Numbers and distribution of individuals and mating type alleles in populations of *Coriolus versicolor*

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SUMMARY

A natural population of the tetrapolar fungus *Coriolus versicolor* (L. ex Fr.) Quel. in a small woodland was observed over 3 years. Dikaryotic members of the population were identified using intraspecific antagonism and mating type markers. Records were kept of the distribution, longevity and fruiting behaviour of 44 individuals. Zone lines between individuals were found to remain constant in position throughout the study, but rates of decay and fruiting times varied between dikaryons and did not seem related to resource size. Detailed maps of the genetic structure of the populations in two stumps are presented. In general the results indicated thousands of alleles at both mating type loci. Repeated occurrences of alleles were very rare, when the data were interpreted rigorously in terms of the probable origins of the nuclei found in individuals. This approach was also applied critically to some published data. Comparisons were made between alleles found in local and more widely gathered samples, and led to estimation of worldwide frequencies but it is concluded that such exercises are of limited value.

1. INTRODUCTION

Ecological genetical studies with fungi have been hampered by poor definition of the structure of populations in nature. Populations have been variously described on the basis of mating type markers (Verrall, 1937; Burnett & Partington, 1957; Brasier, 1970) or interactions between mycelia in culture (Childs, 1963; Adams and Roth, 1967; Barrett & Uscuplic, 1971), but their spatial organization was largely a matter for speculation as no detailed studies were made of mycelia in the field. However, the situation was ameliorated by Rayner & Todd (1977, 1979) who made direct observations on populations of many wood rotting basidiomycetes and showed them to be composed of mutually antagonistic individuals. In their studies on *Coriolus versicolor* (L. ex. Fr.) Quel., evidence from fruit bodies, decay columns in the wood, mating types and mycelial interactions (intraspecific antagonism) was all brought together to describe the spatial and genetic structure of a natural population (Todd & Rayner, 1978). Such an exercise involved damaging the population and consequently temporal aspects were not studied. However, the resulting understanding of population structure formed the basis for

further studies and recently we confirmed the role of mutual antagonism in delimiting dikaryotic individuals during the spatial development of *C. versicolor* populations (Williams, Todd & Rayner, 1981 *b*). Further, and most importantly, by knowing the spatial relationships between individuals, it was possible to avoid unwittingly sampling the same group of fruit bodies or mycelium twice. At the same time, it was possible to include a much higher proportion of relevant individuals in the population study.

Mating type alleles are naturally occurring genetic markers found in both fungi and plants which play a fundamental part in determining what genotypes can and will exist (for review see Pandey, 1977). Most of the published work on mating type in wood rotting fungi involved collecting fruit bodies with scant regard to sampling procedure (see below), and analysing the mating types of their spores. Inter-fruit body crosses revealed any repeated alleles in the sample, and mathematical extrapolation to worldwide frequencies usually followed. For this, the data had to be checked for randomness, theoretically expected for a multiple allele system. Methods commonly used were those of Rao & Chakravata (1956), and worldwide numbers of alleles could then be calculated following, for example, Whitehouse (1949), who derived a formula relating the proportion of different allelomorphs in a sample to the total number in the population. Such extrapolation should, we feel, be regarded extremely critically. First, only potential, and not actual, worldwide allele numbers can be inferred, and then only from cross-allelism between populations, or from worldwide random samples, not from single local samples as has often been the practice. In any case, local populations may be partly inbred, and not display representative allele frequencies. Second, failure to recognize individuals in fungus populations has led to confusion in sampling procedures. In the literature, some samples consisted of several fruit bodies from a single substratum, whereas others consisted of one from each country.

Here we give a detailed description of a local population of *C. versicolor* over a period of time, and examine the numbers and distribution of mating type alleles in local and worldwide samples of this fungus. A novel feature of our analysis of the latter is the use of the concept of nuclei of common or independent origin ('nucleus in common') in assessing the validity of mating type allele repeats for estimating worldwide frequencies, and also in clarifying the historical development of the population. Since *C. versicolor* is unable to spread vegetatively from tree to tree, the 'nucleus in common' test was only necessary with specimens from the same stump.

