Migration of nuclei in tetrapolar *Basidiomycetes*

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When two compatible monokaryotic strains meet, a cytoplasmic connection is established between their hyphae and each mycelium is invaded by nuclei from the other strain. In this way both strains are transformed into dikaryotic mycelia. This invasion of nuclei was first analysed by Buller (1931) in *Coprinus* and was later shown to exist in many species and genera of both *Basidiomycetes* and *Ascomycetes* (Burnett 1956, Snider and Raper 1958, Świeżyński and Day 1960b). The phenomenon is called migration of nuclei.

In tetrapolar *Basidiomycetes* the mating type is determined by two independently inherited loci: *A* and *B*, each with multiple alleles. Only strains with different alleles at both *A* and *B* loci are compatible. Most of the detailed information concerning migration of nuclei comes from research on tetrapolar *Basidiomycetes*. As it appears unlikely that the migration of nuclei has the same mechanism in all groups of fungi in which it has been demonstrated, the discussion in this paper will be limited to tetrapolar *Basidiomycetes*.

The basic facts concerning migration of nuclei in tetrapolar *Basidiomycetes* may be summarised as follows:

1. Hyphae establish cytoplasmic connections more or less independently of mating type. This is shown by the existence in various fungi of common *A*, common *B* and common *AB* heterokaryons (review: Papazian 1958).

2. The *A* and *B* mating type factors are not functionally alike. The difference in *B* alleles appears to be decisive for migration, and difference in *A* alleles — for conjugated divisions of nuclei (Świeżyński and Day 1960a).

3. If nuclei of paired monokaryotic mycelia have different *B* alleles, migration of nuclei is observed (Świeżyński and Day 1960b). As Papazian (1958) points out: "the most acceptable interpretation is that invading nuclei migrate through the cells of a compatible mycelium". The alternative hypothesis, that invading hyphae grow throughout the compatible mycelium is difficult to accept for various reasons:

- a) The rate of migration of nuclei is much higher than the rate of growth of hyphae (Snider and Raper 1958).

b) Migrant nuclei do not colonise densely the invaded mycelium. Migrants may be found in places surrounded by areas in which their presence cannot be detected (Snider and Raper 1958).

c) Mutual inhibition of strains is not directly connected with mating type. It is difficult therefore to accept that mating type has a decisive influence on the intergrowth of hyphae.

For all these reasons it is accepted that nuclei migrate through the cells of the invaded mycelium.

4. Compatible nuclei migrate only if there are no limitations of migration. Primary limitations of migration (Brodie 1948) are found in cases in which a monokaryon is unable to accept foreign nuclei, whether compatible or not. Secondary limitation of migration is observed in mycelia in which migration of nuclei occurs, but is not complete and single hyphae with one type of nuclei may be isolated from heterokaryotised areas (Swieżyński and Day 1960b).

5. Dikaryotic and heterokaryotic mycelia with common *B* factor donate but won't accept nuclei (Swieżyński and Day 1960a).

To the author's knowledge, no general working hypothesis has been published which would explain the phenomena observed in migration of nuclei. An attempt will be made in this paper to formulate such an hypothesis.

It appears, that facts observed in migration of nuclei in tetrapolar *Basidiomycetes* may be explained if the following model of the action of the incompatibility factors is accepted:

1. A single nucleus induces round it a "field" in which all nuclei possessing different *B* alleles are attracted to this nucleus.

2. In conjugated nuclei (situation occurring in dikaryons and common *B* heterokaryons) the forces inducing migration are reduced or are not present. Therefore conjugated nuclei will not attract foreign nuclei. On the other hand conjugated nuclei are liable to attraction by single nuclei. Single nuclei may attract one only or both the conjugated nuclei. The inability to attract foreign nuclei by conjugated ones may be due to the presence of 2 different *A* factors in direct vicinity or to the presence of 2 neighbouring *B* factors (different or alike).

3. There exist factors which limit or completely suppress the "field" exerted by the nucleus. The disappearance of the "field" results in primary and secondary limitation of migration.

4. There exist factors influencing the extent of response of the migrant nucleus to the "field", i.e. factors influencing the rate of migration. Here may operate differences in alleles of the *A* and *B* loci (for instance nuclei with different *A* alleles may be attracted with different force) and other modifying agents, heritable or not.

Summing up, the proposed hypothesis is based on two assumptions: first, that nuclei will migrate only if a force attracting them is present, and second, that the attraction is directed, i.e. if one nucleus is attracted by the other, the reverse may not be true.

If the above model is accepted, it becomes possible to explain several facts observed in experimental work.

THE MIGRATION OF NUCLEI IN COMPATIBLE MONOKARYOTIC MYCELIA

It is explained as follows: After establishment of cytoplasmic connections between hyphae the nuclei will migrate into the foreign mycelium because they are attracted by the nearest single nuclei. If the reaction is not unilateral, it may depend on chance, nutrition (Holton 1942) or other factors which hypha will be invaded in each particular case. As soon as the first dikaryon is formed the mutual attracting forces will dwindle and the migrant nucleus will be attracted by the next single nucleus. In this way the nuclei will migrate in the mycelium of the host. Basing on this model we may understand the observation of Snider and Raper 1958, that migrant nuclei do not colonise densely the host mycelium and there are areas passed by the migrant nuclei in which they cannot be detected.

MIGRATION OF SINGLE NUCLEI IN OTHER COMBINATIONS OF MYCELIA

In several *Basidiomycetes* it could be demonstrated that dikaryons may act as donors of nuclei. The fact was first demonstrated in *Coprinus lagopus* by Buller (1930) and then shown to exist in many other *Basidiomycetes* (Kimura 1958). On the other hand migration of nuclei has never been observed in dikaryotic mycelia (Świeżyński and Day 1960b). These facts are explained simply if the thesis 2 of the proposed model is accepted stating that conjugated nuclei are unable to attract foreign nuclei, but may be attracted by single nuclei.

