VARIATION IN A NATURAL POPULATION OF *SCHIZOPHYLLUM COMMUNE*

II. VARIATION WITHIN THE EXTREME ISOLATES FOR GROWTH RATE

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SUMMARY

Two extreme dikaryotic isolates chosen from a large sample of a localised population of *Schizophyllum commune* exhibited a considerable amount of genetical variation for growth rate at the near ambient temperature of 20°C and at the higher temperature of 30°C. The potential variation within these extreme isolates was greater than the variation observed in the whole sample. Regression analysis of the variation in growth rate of the dikaryotic progeny of the extreme isolates on that of their component monokaryons showed that the nature of gene action was not the same in these two stages of the life cycle.

The simple additive-dominance model of gene action was adequate to explain the variation in growth rate in both of the extreme isolates at both of the temperatures. The small deviations from this model could be accounted for by unequal gene frequencies due to small sample size although a low incidence of non-allelic interactions could not be ruled out. Directional dominance for growth rate was detected in both isolates at the more normal temperature and it was opposing in direction in the two isolates. In the slow growing isolate the dominance was for faster growth and in the fast growing isolate it was for slower growth. This is expected for a character which displays overall ambi-directional dominance if isolates with more extreme growth rates than those recovered in the population sample are eliminated by stabilising selection. The dominance is temperature dependent being ambi-directional in both isolates at the higher temperature.

Environmental heterogeneity, the buffering effects of directional dominance and genotype-environment interactions and opposing selective forces operating on the monokaryotic and dikaryotic stages of the life cycle are possible contributory factors to the considerable free and potential variability displayed in this small, localised population.

I. INTRODUCTION

THE fungi are now being extensively used in the biometrical genetical studies of continuous variation because they offer a number of advantages over the commercially important higher organisms. The application of the biometrical procedures outlined by Simchen and Jinks (1964) and Mather and Jinks (1971) have demonstrated that the phenomena of additivity, dominance and non-allelic interactions exist in the dikaryons of basidiomycetes and behave as in any diploid or amphidiploid organism. These techniques have been mostly applied to study the heritable variation within the progeny of a few dikaryons selected at random from small numbers of wild isolates. They are equally suitable however, for studying the genetical structure of a large

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population as well as for different known segments of a population. In the present study two extreme isolates of a large and genetically variable population of *Schizophyllum commune* were examined to determine:

- (i) the magnitude of the potential variation for growth rate within the extreme isolates;
- (ii) the genetical control of growth rate in the extreme segments of the population and
- (iii) the shifts, if any, in the control in an altered environment not commonly encountered by the organism.

2. MATERIALS AND METHODS

Growth rate and fruiting ability in a random sample of 77 dikaryons of a localised but dense natural population of *Schizophyllum commune* were studied by Brasier (1970). The materials for the present study are two extreme isolates (designated as isolate 25 and isolate 26) chosen from this population. Isolate 25 had the slowest growth rate under the three temperature conditions studied while isolate 26 had above average growth rate at all temperatures and was one of the fastest at 25°C and 30°C. Both were also chosen for their good and fast fruiting.

From each isolate, six monokaryotic progeny of each of the four incompatibility groups were taken at random and all possible matings were made between them. Thus, among the monokaryotic progeny of each dikaryotic isolate, two 6 × 6 series of dikaryotic combinations [designated as (*a-f*) (*g-l*) and (*m-r*) (*s-z*) series] were formed to give rise to 72 dikaryons derived from all possible combinations among 24 monokaryons. The media used, their preparation and composition have been described by Simchen (1965). The techniques of isolation, fruiting and raising of the progeny as well as the measurement of growth rate and biometrical procedures follow closely those of Simchen and Jinks (1964) and Simchen (1966). Two incubators, one at 20°C and the other at 30°C were used in the determination of growth rate. Each of the three shelves of an incubator contained one randomised block and each block contained 97 randomised growth tubes (one tube each of the original dikaryon, 24 monokaryons and 72 dikaryons).

In addition, regression analysis of genotype × environment interaction was carried out as suggested by Perkins and Jinks (1968). However, in this analysis it was used to analyse genotype × genotype interactions, one set of monokaryons say (*a-f*) being considered as the variable environments for the second set of monokaryons (*g-l*) and vice versa.

Directional dominance can be detected directly by comparing the means of each pair of monokaryons and their F_1 dikaryon (Mather and Jinks, 1971) and on averaging over all pairs and their F_1 's it indicates the net directional dominance in the population. This comparison, however, measures directional dominance only if we assume that all differences in gene action between the dikaryotic and monokaryotic states can be attributed to dominance and that there are no differences in gene action *per se* between these two alternative states. This assumption does not appear to hold in general (Simchen and Jinks, 1964) or in these data. While, therefore, we shall compare the growth rates of monokaryotic parents and their F_1 dikaryons they are not used to determine the direction of dominance.

