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Genetic structure of a natural population of *Coriolus versicolor* (L. ex Fr.) Quél.

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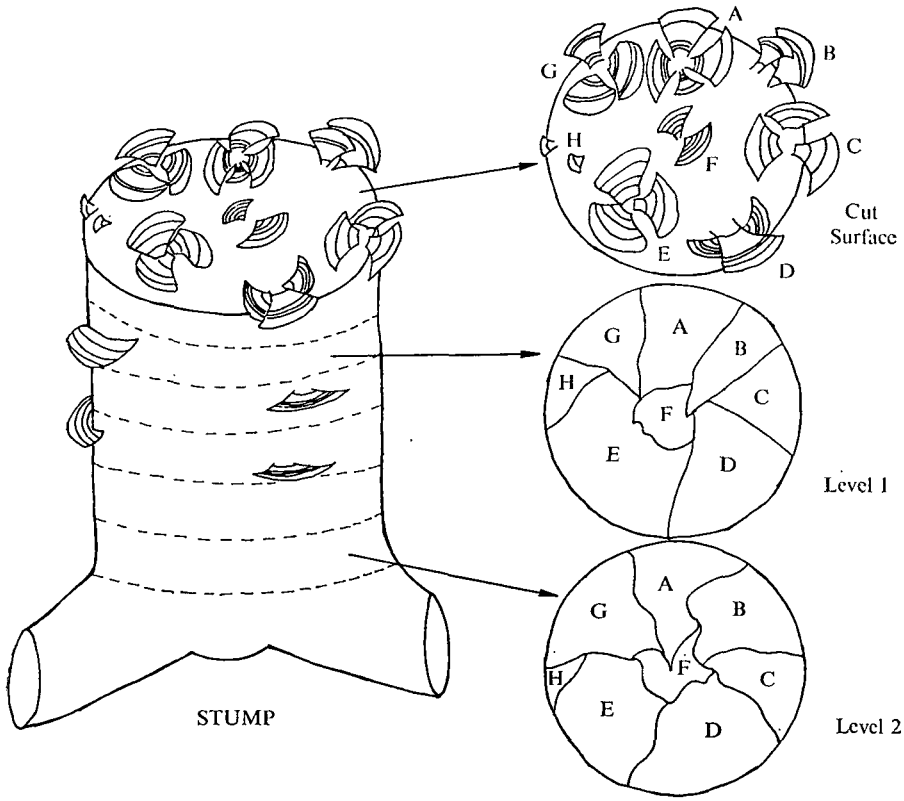
SUMMARY

Experiments were carried out to investigate genetic relationships within a population of *Coriolus versicolor* (a polyporaceous basidiomycete causing white rot of wood) present in a birch stump. The population consisted of individual dikaryons occupying longitudinally continuous columns of decay separated from one another by narrow, dark, relatively undecayed interaction zones. These dikaryons were shown to be genetically homogeneous throughout their respective decay columns by dedikaryotization procedures. They were mutually antagonistic when paired in culture, but monokaryons derived from their fruit-bodies were interfertile. Experiments using synthesized dikaryons indicated that antagonism is inevitable between genetically distinct mycelia, but that the intensity of interaction diminishes with increased relatedness. Results of pairings between synthesized dikaryons and monokaryons varied according to the relatedness of the isolates. Antagonism invariably occurred when the monokaryon contained a nucleus differing from both nuclei in the dikaryon, but this did not necessarily prevent dikaryotization. Often in this situation dikaryotized sectors developed in the monokaryon visibly separated by zones of antagonism ('tracks'). Where the monokaryon contained the same nucleus as one of the components of the dikaryon, antagonism usually occurred initially, but normally the colonies eventually fused.

1. INTRODUCTION

In a recent article (Rayner & Todd, 1977) preliminary results were given of an investigation into the three-dimensional structure of a population of *Coriolus versicolor* (L. ex Fr.) Quél., within an individual birch stump. It was shown that several different individual dikaryons were probably present, occupying spatially defined columns of decay separated by narrow, dark, relatively undecayed interaction zones. When opposed in culture dikaryotic isolates from separate decay columns were invariably antagonistic, clear zones with sparse hyphae developing between them, usually accompanied by brown pigment production. Isolates from the same column merged readily. Monokaryons derived from basidiospores of fruit-bodies corresponding to separate columns were interfertile, forming dikaryons with clamp-connexions when paired in culture, thus demonstrating conspecificity.

