VARIATION IN A DIKARYOTIC POPULATION OF *COLLYBIA VELUTIPES*

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COLLYBIA VELUTIPES is distinguished among the Hymenomycetes by its ability to produce monokaryotic asexual spores (oidia) upon the dikaryotic, as well as upon the monokaryotic mycelia. Thus it is possible to separate a dikaryon collected in the wild into its two parental monokaryons. CROFT and SIMCHEN (1965) have shown the existence of variation within the asexual progeny of each of the parental monokaryons in several wild dikaryotic isolates of *C. velutipes*, and have compared this variation, which is probably cytoplasmic in nature, with the genetic variation among sexual progeny of the same dikaryons.

The character studied by CROFT and SIMCHEN was the growth rate of the monokaryotic mycelium, and the progeny of each wild isolate—sexual or asexual—were grown in a separate experiment and analysed independently of the progenies of the other isolates. On the other hand, SIMCHEN and JINKS (1964) and SIMCHEN (1965) have studied the variation of dikaryotic characters in *Schizophyllum commune* which exists between dikaryons resulting from crosses among the sexual progeny of *single* wild isolates.

The aim of the present paper is to study the variation of dikaryotic characters in a *population* of *C. velutipes*. The wild isolates were collected in a limited area, and can therefore be regarded as sharing in a common gene pool. As *C. velutipes* forms monokaryotic oidia, it can produce many new dikaryotic genotypes by matings of oidial monokaryons, without passing through the sexual stage. This variation was produced here by reisolating the parental monokaryons, and examining all possible dikaryotic combinations between them.

MATERIALS AND METHODS

Six wild isolates of *C. velutipes* have been used in the present study: isolates 7, 9, and 11 were collected during the autumn and winter of 1961–1962, and isolates 12, 13, and 14 were collected in the autumn of 1963. All six isolates were collected in the wild in a region 10 km in diameter in the south and west of Birmingham, England. As reported by CROFT and SIMCHEN (1965), the two parental monokaryons were recovered from each dikaryotic line, by isolating mycelia emerging from single oidia. The growth rates of the oidial progeny of each of these six dikaryons were bimodally distributed, thus the two parental monokaryons were separable on the basis of their growth rates as well as of their morphology and mating reactions. For the present study, one oidial isolate representing each parental monokaryon was taken. As there was variation (which is probably due to changes in the cytoplasm) among oidial progeny of an identical mating type, the choice of these 12 parental monokaryons was made from the means of

the oidial distributions for growth rates (CROFT and SIMCHEN 1965, Figures 1, 2, 3, 5, 6, and 7), thus obtaining lines with "average" cytoplasm.

Hypthal blocks of each pair of monokaryons were inoculated side by side on Petri dishes containing MT medium (2% malt extract and 2% New Zealand agar), resulting in 66 dikaryotic combinations; no selfings are of course possible in this heterothallic (and tetrapolar) fungus. The 66 dikaryons together with the 12 parental monokaryons were inoculated into growth tubes to determine their rates of growth. Four replicate tubes were inoculated with each of the 66 dikaryons and three replicate tubes with each of the 12 monokaryons. The tubes were randomised in four blocks in the incubator at 25°C, so that one block contained 66 tubes only, and the other three blocks contained 78 tubes each. Since the only analysis in which the monokaryons are used is a correlation between dikaryotic and monokaryotic means, the unequal number of replicates for the two phases will not therefore lead to any bias. A more detailed description of a similar experiment is given by SIMCHEN and JINKS (1964). Four days after the inoculation, the front of the mycelial growth was marked, and ten days later, the total linear growth (in mm) from the first mark was recorded.