2. MATERIALS AND METHODS

(i) *Strains, fieldwork, and isolation procedures*

Full details of procedures for sampling and isolating *C. versicolor* from the field have been described elsewhere (Rayner & Todd, 1977). In this study, ten stumps, labelled, A, B, C, D, E, F, G, H, J and K, naturally colonized by *C. versicolor*, and located at Kolora Park, Devon, (N.G. Ref. SX 842886), were visited at frequent intervals between September 1979 and January 1982. Each stump was photographed monthly or more frequently as necessary. Positions of fruit bodies were

noted along with any changes since the previous visit. Four of the stumps were sawn horizontally 2 cm from the top at various times so that the decay columns, separated by dark zone lines, were revealed and could be related to the groups of fruit bodies present. The other stumps were not cut as cutting seemed to induce fruiting (see also Leonard & Dick, 1973, and thus interfered with the natural sequence.

A small specimen was removed from each apparently different group of fruit bodies. From these tissue isolates (dikaryotic) and single spore isolates (monokaryotic) were obtained. In the cut stumps, some decay columns lacked associated fruit bodies. Dikaryons isolated from the wood of such columns would usually fruit in the laboratory (for method see Williams, Todd & Rayner, 1981 *a*), and thus yield spores for inclusion in the data. Recalcitrant dikaryons were dedikaryotized using the method of Kerruish & Da Costa (1963). Some other fruit bodies of *C. versicolor*, collected elsewhere in U.K., in Malawi and sent from Finland and Holland, yielded tissue and spore isolates, and were included in the study for comparison.

(ii) *Experimental pairings*

These were carried out as described by Todd & Rayner (1978), using 3 % malt agar medium at 25 °C. Dikaryons were paired in all possible combinations and any antagonism between them noted. Matings between monokaryons, and di-mon matings were also set up as required.

(iii) *Mating type analysis*

C. versicolor is a tetrapolar heterothallic fungus, but *no distinctive common-A* or common-B mating type allele interactions, such as those described in *Schizophyllum commune* (see Raper, 1966), were observed. Therefore, designation of A and B alleles was arbitrary in this study. One monokaryotic example of each of the four mating type allele combinations found amongst spores from a single fruit body was used as a tester. Thus the four testers derived from one dikaryon had mating type allele combinations designated, for example, A1B1, A2B2, A1B2, and A2B1, the first pair of which could be the compatible parental combinations, while the second pair were the recombinants, or *vice versa*. None of the testers was likely to have the complete parental haploid genotype since they arose by meiosis. A monokaryon derived by dedikaryotization would, however, have both a parental mating type combination and a parental haploid genotype.

Tester monokaryons were paired in almost all possible combinations between and within stumps. Any mating type alleles which occurred in more than one dikaryon were analysed in conjunction with Fig. 1. In particular, isolates from stump K were subjected to the following 'nucleus in common' test in order to clarify the genetic relationships between them.

(iv) *'Nucleus in common' test*

If a monokaryon mates simultaneously with two others, its mycelium may become divided into two dikaryons which have a nucleus in common (see Williams *et al.* 1981 *b*). However, if two neighbouring fruit bodies of a tetrapolar fungus are shown to have two or more mating type alleles in common, it does not necessarily