These findings represented a marked departure from the concept of the unit mycelium first advocated for *C. versicolor* by Burnett & Partington (1957). In this communication we provide results of more detailed genetic studies on this phenomenon, including extensive dedikaryotization, di-mon mating tests and interactions using synthesized dikaryons of known constitution.



Text-fig. 1. Diagram illustrating procedure for analysis of a population of *Coriolus versicolor* in a stump. The stump is first cut into transverse slices as indicated by the dotted lines. The position of the different decay columns, delimited by narrow dark zones, on separate slices is noted, and correlated with that of the fruit-bodies at the surface. The decay columns, and their corresponding fruit-bodies are labelled accordingly, and isolates made from them as follows: (i) from fruit-body tissue; (ii) from single basidiospores from fruit-body used for tissue isolation; (iii) from the decayed wood at different levels.

2. MATERIALS AND METHODS

(i) *Sampling and isolation procedure*

Full details of the procedure for sampling and isolation have been described elsewhere (Rayner & Todd, 1977). This procedure is illustrated diagrammatically in text-fig. 1.

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(ii) *Strains*

The strains of *C. versicolor* used in the present study were the same as those detailed previously (Rayner & Todd, 1977). For each of six adjacent decay columns, four monokaryotic tester strains each representing one of the four possible mating-types (*C. versicolor* is tetrapolar) were obtained from basidiospore isolates of fruit-bodies corresponding to each column.

(iii) *Experimental pairings*

All experimental pairings were carried out at room temperature (approx. 18–20 °C) on 3 % malt agar in 9 cm plastic Petri dishes, using inocula approx. 2 × 2 mm.

(1) Between monokaryons. These were either used in sexual compatibility studies, or for the synthesis of dikaryons of known constitution. In both cases the inocula were placed immediately adjacent. When used for dikaryon synthesis, the pattern of dikaryotization and the position from which dikaryotic inocula were chosen for further pairings were recorded.

(2) Between dikaryons. Here the inocula were placed 1–2 cm apart, to allow for clearest expression of antagonism, the development of which was monitored.

(3) Between dikaryons and monokaryons (di-mon matings). Here again the inocula were placed 1–2 cm apart. The pattern of interaction between the isolates and the extent of dikaryotization of the monokaryon were recorded. Dikaryotization was followed partly by microscopic examination of the plates at frequent intervals after contact between opposing mycelia. In addition, 10 days after contact large portions (up to 15 × 10 mm) of the original monokaryotic colonies were removed and transferred to fresh agar plates. The pattern of outgrowth from these subcultured portions was noted, and the presence or absence of clamp-connexions on the new growth recorded. This latter method, based on subculturing, was finally used because microscopic examination *in situ* subsequently proved unreliable.

Unless otherwise stated results regarding antagonism were recorded 2–3 weeks after contact, i.e. when the interactions had developed to their fullest extent.

(iv) *Dedikaryotization*

Dikaryotic isolates from wood or fruit-body tissue corresponding to each of several different decay columns were dedikaryotized (the purpose of which was to resolve isolated dikaryons into their component monokaryons) using a modified version of the method of Miles & Raper (1956). Whilst being aware of other methods, we nevertheless chose this one because of its obvious reliability and the fact that *C. versicolor* was used in the original study by Miles & Raper (1956). The dikaryotic strains were grown up on 3 % malt agar in 9 cm Petri dishes at 25 °C. After 7 days 10 ml of sterile distilled water was poured on to the mycelium which was then scraped from the agar surface. The resultant suspensions were inoculated into Erhlenmeyer flasks containing 100 ml of dedikaryotization

Table 1. *Number of compatible pairings between monokaryons derived by dedikaryotization, and tester strains*

(For dedikaryotized isolates letters indicate the decay column, numbers 1 and 2 refer to different levels within a decay column and fb indicates that the isolate was derived from fruit-body tissue. For tester strains letters indicate decay column and numbers are isolate numbers. Tester strains for each column are monokaryotic basidiospore isolates each representing one of the four possible mating-types.)