For examining fruiting ability, all 66 combinations were inoculated in four replicates into 250 ml conical flasks containing 25 ml of ASCHAN's (1954) medium: 20.0 g glucose; 9.0 g ammonium tartarate; 7.0 g KH_2PO_4 ; 2.5 g $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$; 0.5 ml of a 1% solution of ferric citrate in 0.64% citric acid; 1.0 ml of a 0.007% solution of thiamine; 20.0 mg $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$; 20.0 mg $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$; 100.0 mg CaCl_2 ; 100.0 mg NaCl ; 20.0 g N.Z. agar; 1 l distilled water. This experiment contained therefore four randomised blocks, each block contained one inoculated flask of any one of the 66 dikaryons, and was confined to a single shelf in the temperature controlled room ($18 \pm 1^\circ\text{C}$). The flasks were continuously illuminated by "day light" fluorescent tubes, with a light intensity at the culture surface of 120 to 150 lumen/square foot. The flasks were examined daily for the appearance of the first sporophore primordia. At 55 days after inoculation all flasks were scored for the number of mature sporophores and for the number of primordia, including mature sporophores. Photographs of flasks containing the six original dikaryons at the time of the final scoring (55 days) are shown in Figure 1.

RESULTS

The matings among the 12 monokaryons succeeded in producing dikaryotic mycelia bearing clamp-connections in all cases but one. This exceptional combination involves the two monokaryons extracted from isolate 13. The reason for the failure of this mating is not clear and will not be discussed here. In the present study, the original isolate 13 was inoculated and scored instead of the combination 13S + 13F (where 13S refers to the slower parental monokaryon and 13F refers to the faster parental monokaryon, both of which were extracted from oidial progeny of the wild isolate 13). Isolate 13 itself is known to be a dikaryon since it bears clamp-connections, and has fruited previously in this laboratory (CROFT and SIMCHEN 1965).

The data collected in the experiments described above are summarized in Tables 1 and 2 in the form of the means of the four replicates. For one character, number of primordia per flask, rescaling of the original data was necessary because the variances within replicates for each dikaryon were correlated with their means. The square root of the number of primordia was therefore used and was found to be a suitable metric in the subsequent analyses. It is indeed possible that the number of primordia reflects some characteristics of the mycelium surface, and is therefore correlated with a squared metric.

One further fact that requires comment is the superiority in growth rate of the

FIGURE 1.—Photographs of the six original dikaryons taken after 55 days in flasks, i.e. at the end of the experiment (the early fruiterers have already begun to degenerate). $\times 0.90$.

monokaryon 14S to the monokaryon 14F, in contrast to the original behaviour of those lines reported by CROFT and SIMCHEN (1965). 14S originally contained the m_2 gene which resulted in a sectoring of the mycelium. It has changed and lost this sectoring morphology in the time which passed between the previous and the present experiment, so that it now grows faster than 14F.

General and specific combining abilities: The data summarized in Tables 1 and 2 may be analyzed in such a way that the genotypic variation is partitioned into two components, the general combining ability (GCA) and the specific combining ability (SCA). GCA represents the additive genetic effects which are common to all combinations of the same parent, and SCA represents the non-additive genetic effects—dominance and other types of genic interaction. The analysis of variance is according to GRIFFING (1956, 1958), although some minor modifications are required because of the randomized block design.

In the analysis of variance x_{ijk} is a single observation of the dikaryotic combination of parents i and j in the block k (there are p parental monokaryons and n

TABLE 1

Results of the experiments for the growth rate (upper right) and the number of primordia (lower left), averaged over blocks. The row marked by M contains the monokaryotic growth rates

Parents	7S	7F	9S	9F	11S	11F	12S	12F	13S	13F	14S	14F
M	37.33	62.33	57.00	66.33	56.33	79.00	56.67	94.67	24.67	51.00	43.67	40.33
7S	...	78.25	84.75	84.25	86.75	90.75	87.25	100.25	90.50	81.00	80.50	83.50
7F	3.22	...	89.00	83.00	87.25	98.25	92.00	97.50	77.00	74.25	80.25	85.75
9S	5.70	11.25	...	91.25	82.00	96.00	94.50	101.00	87.75	89.00	83.75	91.00
9F	2.58	3.60	6.87	...	89.75	96.25	93.00	97.00	81.00	86.25	84.25	84.75
11S	5.06	1.97	5.13	6.66	...	96.00	91.00	97.50	86.25	89.00	83.25	85.50
11F	1.72	2.16	2.59	2.73	2.61	...	105.75	98.50	103.50	100.75	92.00	97.50
12S	1.41	2.45	0.35	7.07	1.17	0.68	...	99.25	97.00	96.25	91.50	94.75
12F	5.50	6.14	5.30	3.95	5.36	5.95	5.34	...	100.25	97.50	100.00	100.25
13S	2.94	1.29	2.80	6.47	0.35	0.50	0.00	5.65	...	87.50	80.00	93.75
13F	2.61	0.85	3.63	1.70	0.00	1.00	0.56	5.55	0.00	...	76.50	94.50
14S	5.64	7.62	15.06	5.74	6.10	6.12	0.35	4.77	5.58	4.99	...	88.50
14F	2.79	8.76	11.06	9.68	6.49	4.74	5.82	4.86	3.95	2.95	15.51	...

