*, **1**, 114–128.