Dedikaryotized isolates	Total number of derived monokaryons tested	Tester strains			
		O3	O4	O6	O11
O1	31	0	0	0	31
O2	35	0	2	0	33
Ofb	26	0	11	0	15
		N8	N4	N36	N31
N1	28	0	0	0	28
N2	47	0	0	0	47
Nfb	20	0	0	0	20
		A29	A36	A26	A23
A1	35	0	0	0	35
Afb	52	0	52	0	0
		F2	F4	F40	F38
Ffb	10	0	8	0	2
		J3	J6	J13	J19
J1	23	0	0	0	23

medium (*Coprinus* liquid minimal medium (Lewis, 1961) plus 0·1 % cholic acid). The flasks were then incubated on a rotary shaker at 25 °C for 28 days. For each isolate macerates suspended at various dilutions in sterile distilled water were then prepared from the resultant colonies using a Wareing blender. 0·15 ml aliquots of the suspensions were then added to 150 ml of molten 3 % malt agar at 46 °C, which was then poured into ten Petri dishes. The plates were incubated at 25 °C and colonies subcultured as soon as they appeared. These isolates were grown up and examined for the presence or absence of clamp-connexions. Those without clamps were used for compatibility tests with tester strains of known mating type from each decay column.

3. RESULTS

(i) *Dedikaryotization*

The results obtained from dedikaryotization experiments are given in Table 1. For a particular decay column each derived monokaryon, irrespective of origin, was compatible with only one tester strain. Further, all such monokaryons were either compatible with only one of the testers, as from column N, or with two testers of opposite mating-type, as with column O. This is consistent with the hypothesis that each decay column contained a single, pure dikaryon. In addition these results indicate strong selection of one of the conjugate nuclear types during dedikaryotization.

(ii) *Pairings between synthesized dikaryons*

The results of these pairings are summarized in Table 2.

Antagonism occured in all instances (except in control pairings between the same dikaryons, these fusing readily), but there was a marked tendency of decreased intensity of interaction with increased relatedness, associated with decreased pigment production. In pairings between non-sibcomposed dikaryons, 30 such isolates derived from monokaryons corresponding to six adjacent decay columns were paired in 30×30 matrix. Pigment production varied according to the type of pairing. Pairings in which all the monokaryotic components were of different origin (type A.a) showed a greater incidence of pigment production (80%) than those involving either common, or sibrelated monokaryotic components. A 4×2 contingency table gave a $\chi^2_{[3]}$ value with a probability of $< 0{\cdot}01$ that pigment production was independent of pairing type. By inspection it is clear that the non-randomness was due to results from type A.a pairings. Percentage occurrence of pigment production in the other classes were as follows: type A.b

Table 2. *Occurrence of antagonism in pairings between synthesized dikaryons*

(Symbols: ○, pairings showing antagonism; △, pairings showing antagonism accompanied by pigment production.)

Pairing type	No. of pairings	No. △	No. ○	% △
(A) Dikaryons not sibcomposed				
(*a*) All monokaryotic components from different decay columns	180	144	36	80·0
(*b*) One pair monokaryotic components in common	79	48	31	60·8
(*c*) One pair monokaryotic components sibrelated	160	104	56	65·0
(*d*) Two pairs monokaryotic components sibrelated	13	8	5	61·5
(B) Dikaryons sibcomposed				
(*a*) Dikaryons from different decay column	50	39	11	78·0
(*b*) Dikaryons from same decay column	67	3	64	4·5

(one pair monokaryotic components in common) 60·8; type A.c (one pair monokaryotic components sibrelated) 65; type A.d (two pairs monokaryotic components sibrelated) 61·5. Whilst there is an apparent trend for reduction of pigment production with increased relatedness, i.e. type A.c > type A.d > type A.b, the differences between these classes were not statistically significant.

In pairings between sibcomposed dikaryons (type B.a), 11 such isolates corresponding to the same six adjacent decay columns as above were paired in an 11×11 matrix. As mentioned previously antagonism occurred in all pairings. The incidence of pigment production was 78%, corresponding closely to the value

obtained in type A.a pairings between non-sibcomposed dikaryons. However, insufficient data were available for meaningful statistical comparisons.