Alleles in common	Second dikaryon testers	First dikaryon testers				Number of compatible matings
		A1B1	A2B2	A1B2	A2B1	
0	A3B3	+	+	+	+	
	A4B4	+	+	+	+	
	A3B4	+	+	+	+	16
	A4B3	+	+	+	+	
1 (a or b)	A3B3	+	+	+	+	
	A1B4	−	+	−	+	
	A3B4	+	+	+	+	12
	A1B3	−	+	−	+	
2 (both A or both B)	A1B3	−	+	−	+	
	A2B4	+	−	+	−	
	A1B4	−	+	−	+	8
	A2B3	+	−	+	−	
2 (an A and a B)	A3B3	+	+	+	+	
	A1B1	−	+	−	−	
	A1B3	−	+	−	+	9
	A3B1	−	+	+	−	
3	A1B1	−	+	−	−	
	A2B3	+	−	+	−	
	A1B3	−	+	−	+	6
	A2B1	−	−	+	−	
4	A1B1	−	+	−	−	
	A2B2	+	−	−	−	
	A1B2	−	−	−	+	4
	A2B1	−	−	+	−	

follow that the two dikaryons have a common nucleus. Common origin in a single monokaryon is only indicated if members of a pair of common alleles are together in one nucleus in both dikaryons. Therefore the pair must consist of one A and one B allele. In addition the rest of the haploid genome of that nucleus must be identical in both dikaryons.

Fig. 1 shows all possible patterns of compatible and incompatible matings to be observed when intercrossing sets of tester monokaryons. When the results of a set of 16 crosses between testers from two dikaryons were compared with Fig. 1, the total number of compatible pairings immediately indicated how many common alleles were present. If the number of common alleles was 2 (an A and a B), 3 or 4, closer examination of the pattern was required to determine which pairs of testers gave rise to the quadrants outlined in Fig. 1. These pairs had then to be identified as parental or recombinant combinations by crossing each to a monokaryon obtained by dedikaryotization of each parent dikaryon. Such a monokaryon would be compatible only with the tester of the opposite parental combination. A nucleus in common was only possible if the parental combinations of both dikaryons were those giving rise to an outlined quadrant. If so, the rest of the haploid genomes associated with the common parental mating type combination had to be compared. If the monokaryons already obtained by dedikaryotization of both parent dikaryons happened to contain the suspected common nucleus, they should behave identically in pairing reactions. For example, each could be mated to the same unrelated monokaryon, and the resulting dikaryons would intermingle without antagonism. Since dedikaryotization tended to be unilateral, the probability of getting both the required nuclei was only 0·25. An alternative test was to di-mon mate both parent dikaryons to the same unrelated monokaryon. If, as usually occurred, tracks (narrow lines of antagonism separating different dikaryotic sectors, see Todd & Rayner (1978)), appeared in the monokaryotic area of the culture dishes, both pairs of product dikaryons could be isolated. When these are tested for mutual antagonism to each other, one pair will intermingle if there had been a nucleus in common. An example is shown in Table 1. If a nucleus in common is confirmed in two adjoining dikaryons in a stump, the common A and B alleles were considered spurious repeats in allele frequency data. In this study the definition of a genuine repeat came to be taken as one which arrived at the substratum in a separate spore.

Fig. 1. Four monokaryotic tester strains (each representing one of the four possible mating types) from the first dikaryon are crossed to similar sets obtained from other dikaryons with 0, 1, 2, 3 and 4 mating type alleles in common with the first. + indicates compatible reaction, − incompatible reaction. The total number of compatible matings is given for each 4 × 4 matrix. For each dikaryon, the testers are listed as two compatible pairs, each bracketed, either of which could represent the parental mating type allele combination in the original dikaryon, the other being the recombinants. If, in practice, the two pairs of parental combinations give rise to an outlined quadrant in a matrix, there exists a possibility that the two dikaryons have a nucleus in common (see text). These quadrants are distinguishable from others in the same matrix by the pattern of + and − reactions within them. When the above condition applies to cases where 4 mating type alleles are common, it is theoretically possible that the two dikaryons have not only one, but two, nuclei in common, i.e. are identical. In practice this would already have been recognized from their lack of vegetative antagonism.