3. RESULTS

(i) *Genetic variation for growth rate*

The analysis of variance in respect of growth rate of the dikaryotic progeny of the two isolates at 20°C and 30°C is presented in tables 1 and 2. The significant differences among the dikaryons in both duplicate series of both the isolates in each environment suggests the existence of genetic

TABLE 1

Analysis of variance of growth rate in two duplicate series of two isolates under normal and high temperature conditions

Isolate	Item	d.f.	Mean squares			
			20°C		30°C	
			Series: (a-f)(g-l)	(m-r)(s-z)	(a-f)(g-l)	(m-r)(s-z)
25	Blocks	2	3.20	3.30	346.00**	157.00*
	Dikaryons	35	35.30***	31.50***	760.20***	791.50***
	Error	70	4.27	4.25	63.29	42.54
26	Blocks	2	18.30	7.20	92.20	47.15
	Dikaryons	35	93.50***	42.70***	765.80***	376.90***
	Error	70	11.04	13.45	40.41	39.39

*, **, *** Probability less than 0.05, 0.01 and 0.001 respectively.

TABLE 2

(a) *Pooled analysis of variance over duplicate series for growth rate of two isolates under normal and high temperature conditions*

Item	d.f.	Mean squares			
		Isolate 25		Isolate 26	
		20°C	30°C	20°C	30°C
Blocks within series	4	3.2500	251.5000	12.7500	69.6750
Between series	1	53.0046	44.4629	196.4629	67.7824
Dikaryons within series	70	33.4000***	775.8500***	68.1000***	571.3500***
Error	140	4.2500	52.9000	12.2000	39.9000

(b) *Pooled analysis of variance over duplicates and temperatures*

Blocks within series	8	127.3750	41.2125
within temp.			
Between series	1	97.2801	247.5209
Between temperatures	1	182821.2245***	247537.6875***
Series × temperature	1	0.1875	16.7245
Dikaryons within series	140	404.6250***	319.7250***
within temp.			
Error	280	28.5750	26.0500

diversity for growth rate. The variation between duplicate series within each isolate when tested against the variation between dikaryons within the series was not statistically significant (table 2a) suggesting that the duplicates could be considered together. The pooled analysis over duplicates and temperatures (table 2b) revealed that the variation in temperature had a

tremendous effect on growth rate of both of the isolates and that the duplicates within an isolate did not interact with the temperature. The total genetic variation present in each duplicate series was partitioned into additive, non-additive and the environmental components (tables 3 and 4). The differences due to common parents were significant for six out of eight possible cases for each of the two isolates suggesting the presence of additive variation for growth rate. The highly significant interaction item for all the

TABLE 3
Partitioning of variation between dikaryotic combinations in duplicate series of two isolates

Isolate	Item	d.f.	Mean squares			
			20°C		30°C	
			(a-f)(g-l)	(m-r)(s-z)	(a-f)(g-l)	(m-r)(s-z)
25	Common parents	5	159.30***	68.40**	881.40	1720.40*
	Common parents	5	34.10*	88.40***	2019.10**	890.20
	Parents interaction	25	10.66**	12.87***	484.20***	586.01***
	Error	70	4.27	4.25	63.29	42.54
26	Common parents	5	195.00**	73.00	1550.10**	982.30*
	Common parents	5	218.50**	81.50*	1916.70**	163.10
	Parents interaction	25	48.24***	28.84**	378.73***	298.59***
	Error	70	11.04	13.45	40.41	39.39

TABLE 4
Components of variation for growth rate of two isolates under normal and high temperature conditions

Isolate	Temperature	Series	Components			Total variance
			Environmental	Non-additive	Additive	
25	20°C	(a-f)(g-l)	4.27 (26.75)	2.13 (13.35)	9.55 (59.90)	15.96
		(m-r)(s-z)	4.25 (29.49)	2.87 (20.00)	7.28 (50.55)	14.40
	30°C	(a-f)(g-l)	63.29 (20.35)	140.31 (45.12)	107.35 (34.53)	310.93
		(m-r)(s-z)	42.54 (14.01)	181.16 (59.67)	79.92 (26.32)	303.62
26	20°C	(a-f)(g-l)	11.04 (26.90)	12.40 (30.20)	17.61 (42.90)	41.06
		(m-r)(s-z)	13.45 (56.12)	5.13 (21.43)	5.38 (22.45)	23.96
	30°C	(a-f)(g-l)	40.41 (13.31)	112.77 (37.13)	150.51 (49.56)	303.70
		(m-r)(s-z)	39.39 (25.21)	86.40 (55.30)	30.46 (19.49)	156.26

comparisons reflected the importance of non-additive genetic variation determining growth rate under both temperature conditions in both isolates. The estimates of components of variation determined from the mean squares in this analysis were in good agreement for isolate 25 but not for isolate 26. At 20°C, isolate 26 exhibited higher variation than isolate 25. However, at the higher temperature, the total variation in isolate 25 was similar to that in isolate 26 [with the exception of the series (m-r)(s-z)]. In isolate 25, the additive component was larger than the non-additive component at 20°C but it was smaller at 30°C. The ratio of the non-additive to the additive component was relatively larger in isolate 26 than in isolate 25 under both temperature conditions.