In pairings between sibcomposed dikaryons from same decay column (type B.b), pairings between dikaryons corresponding to two columns, A and N, were tested, in a 10×10 and 7×7 matrix respectively. Antagonism occurred regardless of whether the component nuclei were of identical mating-type, and regardless of relatedness between dikaryons. However, there was striking evidence for reduced occurrence of pigment production in these pairings (4·5 %) when compared with those involving less closely related dikaryons. In certain cases, particularly in pairings involving dikaryons with nuclei in common, only rather faint interactions (but nonetheless present) were observed.

(iii) *Di-mon matings*

The results of di-mon matings are summarized in Table 3.

Table 3. *Numbers of pairings between synthesized dikaryons and monokaryons showing antagonism and other features*

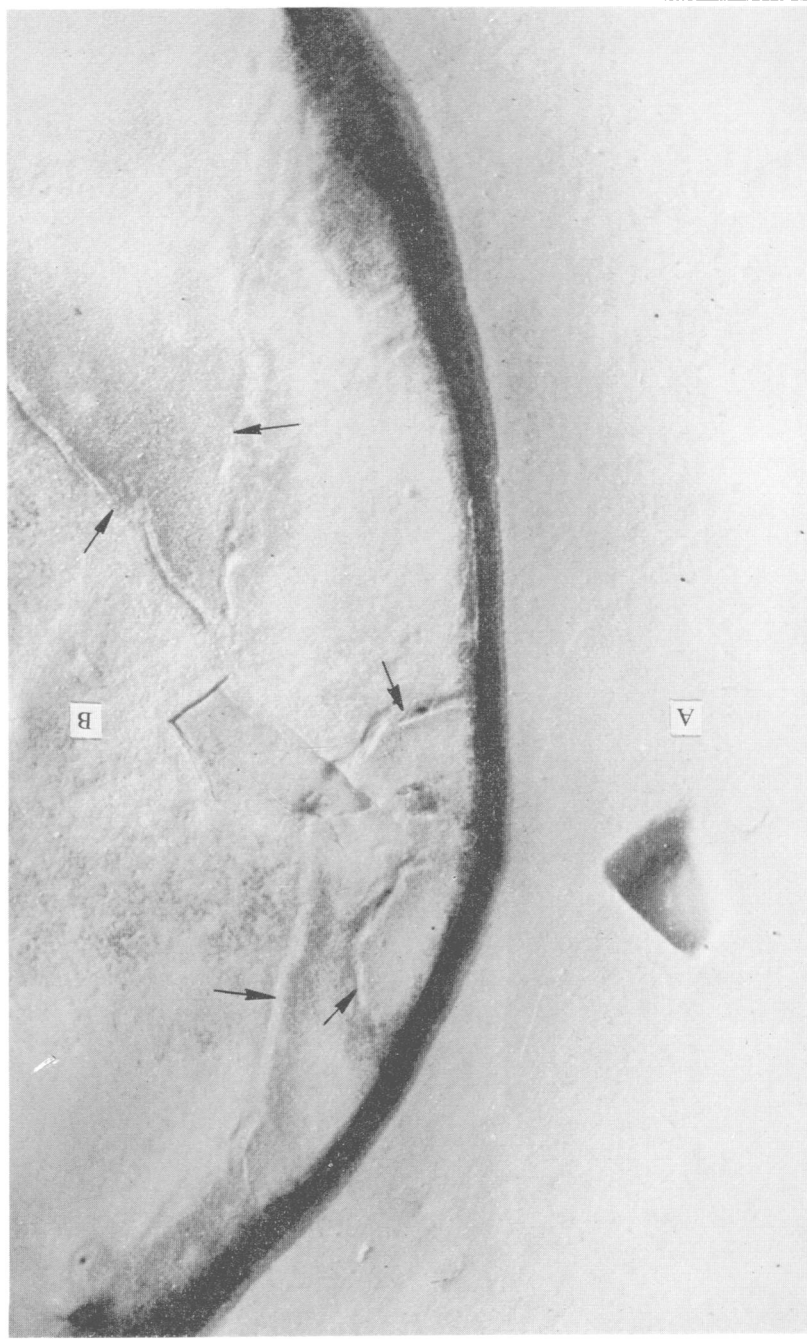
(Symbols: ●, pairings showing complete fusion; otherwise as in Table 2.)