Table 1. *Detection of the presence of a common nucleus in two dikaryons by means of di-mon mating*

Dikaryon	Monokaryotic mate	Tracks formed
A1B1 + A2B2	A4B4	A1B1 + A4B4, A2B2 + A4B4
A1B1 + A3B3	A4B4	A1B1 + A4B4, A3B3 + A4B4

Interpretation; The A1B1 + A4B4 tracks formed in each mating will intermingle if the genotypes as well as the mating types are identical. Other pairings will be antagonistic.

3. RESULTS

Numbers of dikaryons, their mating type alleles and fruiting behaviour are summarized in Table 2. In addition, details of the spatial arrangements and mating types of the dikaryons found in stumps A and K are shown in Figure 2. In stump A, no mycelium could be isolated from the columns designated X and Y during the survey period, but later in 1982 both fruited in the field. At this time columns which had already fruited were almost completely rotten, while X and Y were hard and white. However, zone lines could still be detected as hard bands even in completely rotten wood. Further information about fruiting behaviour is given in Fig. 3 which has been compiled from serial photographs and field notes. The progress of 44 groups of fruit bodies, each known to arise from a separate dikaryon, is shown quantitatively.

The mating type allele distribution does not differ from random at any location. When tester types from different locations were crossed they were all completely compatible and interfertile. It was not possible to check all combinations of all four testers but more than 7000 crosses were set up, so that the results are stated with

Table 2. *Numbers of dikaryons, their mating type alleles and fruiting behaviour*

Location	Stump	Number of dikaryons			Mating type alleles	
		present	*fruited*	*analysed*	*observed*	*possible*
Kolora Park	A	16	8	7	27	28
	B	—	5	4	16	16
	C	—	5	3	12	12
	D	—	4	3	12	12
	E	—	3	1	4	4
	F	—	5	4	16	16
	G	—	2	2	8	8
	H	4	3	1	4	4
	J	19	4	3	12	12
	K	6	5	6	18	20
Haldon		32	16	6	22	24
UK		—	—	15	60	60
Europe		—	—	3	12	12
Malawi		—	—	3	10	12

U.K., Europe and Malawi strains came from separate substrata, the rest from single stumps as listed. In cut stumps the number of dikaryons present was estimated from the decay columns observed. The number fruiting during 1979–82 is recorded alongside the number analysed for mating type. The total number of A and B mating type alleles found is shown beside the theoretical maximum for the sample.
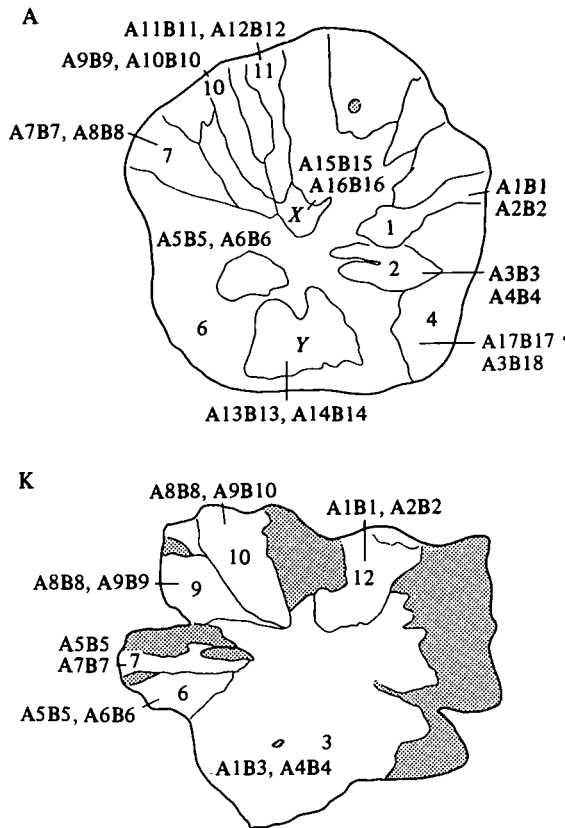
Fig. 2. Maps of decay columns observed in cut surfaces of stumps A and K. Dikaryons of *C. versicolor* were isolated from numbered and lettered areas. Mating type alleles of these dikaryons are also shown, using separate, arbitrary, designations in each stump. Shaded areas appear to be occupied by other fungi.

confidence. It therefore seemed reasonable to assume that there were virtually no repeated alleles between locations. Whitehouse's (1949) calculation applied cautiously to these data indicated the existence of several thousand A and B alleles for the species worldwide.