TABLE 2

Results of the experiments for the number of sporophores (upper right) and the time to appearance of first primordium (lower left), averaged over blocks

Parents	7S	7F	9S	9F	11S	11F	12S	12F	13S	13F	14S	14F
7S	...	2.25	4.75	0.00	2.25	0.50	0.00	2.25	1.25	1.25	1.25	2.50
7F	22.00	...	1.50	2.00	1.75	1.00	0.00	2.50	0.00	0.25	2.25	2.00
9S	19.00	23.25	...	4.00	2.25	2.75	0.00	2.00	0.00	1.00	1.50	3.50
9F	20.25	22.25	25.50	...	6.25	4.25	5.75	1.25	2.25	0.00	4.00	6.00
11S	21.75	23.25	21.25	19.75	...	2.50	0.00	1.75	0.00	0.00	2.50	3.00
11F	34.50	21.00	18.75	17.75	21.50	...	0.00	2.25	0.25	0.00	1.00	4.50
12S	38.25	25.25	53.75	20.25	39.25	46.25	...	1.25	0.00	0.00	0.00	1.00
12F	22.25	20.25	23.50	25.25	21.75	22.50	21.50	...	2.00	3.50	1.25	2.00
13S	26.00	28.75	30.50	28.50	49.00	49.00	55.00	26.50	...	0.00	2.00	2.00
13F	26.50	31.00	30.25	33.50	51.25	47.50	47.50	25.50	55.00	...	1.25	3.50
14S	19.50	19.25	18.50	19.00	20.25	22.25	54.25	20.50	19.75	19.00	...	4.00
14F	20.50	19.50	19.00	16.75	19.00	19.00	20.00	23.50	23.75	25.50	16.75	...

randomized blocks). Therefore $x_{ijk} = \mu + g_i + g_j + s_{ij} + v_k + (e_{ik} + e_{jk} + e_{ijk})$ where μ is the population mean, g_i and g_j are the additive genetic effects of parents i and j , s_{ij} is the nonadditive genetic effect (or interaction between the additive effects of both parents), v_k is the (additive) effect of block k , and $(e_{ik} + e_{jk} + e_{ijk})$ is the combined interaction of the genetic effects with the effect of the block k .

The procedure of calculating the sums of squares in the analysis of variance and the appropriate degrees of freedom are given in Table 3.

Assuming a model II situation (EISENHART 1947), i.e. that the parental lines

TABLE 3

The computation of sums of squares in the analysis of variance

Item	d.f.	sum of squares
Dikaryons	$\frac{(p-1)p}{2} - 1$	$\frac{1}{n} \sum \sum_{i < j} X_{ij}^2 - \frac{2}{n(p-1)p} X_{...}^2$
Blocks	$n - 1$	$\frac{2}{(p-1)p} \sum_k X_{..k}^2 - \frac{2}{n(p-1)p} X_{...}^2$
Error	$(\frac{(p-1)p}{2} - 1)(n-1)$	$\sum \sum_{i < j} \sum_k X_{ijk}^2 - \frac{1}{n} \sum \sum_{i < j} X_{ij.}^2 - \frac{2}{(p-1)p} \sum_k X_{..k}^2 + \frac{2}{n(p-1)p} X_{...}^2$
G C A	$p - 1$	$\frac{1}{n(p-2)} \sum_i X_{i..}^2 - \frac{4}{np(p-2)} X_{...}^2$
S C A	$\frac{(p-3)p}{2}$	$\frac{1}{n} \sum \sum_{i < j} X_{ij.}^2 - \frac{1}{n(p-2)} \sum_i X_{i..}^2 + \frac{2}{n(p-1)(p-2)} X_{...}^2$
<p>Where $X_{i..} = \sum_j \sum_k X_{ijk}$ $X_{ij.} = \sum_k X_{ijk}$ $X_{..k} = \sum_{i < j} X_{ijk}$</p> <p>$X_{...} = \sum_{i < j} \sum_k X_{ijk}$ and in our design $X_{...} = \frac{1}{2} \sum_i X_{i..}$</p>		

are a random sample of lines from the population and g_i , g_j and s_{ij} are random variables, the expectations are:

Mean Square for General Combining Ability	$\sigma_E^2 + n\sigma_{SCA}^2 + n(p-2)\sigma_{GCA}^2$
Mean Square for Specific Combining Ability	$\sigma_E^2 + n\sigma_{SCA}^2$
Mean Square for Error	σ_E^2

It is possible to divide the total observed variance (excluding the blocks' component in which we are not interested) into three components—two genetic, V_{GCA} and V_{SCA} , and one environmental V_E , such that $V_T = V_{GCA} + V_{SCA} + V_E$ (see also SIMCHEN and JINKS 1964, p. 635), where V_{GCA} is an estimate of $2\sigma_{GCA}^2$, V_{SCA} is an estimate of σ_{SCA}^2 , and V_E is an estimate of σ_E^2 .

Table 4 gives the analysis of variance for the four characters and Table 5 contains the estimates of the variance components following this analysis. All four characters show significance for both additive (GCA) and nonadditive (SCA) genetic variation. Growth rate and the number of primordia both have a small proportion of the environmental component, and are therefore comparable to growth rate in *Schizophyllum*, which was the character with the highest proportion of heritable variation in that fungus (SIMCHEN 1965).

TABLE 4
Analysis of variance

	Dikaryons-GCA (11 df)		Dikaryons-SCA (54 df)		Blocks (3 df)		Error (Dik × Block) (195 df)†
	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.
Growth rate	986.92	16.38**	60.24	11.32**	89.46	16.82**	5.32
Number of primordia	153.41	7.38**	20.78	15.23**	2.07	1.52	1.36
Number of sporophores	26.73	4.25**	6.29	5.46**	2.80	2.43	1.15
Time	1765.52	7.60**	232.25	6.67**	42.23	1.21	34.82

** Significant at the 0.001 level: GCA—when tested against SCA; SCA and Blocks—when tested against Error.

† For one character, that is Time, the number of degrees of freedom is only 174 because a score of 55 days was given to all combinations which did not fruit during the course of the experiment; an appropriate allowance was therefore necessary in the degrees of freedom.

TABLE 5
The components of variation

	V _{GCA}	V _{SCA}	V _E	V _T
Growth rate	46.28 (70.84%)	13.73 (21.02%)	5.32 (8.14%)	65.33
Number of primordia	6.632 (51.61%)	4.854 (37.77%)	1.364 (10.62%)	12.850
Number of sporophores	1.022 (29.56%)	1.284 (37.13%)	1.152 (33.31%)	3.458
Time	76.66 (47.66%)	49.36 (30.69%)	34.82 (21.65%)	160.84

Dominance and nonallelic interaction: So far, genetic variation due to additive effects and to nonadditive effects (GCA and SCA) has been demonstrated. As in all analyses which divide the genetic variation into components of general and specific combining abilities, one cannot determine the nature of the genic interaction which results in the specific combining ability without further analysis. SIMCHEN and JINKS (1964) have shown that in certain circumstances, an hypothesis assuming additivity and dominance only is testable. When the conditions laid out by SIMCHEN and JINKS hold, that is homozygosity (or haploidy) of the parental lines and two equally frequent alleles for each locus, a W'_r/V_r graph should show a slope of $\frac{1}{2}$ as long as additivity and dominance are the only sources of genetic variation. (V_r is defined as variance within an array, W_r as covariance of an array with the noncommon parents, and W'_r is defined as covariance of an array with the means of noncommon arrays.) Although in the present case one has *a priori* no reason to believe that all loci contain only two, and equally frequent alleles, there is at least the certainty about the haploidy of the parental lines, and hence this way of analysis is worth trying. The W'_r/V_r graphs for the four characters are given in Figure 2.