Pairing type	No. of pairings	No. △	No. ○	No. ●	Status of monokaryon following subculturing after 10 days: No. Clamps	No. clamps	Track-formation*
(A) Dikaryon not sibcomposed, monokaryon neither component nor sibrelated	111	79	32	0	87	21	20
(B) Dikaryons paired with component monokaryons							
(*a*) Dikaryons not sibcomposed	57	7	29	21	55	2	0
(*b*) Dikaryons sibcomposed	23	1	12	10	22	1	0

* For explanation see text.

The discrepancy between total numbers of pairings and observations regarding status of monokaryon is due to practical difficulties resulting from comparatively slow growth of monokaryon in certain pairings.

Between non-sibcomposed dikaryons and non-component, non-sibrelated monokaryons (type A pairings) antagonism was observed in all matings and, in the majority (71·2 %) was accompanied by pigment production. In most cases this antagonism resembled that observed between dikaryons. However, in a few instances rather than a clear zone developing between colonies, a narrow zone of mycelial build-up occurred. This latter was particularly prominent in those pairings where the monokaryon was not dikaryotized. Further, in many pairings, whilst typical antagonism was observed in distal positions along the line of



'Track-formation' in a di-mon mating. A non-sibcomposed dikaryon (A) has been paired with a non-component, non-sibrelated monokaryon (B). A pigmented band of antagonism has developed between the colonies, and within the originally monokaryotic colony lines of antagonism, 'tracks' (arrowed) are present separating different dikaryotic sectors.

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contact between colonies, at the initial point of contact mycelial build-up occurred instead. In the majority of pairings the monokaryon eventually became dikaryotized (assuming that the occurrence of clamps was not due to growth of the dikaryon through the monokaryon: from the pattern of growth and interaction on the plates we believe this very unlikely, but the rate of dikaryotization was no faster than could be accounted for by this means). However, there was evidence for certain isolates (e.g. Cl and A26) that these could persist as monokaryons for an extended period when confronted with a theoretically compatible dikaryon.

In several pairings we observed what we have termed 'track-formation' (Plate 1). Here the process of dikaryotization appeared to be such what different dikaryotic sectors occurred, spreading from the initial point of contact, and separated from each other by narrow lines of antagonism ('tracks'). On subculturing, newly grown mycelia from either side of such a track showed antagonism typical of that normally observed between different dikaryons. This phenomenon would be expected if both nuclei of the opposing dikaryon are able to dikaryotize the monokaryon. Track-formation was most often observed with monokaryons J13 and O4 which also showed a greater propensity for pigment production in interactions than the others.

Matings between both non-sibcomposed and sibcomposed dikaryons and their corresponding monokaryotic components (type B pairings) showed antagonism in virtually all pairings, at least initially (i.e. within 3–4 days). However, in many cases this was superseded by complete fusion of the isolates. In these instances traces of the original antagonistic interaction were still discernible on the plates when viewed from below. In other cases definite zones of antagonism developed, sometimes accompanied by pigment production, which were persistent. Even in these instances, however, the antagonism was only clear along distal portions of the interaction interface: at the point of initial contact the mycelia fused imperceptibly. There was slight evidence for greater pigment production in pairings involving non-sibcomposed dikaryons but this was by no means statistically significant.

In virtually all cases the original monokaryons were dikaryotized (making the assumptions previously mentioned), the three exceptions being in pairings involving Cl monokaryotic components. As might be expected, since any dikaryons formed would be identical in nuclear constitution to the parent dikaryons, no instances of track-formation were observed.

4. DISCUSSION

In other articles (Rayner & Todd, 1977, 1978) we have provided evidence that populations of *C. versicolor* occurring in natural substrata are made up of individual, mutually antagonistic dikaryons, whose genetic differences are often externally manifest in the polymorphism between their fruit-bodies. These conclusions differ markedly from the concept of the unit mycelium advocated for this fungus by Burnett (e.g. Burnett, 1976) which supposes that different mycelia will fuse to form a genetically heterogeneous ecological and physiological unit. Nonetheless

our conclusions are strongly supported by the findings reported in this paper concerning the detailed genetic structure of a population of *C. versicolor* within a single stump. These results also provide what we believe to be a key to understanding the basis of the antagonistic phenomena operating to delimit individual mycelia in nature.