The locations at which allele repeats were found were stumps A and K, Haldon and Malawi. Stump K exhibited almost all the possible genetic relationships between pairs of dikaryons. There were six sizeable dikaryons present, of which two pairs had nuclei in common (dikaryons 6 and 7, and 9 and 10). There were therefore considered to be only 20 independent A and B alleles in the stump, and not 24. Two of the pairs of dikaryons also have a different single allele in common (12 and 3, 9 and 10). These are genuine repeats. Thus there are 18 different alleles present out of a possible 20.

In stump A two adjoining dikaryons have one allele in common, and at Haldon, two pairs of dikaryons had different alleles in common. The three Malawi isolates have the mating type configuration A1B1 + A2B2, A1B3 + A4B4, and
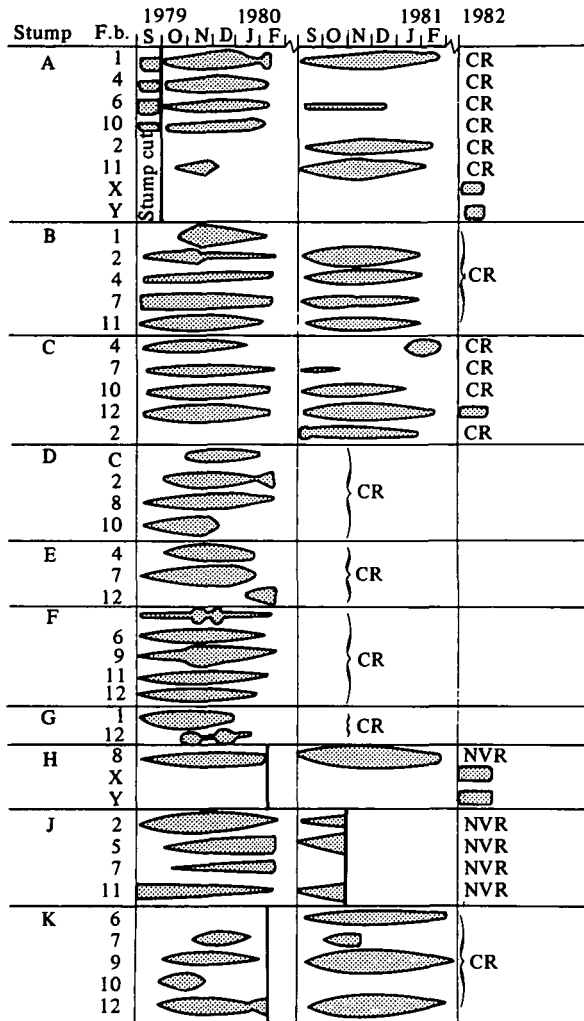
Fig. 3. Fruiting of 44 dikaryons of *C. versicolor* on stumps in a woodland during 1979/82. The width of the bars indicates the quantity of fruit body tissue present. Heavy vertical lines shown when stumps A, H, J and K were sliced to examine decay columns within the cut surface. CR and NVR mean completely rotten and not very rotten.

A2B5 + A6B6. These fruit bodies were collected from different logs, and had no nuclei in common. Three further fruit bodies from the same forest in Malawi only yielded a few spores of one or two tester types. These were, however, completely fertile with the other Malawi testers. When Malawi monokaryons were crossed to European ones, dikaryotisation was rather slow, but occurred in all cases.