The sensitivity of the W'_r/V_r test to gene frequencies could be overcome by

FIGURE 2.— W'_r/V_r graphs of the data represented in Tables 1 and 2. Each point represents an array of a common monokaryotic parent.

using W_r/V_r graphs as devised by JINKS (1954), but it is not possible in the present situation because the monokaryotic parental lines cannot be selfed. One could, however, arrange the results represented in Tables 1 and 2 in the form of 6×6 diallel tables, in which the six original dikaryons are the parents, and those parents are crossed among themselves in all possible combinations. The two parental monokaryons can be regarded as two types of gametes, and a cross between two dikaryons will therefore produce a "family" of four dikaryotic progeny (2×2). A selfing "family" (which is placed on the leading diagonal) will include only one offspring, that is the original dikaryon, because the selfing of a gamete (monokaryon) is not possible here. The "families" obtained in this way are not homogeneous (except on the leading diagonal) and indeed the

original dikaryons are heterozygous as demonstrated in Tables 1 and 2 (compare, for example, combinations of 12S with combinations of 12F, 14S with 14F, etc.). Thus we have to regard the 6×6 tables obtained by the grouping of combinations to "families" as equivalent to heterozygous diallel tables, and treat them accordingly (DICKINSON and JINKS 1956). The heterozygosity weakens the analysis and only intense nonallelic interaction can be detected without ambiguity. The W_r/V_r graphs, when calculated from the means of the "families", are given in Figure 3.

The genetic interpretation of the W'_r/V_r and W_r/V_r graphs is as follows. For three characters, that is growth rate, number of primordia and time to first primordium, additivity and dominance are sufficient explanations of the genetic variation. For the number of sporophores, the slope of the W'_r/V_r graph does not differ significantly from zero; the W_r/V_r graph for this character is also more scattered than the other three, and it is perhaps possible to claim that nonallelic interaction is present. Both genetical analyses, the W'_r/V_r and the W_r/V_r for

FIGURE 3.— W_r/V_r graphs of the data represented in Tables 1 and 2, grouped as described in the text. Each point represents an array of a common dikaryotic parent.

this character are probably influenced also by its high environmental component and low heritability: $V_E = 33.31\%$ and $V_{GCA} = 29.56\%$ (Table 5). The W_r/V_r graphs of the number of primordia and the time give lower regression coefficients than expected (both differ significantly from $b = 0.5$), although they are significantly different from zero. The reason for this could be either unequal gene frequencies or nonallelic interaction. There is in fact an indication of duplicate gene interaction in the W_r/V_r graphs, which results in a concentration of the points towards the lower parts of the graphs. This does not exclude the possibility of unequal gene frequencies, to which the slope of the graph in the W_r/V_r test is not sensitive. Growth rate behaves as expected in both tests, and it can be concluded that neither nonallelic interaction nor unequal gene frequencies are present for this character.

The heterozygosity has only a slight effect on the W_r/V_r graphs, although for the number of primordia it results in the expected triangulation (DICKINSON and JINKS 1956).

The analysis of array variances and covariances also provides us with information about the direction of dominance since the most dominant arrays have the lowest values for the variance and covariances (JINKS 1954). One of the characters, that is time to the first primordium shows unidirectional dominance, while for the other three characters dominance is ambidirectional. This suggests that fruiting time which is probably a fitness character has been subjected to directional selection in favour of shortening the period to appearance of the first primordium, while the other three characters have been subjected to stabilizing selection (MATHER 1960).

Correlations: The data collected in the present study provide us with information about the correlations between the different characters which were measured. There are two possible genetic causes of such correlations (MATHER and HARRISON 1949). First, pleiotropy of genes which affect two or more characters simultaneously. Second, linkage or association of genes in certain phases which occur more often than expected, either by chance or as a result of natural selection; for example the association phase $c^+ d^+$ and $c^- d^-$ being more frequent than the alternative phase $c^+ d^-$ and $c^- d^+$. In the present study it is not possible to distinguish between pleiotropy, and linkage or association, since this requires recombination cycles, genetic markers and screening methods.