Extensive dedikaryotization tests were invariably consistent with the hypothesis that individual decay columns contain genetically pure, individual dikaryons. The comparative ease with which these tests were carried out, and the consistency of the results obtained, suggest that the procedure is an invaluable aid to studying the genetic structure of individual mycelia obtained from nature. It is surprising, in this light, that such work should not have been attempted on a much greater scale than it appears to have been at the present time. A surprising feature of the results we obtained was the apparent selection, in a seemingly regular fashion, of one of the conjugate nuclear types during dedikaryotization. Further work is required to investigate the basis of this phenomenon: this might lead to a deeper understanding of the processes maintaining the dikaryotic state.

Pairings between synthesized dikaryons provided several points of interest. That the antagonism is principally a dikaryotic phenomenon independent of homogenic incompatibility mechanisms, was confirmed by the fact that it was observed in all pairings between genetically different dikaryons regardless of their relatedness. There was much evidence that the degree of relatedness between opposed dikaryons affected the intensity of the interaction, especially with regard to pigment production: closely related dikaryons were usually less strongly antagonistic than others.

Dimon matings also provided interesting information. In pairings between non-sibcomposed dikaryons and non-component, non-sibrelated monokaryons, antagonism similar to that between different dikaryons was usually observed, but this did not appear to interfere with dikaryotization. It was not always clear, however, whether the interaction finally observed resulted directly from the confrontation between monokaryon and dikaryon or whether it developed subsequent to dikaryotization. Two of the monokaryons tested, A26 and especially C1, persisted as monokaryons for considerable periods after contact in certain pairings. The consistency of these findings, especially for C1 which also failed to be dikaryotized in pairings with dikaryons of which it was a component, is suggestive of some mechanism, which we do not understand, preventing nuclear exchange with dikaryons. In several of the pairings where C1 failed to become dikaryotized, the interaction with the dikaryon was of a different type from normal: instead of a clear zone developing between the isolates later accompanied by pigment production, a narrow zone of mycelial build-up occurred. Two of the monokaryons tested, J13 and O4, showed a particularly strong tendency towards pigment production. This is of some interest since pairings between synthesized dikaryons involving either of these as monokaryotic components also showed this feature. These two monokaryons also showed the greatest tendency for the phenomenon we have described as track-formation. We believe this to be an extremely interest-

ing phenomenon for a variety of reasons. The simplest interpretation is that the tracks represent lines of antagonism between different dikaryons formed following movement into the monokaryon of the two different nuclei from the parent dikaryon. This hypothesis is currently being tested. If this is so then the pattern of track-formation is likely to reflect the pattern of dikaryotization from the point of contact between the dikaryon and monokaryon, and may provide us with a convenient, easily observed feature by which we can follow dikaryotization. In addition it shows that if a dikaryon is formed containing different dikaryotic components it is likely that this could be observed readily on subculturing: different sectors would be expected to grow out separated by zones of antagonism. Since such a phenomenon has never been detected in isolates derived from the field, or from dikaryotic isolates subcultured after interaction in culture, it seems highly probable that no nuclear exchange can take place between interacting dikaryons. Clearly this phenomenon of track-formation is worthy of further investigation, which we are currently undertaking.

In pairings between dikaryons and their component monokaryons, a high incidence of complete fusion between isolates was observed. This would be expected since any dikaryon formed would have the same nuclear constitution as the parent. Nonetheless, in many pairings antagonism still occurred, albeit slightly different from that observed between different dikaryons. Most often such antagonism was seen along distal portions of the interaction interface, whilst near the point of contact, complete fusion occurred between the mycelia. This may suggest the operation of some kind of cytoplasmic factor and/or the production of some persistent inhibitory substance.

So far as we know, only two other detailed genetic investigations of intraspecific antagonistic phenomena in wood-rotting basidiomycetes have been made; those of Adams & Roth (1967) on *Fomes cajanderi* Karst. and of Barrett & Uscuplic (1971) on *Phaeolus schweinitzii* (Fr.) Pat. Both these studies show a number of features in common with our own. However Barrett & Uscuplic, whilst finding antagonistic isolates of *P. schweinitzii*, never found more than one such isolate in an individual tree. In contrast Adams & Roth found more than one antagonistic isolate per tree in several instances (Adams & Roth, 1969), but unfortunately they did not sufficiently correlate their field sampling procedures with their genetic studies in culture: these latter were carried out with four isolates derived from heartwood of two glaze-damaged Douglas firs, which were obtained without reference to their position in decay columns. Both studies mention a greater intensity of interaction in pairings between more distantly related heterokaryons, much as we have reported in this article. In di-mon matings between isolates of *F. cajanderi* Adams & Roth reported that dikaryons were completely unable to dikaryotize monokaryons against which they were opposed. They only used microscopic examination, and not subculturing, as a means for assessing this however. Both these studies serve to emphasize the possibility that intraspecific antagonism of the type we have described may be general amongst the wood-rotting basidiomycetes rather than exceptional. We ourselves have seen