4. DISCUSSION

In ecological genetics and population biology, an essential preliminary step in any study is enumeration and location of individual members of the chosen

population. The combination of approaches described here is potentially very useful when those studies embrace wood rotting fungi. A dynamic quantitative description of a local population can be built up by inter-relating observations of fruit bodies, decay columns and interactions between mycelia. The results reported in this paper implied that fruit body samples collected on a single occasion may not fully represent the population. Evidence from cut stumps indicated that only about half the dikaryons fruited during the three year study period. If this is generally the case, there is justification for being wary of genetical and variation work carried out after a single field trip.

In this context it is worth noting that the Kolora Park stumps were all exposed at roughly the same time prior to 1975. The dikaryons found in them during 1979–82 were either established at different times, or utilized the wood at different rates because not all the columns were equally rotten. Further, the smaller columns were not always the most decayed, as might be expected if simultaneous establishment of unequally sized columns was followed by uniform rates of decay. Since simultaneous establishment is indicated in the field (Williams, 1982 and unpublished observations), rates of decay must vary between dikaryons. The fact that zone lines could still be detected in really rotten wood further implied that boundaries between individuals remained constant throughout the period of habitation.

Times of fruiting also varied between dikaryons and did not seem to relate to resource (column) size. Presumably some of the dikaryons had fruited before the survey began, and may or may not have fruited again during 1979–82. Very little fruiting was observed during the summer months but these stumps were in an exposed position susceptible to desiccation. Other stumps in the wetter parts of the woodland bore fruit bodies throughout the year. However, the mycelia in the ten stumps obviously remained viable since many of them fruited again the following autumn. For some reason it was not always possible to isolate mycelium from decay columns but subsequently fruiting indicated the continuing presence of a live dikaryon of *C. versicolor*. With experience it was usually possible to guess correctly the presence of the species in columns without fruit bodies or isolatable mycelium. A few other species were found on or near these stumps but their effect was negligible compared to that of *C. versicolor* which took the stumps to complete destruction.

In summary, the dikaryons seemed to become established soon after newly exposed substrata became available, then utilized the wood at characteristic rates, fruited in their own time subject to environmental stimuli, and remained totally separate from their neighbours. Such independence and variability is greater than commonly suspected in the fungi, and has aspects that need serious consideration during field studies.

Another purpose of this work was to establish the level of repetition of mating type alleles within a population. It appeared to be minimal, but an exact and exhaustive survey is tedious with a tetrapolar species, and was not intended. The main aim was assessment of the method of determining allele frequency in basidiomycetes in terms of nuclei of independent origin. This was proved less confusing than working at the level of fruit bodies, or, indeed, mycelia. Since

monokaryotic forms can exist independently, if briefly, in nature, consideration of individual nuclei has ecological genetical relevance and aids understanding of population establishment.

Amongst data on tetrapolar species, that on *S. commune* is most significant. Raper *et al.* (1958) collected this species all over the world and their data contributed to a recent estimate of 450 A and 95 B alleles in existence (see Fincham, Day & Radford, 1979). However, Brasier (1970) found several repeated alleles, and hence a much lower estimate of worldwide numbers, in a sample collected from a single log. Amongst data on other tetrapolar species, Eggertson (1953) obtained an estimate of 112 alleles at each locus in *Polyporus obtusus*. He carefully avoided using more than one fruit body per substratum. Burnett (1964) presented a summary of mating type surveys for several species including Partington's (1959) figures for *C. versicolor*. These will now be discussed in direct comparison with the results given in this paper.