The correlations were calculated on the means of the four replicates for each metric, so that the intragenotype correlation is minimized, and are represented in Table 6. Three of the characters were found to be correlated, therefore a partial correlation was calculated as suggested by FISHER (1958, p. 188). The partial correlation excludes the correlations of the two characters with a third character, that is it measures the correlation between two characters when a third (correlated) character is held constant. For all three significant correlations, the partial correlations are also significant. This could be explained on linkage or association but at the same time pleiotropy would not be surprising for related fruiting characters, and it would also explain the partial correlations. We would have to assume that there are genes which affect both the number of primordia

TABLE 6
Correlations between characters

The characters	Correlation		Partial correlation	
	<i>r</i>	P	<i>r</i>	P
<i>Uncorrelated:</i>				
Growth rate-Number of primordia	-0.1418	>0.10		
Grow rate-Number of sporophores	-0.0265	>0.10		
Growth rate-Time	0.2143	0.10-0.05		
<i>Correlated:</i>				
Number of primordia-Number of sporophores	0.5624	<0.001	0.2523	0.05-0.02
Number of primordia-Time	-0.6640	<0.001	-0.4842	<0.001
Number of sporophores-Time	-0.6253	<0.001	-0.4076	<0.001

The partial correlation is calculated for the correlated characters only. *r* is the correlation coefficient, *P* is its level of significance.

and the time to the first primordium, but do not affect the number of sporophores, and so on.

Growth rate is not correlated with any of the fruiting characters.

Whether the significant correlations include only additive effects of genes or whether dominance relationships are also correlated is not possible to decide. An indication of some correlation in dominance relationships is given in Figure 2, since the most dominant parent for all characters is 12F.

SIMCHEN and JINKS (1964) have calculated the correlation between the growth rates of dikaryons and the growth rates of parental monokaryons, and related a proportion, which equals r^2 , of the heritable variation among dikaryons to genes acting in both mono- and dikaryotic phases of the life cycle of the fungus. The same calculation for growth rates was carried out here. The r^2 between dikaryotic values (means of four replicates) and midvalues of monokaryotic parents (means of three replicates) was found to be 0.3375, and the heritable variation in dikaryons due to this correlation $V_M = r^2(V_{GCA} + V_{SCA}) = 20.25$ which is 31.00% of V_T . Here again $V_M < V_{GCA}$, and even if we accept that V_{SCA} is the result of dominance only, which cannot be expressed in monokaryons, the majority of the additive effects in dikaryons is still uncorrelated with the genetic (additive) effects in the parental monokaryons.

The conclusion here is identical with the one reached by SIMCHEN and JINKS: most genes which determine growth rate in dikaryons of *C. velutipes*, either do not act in monokaryons or act in a different and independent way.

DISCUSSION

At the present time little is known about the genetical structure of populations of the higher Basidiomycetes. The significance of the dikaryotic stage in these fungi lies mainly in the ability of each of the two nuclei to migrate independently in a compatible monokaryotic mycelium and to form new dikaryotic combinations by means of di-mon matings (BULLER 1931). Thus we can regard such a

population of dikaryons as a gametic population in which the gametes are organized in pairs but still preserve their independence and the ability to form new pairs, should the opportunity arise. The genetic flexibility of this type of population is potentially enormous, and is limited only by the necessity of successful hyphal fusion following contact between different mycelia. *Collybia velutipes* overcomes this limitation by having monokaryotic oidia upon the dikaryotic mycelium, so that physical contact between mycelia of the members of the population is no longer essential. The flexibility of populations of *C. velutipes* is further extended by the existence of clonal variation between oidial monokaryons possessing identical nuclei (CROFT and SIMCHEN 1965) and probably representing variation in cytoplasmic systems. The Hymenomycetes, and especially *C. velutipes*, maintain therefore high genetic flexibility in their vegetative populations in addition to the flexibility that they maintain by the sexual cycle and basidiospore dispersion (as other organisms do).

The incompatibility factors in the Hymenomycetes prevent close inbreeding and the formation of a dikaryon from two identical haploid nuclei. Here, as in *Schizophyllum commune* (RAPER, KRONGELB and BAXTER 1958) and in other Hymenomycetes (WHITEHOUSE 1949), the number of alleles for each of the two factors *A* and *B* is large, so that the self incompatibility system does not restrict the possibilities of matings between different nuclei. Our estimates of the number of alleles of each factor in *C. velutipes* are high, because no repetition of the incompatibility factors was found among the 12 monokaryons analyzed.