The common *B* heterokaryons act as donors but not as acceptors of nuclei in the same way as dikaryons do it (Świeżyński and Day 1960a) and the explanation of the facts seems to be similar.

Common *A* and common *AB* heterokaryons will usually act as donors and as acceptors of nuclei (Świeżyński and Day 1960a). Such heterokaryons are much less stable than dikaryons and common *B* heterokaryons and frequently produce hyphae with only one type of nucleus (Raper and San Antonio 1954, Świeżyński and Day 1960a), what may account for the fact that they usually behave like monokaryons as far as migration of nuclei is concerned.

MIGRATION OF BOTH NUCLEI IN COMPATIBLE AND DOUBLY COMPATIBLE DI — MON MATINGS

It has been shown that if a small dikaryotic inoculum is added to a large monokaryotic mycelium, occasionally both nuclei of the added dikaryon migrate through the monokaryotic mycelium and establish on its margin the original dikaryon. It may happen in doubly compatible i.e. $(A_1B_1 \times A_2B_2) \times A_3B_3$, compatible, i.e. $(A_1B_1 \times A_2B_2) \times A_2B_2$ and incompatible, i.e. $(A_1B_1 \times A_2B_2) \times A_1B_2$ matings.

Migration of both nuclei in an incompatible mating has been explained in a simple way elsewhere (Świeżyński and Day 1960b). In *Coprinus fimetarius*, *C. macrorrhizus*, *Galera tenera* and *Schizophyllum commune* it has been demonstrated (Quintanilha 1939, Oikawa 1939, Papazian 1950, Crowe 1958, Kimura 1958) that both nuclei may migrate in compatible and doubly compatible matings. The explanation of migration of both nuclei in doubly compatible matings may be fairly simple. It is enough to assume that by chance some hyphae are invaded by one type and other hyphae by the other type of nucleus of the dikaryon. Oikawa demonstrated that this may happen. In a doubly compatible cross he observed that one part of the monokaryotic strain was dikaryotised by one and another part by the other nucleus of the original dikaryon. As dikaryons may exchange nuclei to form recombinant dikaryons (Świeżyński 1961) it may be inferred that migration of both nuclei results from individual migration of single nuclei and then formation of a recombinant dikaryon. This reasoning will not explain the migration of both nuclei in compatible crosses of the type: $(A_1B_1 \times A_2B_2) \times A_3B_2$. Kimura (1958) demonstrated that also in such combinations both nuclei may migrate. It appears that this fact may be understood only by assuming that both conjugated nuclei of the dikaryon migrate as one unit, being jointly attracted by single nuclei with a *B* allele common to one of the nuclei of the dikaryon. It is possible that this happens if a diploid nucleus is formed. The existence of such nuclei is not improbable as recombinant nuclei have also been observed in such matings (Papazian 1950, Crowe 1958, Kimura 1958). This alternative explanation may apply also to migration of both nuclei in doubly compatible matings.

LIMITATIONS AND VARIATIONS IN RATE OF MIGRATION

Fulton (1950) suggested that in *Cyathus stercoreus* limitations of migration may be connected with the existence of loose pairing of nuclei, which appears to be due not to the factors determining mating type but to some other factors. Mycelia with such associations of nuclei acted as acceptors and not as donors of nuclei.

Various authors observed dikaryotisation and secondary limitations of migration (Świeżyński 1961, reviews: Buller 1941, Raper 1953). This indicates that limitations of migration may evolve during the development of dikaryotic and heterokaryotic mycelia. The nature of these limitations is not yet clear.

Quintanilha (1938, 1939), Papazian (1950) and Kimura (1958) demonstrated that in doubly compatible matings the nuclei do not migrate at random, but that definite combinations of nuclei are prevalent. The results of Papazian cannot be explained on the assumption that only differences in *B* alleles are responsible for this fact. The results of Quintanilha and Kimura indicate that some modifiers, inherited independently from the mating type loci, are in operation.

All these data show that mating type loci are not the only factors influencing the migration of nuclei. The existence of some modifying factors must be assumed as well, but their nature still remains obscure.

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The proposed model is based mainly on genetical evidence due to the fact that cytological and biochemical evidence is still very scarce. The studies of Snider and Raper (1958) indicate that the migration is due to chemical rather than physical processes. In formulating the model the idea of Quintanilha (1939) that different mating factors may attract each other has been accepted as well as the idea of Lewis (1954) that these forces may be neutralised in conjugated nuclei. There is no need to accept any kind of repulsion between mating type loci to explain phenomena of migration and it appears still to be an open question whether differences in the rate of migration may be ascribed to differences in *B* alleles or are due exclusively to other factors.

The proposed model may be proved only if a material basis for the attraction of nuclei may be demonstrated and if it will function in the predicted way. On the other hand the model may be shown to be wrong or require alterations if contradictory facts are found.

It has been formulated in the hope that it may help to define the points which still remain obscure and establish the material basis of the facts observed.

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At the same time the author wants to state that he is solely responsible for the opinions presented in this paper.

SUMMARY

A hypothetical model of nuclear migration in tetrapolar *Basidiomycetes* is suggested. It is based on two assumptions: first, that nuclei will migrate only if a force attracting them is present, and second, that the attraction is directed, i.e. if one nucleus is attracted by the other, the reverse may not be true.

It is attempted to explain basic facts observed in migration of nuclei with the use of this model.

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