intraspecific antagonistic phenomena apparently paralleling that described for *C. versicolor* in a wide variety of common wood-decaying basidiomycetes including *Bjerkandera adusta* (Willd. ex Fr.) Karst., *Hypholoma fasciculare* (Huds. ex Fr.) Kummer, *Phlebia merismoides* Fr., *Phanerochaete velutina* (DC ex Pers.) Parmasto and *Stereum hirsutum* (Willd. ex Fr.) S. F. Gray. It is interesting that these probably have a wide variety of mating and nuclear behaviours ranging from homothallic, holocoenocytic as with *S. hirsutum* and *P. velutina*, through bipolar, astatocoenocytic as with *P. merismoides*, to tetrapolar, normal in *C. versicolor* (Boidin, 1971).

The mechanism underlying intraspecific antagonism requires investigation. It would appear from the results presented in this article that the antagonism in *C. versicolor* is primarily a dikaryotic phenomenon, and serves to 'protect' dikaryons from nuclear or other exchange of information when in contact with other mycelia. One observation we believe likely to be relevant is that when antagonistic isolates are opposed in culture, hyphal anastomosis between them does at first occur, but subsequently the fusion segments change in refractive properties and swell to form spindle-shaped cells, constricted at either end at the septa. We believe this may be due to an incompatible reaction between nuclei and cytoplasm resulting in the closure of the affected segments from the rest of the mycelial system.

Finally we must ask what the significance of intraspecific antagonism in fungi may be in terms of evolution and adaption. Before we speculate on this issue, however, we must point out the need for a much deeper understanding of mating and nuclear behaviour during the life-cycles, especially in nature, of a much wider range of species than we possess at present. Certain work (e.g. see Boidin, 1971; Kühner, 1977) has shown that these features may show much more variability and complexity than many suppose.

The widespread acceptance (conscious or unconscious) of the concept of the unit mycelium has, apart from perhaps preventing further work on its occurrence (the need for which has however been repeatedly expressed by Burnett (e.g. Burnett, 1976), caused many to consider the advantages of such a system, possibly forgetting any disadvantages. The ecological advantages of the unit mycelium in terms of communal exploitation of the substrate are of course obvious and highly attractive, implying a degree of social organization in higher fungi unique amongst organisms. The possible opportunity for somatic recombination and hence production of new variants to exploit the substrate (Burnett, 1965) could also be seen as an advantage. In a fungus such as *C. versicolor* which is a highly effective agent of wood decay, individual isolates being capable of bringing about the virtually complete destruction of wood on their own (Findlay, 1940), we believe that such production of new variants may not be particularly necessary in terms of exploitation of the substrate.

In spite of these possible ecological advantages we believe that the unit mycelium may have certain inherent disadvantages, for example in terms of genetic variation. One obvious circumstance where such variation might be reduced is where

one component of a unit mycelium begins to fruit, drawing on the rest of the mycelium for the necessary nutrients, at the expense of the fruiting capacity of other components. In such instances fruit-bodies of only one or a few components might predominate with consequently greatly reduced expression of the variation potential of the population. In cases where dikaryons remain physically separated, as we have suggested in *C. versicolor*, each would be able to fruit separately, albeit that in a population with numerous individuals, and hence separate decay columns, the fruit-bodies might be reduced in size. We have found evidence that this may indeed be the case with *C. versicolor* (Rayner & Todd, 1977). Another possibility which needs exploration is that the formation of a unit mycelium, by blurring the distinction between individuals, may reduce genetic variability in the population.

Clearly the clarification of these issues, which are so fundamental to understanding the behaviour of fungi in nature (as pointed out by Buller (1931) and Burnett (1976)) require far more investigation.

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