The variation found in the present study (Table 5) is comparable in magnitude to the variation found in *S. commune* (SIMCHEN and JINKS 1964), in spite of the fact that the *Collybia* monokaryons, unlike those of *Schizophyllum* in the earlier experiments, have already been subjected to natural selection. It appears that the effect of natural selection is too small to be detected directly by comparing the variation found within the progenies of single wild isolates with the variation found in a population of wild isolates which have been exposed to natural selection. Such an effect can perhaps be demonstrated by comparing the components of variation found within populations with those found in crosses between populations.

One significant difference between the present study and the *Schizophyllum* studies is the relationship between growth rates of dikaryons and parental monokaryons. As SIMCHEN and JINKS (1964) pointed out, most dikaryons in *S. commune* grow faster than the parental monokaryons, but some have an intermediate growth rate or even grow more slowly than both parental monokaryons. They suggest that this relationship depends on the genotypic constitution of the lines. This is supported by later results (SIMCHEN 1965) which show that in other lines of *S. commune* the majority of dikaryotic combinations grow more slowly than both parental monokaryons. In the present study (see Table 1), all 66 dikaryotic combinations grow faster than both their parental monokaryons, in contrast to the *Schizophyllum* results and to those of ASCHAN-ÅBERG (1960) who measured the growth rate of *C. velutipes*. The explanation of this apparent disagreement possibly lies in the growth habit of *C. velutipes*. The monokaryotic

oidia are formed on monokaryotic hyphal branches of the dikaryon, hence the dikaryons will break down regularly to their monokaryotic components unless the dikaryons outgrow the component monokaryons. Natural selection will favour therefore combinations in which the dikaryon grows faster than the parental monokaryons, and indeed in those combinations of ASCHAN-ÅBERG in which the dikaryon was intermediate, at least one of the parental monokaryons was derived from a basidiospore isolated in the laboratory, and hence not subjected to natural selection.

The genetic interpretation of diallel sets of crosses by means of W_r/V_r graphs has been used in recent years by several authors for different organisms. One of the unknown factors, which applies mainly to the study of variation in populations, is the extent to which heterozygosity will affect these graphs. Theoretically (DICKINSON and JINKS 1956), triangulation of the points within the limiting parabola is the expected result. The diallel tables constructed from "families" of four individuals each, presents us with heterozygous W_r/V_r graphs which show only very slight triangulation. In fact, the present situation is almost an ideal heterozygous diallel, since the two "gametes" produced by each dikaryon are complementary, equally frequent, and common to the combinations with all other dikaryons. The heterozygosity of a dikaryon can be demonstrated directly by comparing dikaryotic combinations of one monokaryotic parent with those of the other parent. One can see also that different levels of heterozygosity exist among the parental dikaryons, as required for the triangulation of points. In spite of these ideal conditions the discrepancies from slopes of 1.0 are small and the triangulation only slight. This confirms previous experience that nonallelic interactions have probably a much more marked effect on the W_r/V_r graph than has heterozygosity.

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SUMMARY

Twelve monokaryons were isolated from oidia of six dikaryons of *C. velutipes*, all of which were collected within a limited area in England. The monokaryons were crossed in all possible combinations, resulting in 66 dikaryons which were scored for linear growth rate and three measures of fruiting ability. The components of variation have been estimated by an analysis of variance, and the heritable variation partitioned into general and specific combining ability, which are estimates of the additive and nonadditive (dominance and/or nonallelic interaction) genetic effects, respectively. The nature of the genetic interaction has been analyzed by W'_r/V_r and W_r/V_r regressions. Growth rate shows additivity and dominance only. Number of primordia and time to the appearance of the first primordium show some indication of the duplicate type of genic interaction, although additivity and dominance are sufficient as sources of the heritable variation. Number of sporophores shows low heritability and nonallelic interaction

may exist for this character. Dominance is unidirectional for time of appearance of the first primordium, which is a fitness character. The three fruiting characters are correlated, thus pleiotrophy and/or linkage-association exist. The low correlation between growth rate of dikaryons and parental monokaryons indicates that many of the genes which determine the growth of dikaryons do not act in the monokaryotic stage.

The population concept in the Hymenomycetes is discussed in relation to the high potential genetic flexibility of *C. velutipes*, as well as the effects of natural selection on populations of this fungus.

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