Our study predicted thousands of mating type alleles for *C. versicolor*, whereas Partington (1959) predicted 25 A and 25 B alleles from her sample of 46 fruit bodies. The vast difference stems from the method of deciding which occurrences of repeated alleles were genuine. Close examination of her data revealed that 9 of her 23 fruit bodies contained mating type combinations identical to others on the same substratum. Since she gave a diagram of the exact spatial relationships of the fruit bodies, it was possible to say that these 9 were repeat sampling of the same mycelia. Anyway the chance of independently getting two dikaryons of absolutely identical mating genotype, even with her low estimate of 25 alleles per locus, is extremely small. The number of individuals she sampled was probably only 14. On this basis her estimate of the number of alleles in the world should go up to 40 per locus. Further examination of neighbours in her data showed that there need only have been 20 nuclei involved in the formation of the observed fruit bodies. Some of the dikaryons probably had a nucleus in common, as in stump K, but there is no way of proving this now. If this had been true, 20 nuclei containing 20 alleles at each locus would have been indicative of an extremely large number of alleles, and in agreement with the present results. Most other tetrapolar species seem to have at least hundreds, if not thousands, of alleles at both loci. This re-interpretation of Partington's data augers well for the use of the method of counting nuclei of independent origin in surveys of mating type, rather than fruit bodies *per se*.

Workers on bipolar species had a less arduous task than those using tetrapolar species, as the number of test crosses involved is four times smaller. However, bipolar species other than *Piptoporus betulinus* have not been extensively examined. A large sample of *P. betulinus* was collected by Saunders (1956). She was aware of the problem of interpreting repeated mating type factors found in the same tree. After devising a method of correcting the data for this, she arrived at an estimate of 30 alleles worldwide. Cant (1980) also collected a large sample of *P. betulinus*. Re-examination of her data indicated that she probably only collected 116 different individuals, not 215. The other 99 were of identical mating type to others found on the same tree. However, this did not increase the worldwide estimate of the number of alleles much, as the sample was still large. Consideration of the number of nuclei of (probably) independent origin in her data reduced the number

of individuals to 100·5, or 201 nuclei. Again the sample size was still sufficiently large for the prediction of 35 alleles from the observed 33 to be acceptable. In this case, application of the rigorous procedure advocated in this paper did not affect the final result. The figure of 35 alleles for the species also agrees with that of Adams (1982) in a study being carried out parallel to this. It seems that bipolar species in general tend to have fewer mating type alleles.

Two other features of the results merit comment. The Malawi sample, in which 10 out of a possible 12 alleles were found, might indicate limited heterogeneity at that site. A total of only 40 alleles is predictable from the sample data. The site was a small forest on a narrow ledge at 2500 m on an isolated mountain. The sample was very small but there were other signs, such as reduced variability, that the population was more inbred that European ones. Part of the same argument could be applied to stump K. The genuine repeats observed there could be due to sibling spores originating close by and not yet dispersed by turbulence. It is perhaps surprising that the other stumps in the group did not show many repeated alleles if the spores of a nearby fruit body were predominating locally at the time of felling. However, spore trapping experiments (Williams, Todd & Rayner, 1984) at Kolora Park on a number of occasions indicated that the spore rain contained no repeats of any alleles throughout the year even when the traps were within 20 m of a sporulating fruit body of *C. versicolor*.

Returning to worldwide considerations, Malawi and UK strains were found to be interfertile, and to have no alleles in common. It is doubtful that spores actually travel between these populations, although they might interact via intervening populations. Worldwide allele numbers are used to estimate the outbreeding potential of species. However, such estimates fail to take into account external (ecological and geographic factors) and internal (genetical factors) breeding barriers. Therefore, worldwide allele numbers alone are virtually meaningless. In any case, in the absence of repeats, accurate estimation of allele numbers is impossible. Numbers must be large, and in order to maintain such large numbers of alleles the effective size of the interbreeding population must be enormous, worldwide or not. Otherwise, alleles would be lost by genetic drift probably faster than they could be replaced by mutation. Competent mating type alleles are very difficult to produce by standard mutational techniques (Raper, 1978), therefore it is possible to speculate that the large numbers and distribution of mating type alleles in species such as *C. versicolor* reflect their ubiquity, and the millenia during which the alleles have accumulated.

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