The relative importance of the linear and the non-linear components of variation in the two isolates can also be demonstrated by an alternative technique of regression analysis. The interaction component between the two sets of parents (genotype-genotype interaction) can be partitioned in two ways *i.e.* considering the interaction of one set of monokaryons (*a-f*) with the genetic environments of another set of monokaryons (*g-l*) and vice versa. The results of such analyses are presented in table 5. For isolate 25 at 20°C,

TABLE 5
Partitioning of the parents (genotype-genotype) interaction

Isolate	Temperature	Genotypes	Genetic environments	Mean squares			
				Parents interaction (25)	Hets. bet. regressions (5)	Remainder (20)	Error (70)
25	20°C	(<i>a-f</i>)	(<i>g-l</i>)	10·6635**	7·1100 ($\frac{n.s.}{n.s.}$)	11·5518**	4·2700
		(<i>g-l</i>)	(<i>a-f</i>)	10·6635**	7·3923 ($\frac{n.s.}{n.s.}$)	11·4816**	4·2700
		(<i>m-r</i>)	(<i>s-z</i>)	12·8715**	8·0637 ($\frac{n.s.}{n.s.}$)	14·0733	4·2500
		(<i>s-z</i>)	(<i>m-r</i>)	12·8715**	24·3609 ($\frac{n.s.}{**}$)	9·9987**	4·2500
		χ^2 homogeneity			1·5308 n.s.	0·6885 n.s.	
		(<i>a-f</i>)	(<i>g-l</i>)	484·2018**	260·9947 ($\frac{n.s.}{**}$)	540·0063**	63·2900
		(<i>g-l</i>)	(<i>a-f</i>)	484·2018**	530·1078 ($\frac{n.s.}{**}$)	472·7250**	63·2900
		(<i>m-r</i>)	(<i>s-z</i>)	586·0056**	542·8110 ($\frac{n.s.}{**}$)	596·8044**	42·5400
		(<i>s-z</i>)	(<i>m-r</i>)	586·0056**	214·7157 ($\frac{n.s.}{**}$)	678·8280**	42·5400
		χ^2 homogeneity			2·8014 n.s.	0·5888 n.s.	
	30°C	(<i>a-f</i>)	(<i>g-l</i>)	48·2448**	46·5858 ($\frac{n.s.}{**}$)	48·6597**	11·0400
		(<i>g-l</i>)	(<i>a-f</i>)	48·2448**	55·9083 ($\frac{n.s.}{**}$)	46·3284**	11·0400
		(<i>m-r</i>)	(<i>s-z</i>)	28·8444**	16·4862 ($\frac{n.s.}{**}$)	31·9341**	13·4500
		(<i>s-z</i>)	(<i>m-r</i>)	28·8444**	74·1039 ($\frac{**}{**}$)	17·5302	13·4500
		χ^2 homogeneity			2·4661 n.s.	5·8465 n.s.	
		(<i>a-f</i>)	(<i>g-l</i>)	378·7275**	431·7207 ($\frac{n.s.}{**}$)	365·4804**	40·4100
		(<i>g-l</i>)	(<i>a-f</i>)	378·7275**	259·9044 ($\frac{n.s.}{**}$)	408·4332**	40·4100
		(<i>m-r</i>)	(<i>s-z</i>)	298·5885**	481·0812 ($\frac{n.s.}{**}$)	252·9651**	39·3900
		(<i>s-z</i>)	(<i>m-r</i>)	298·5885**	43·1184 ($\frac{n.s.}{n.s.}$)	362·4558**	39·3900
		χ^2 homogeneity			5·9975 n.s.	1·2039 n.s.	
26	20°C	(<i>a-f</i>)	(<i>g-l</i>)	48·2448**	46·5858 ($\frac{n.s.}{**}$)	48·6597**	11·0400
		(<i>g-l</i>)	(<i>a-f</i>)	48·2448**	55·9083 ($\frac{n.s.}{**}$)	46·3284**	11·0400
		(<i>m-r</i>)	(<i>s-z</i>)	28·8444**	16·4862 ($\frac{n.s.}{**}$)	31·9341**	13·4500
		(<i>s-z</i>)	(<i>m-r</i>)	28·8444**	74·1039 ($\frac{**}{**}$)	17·5302	13·4500
		χ^2 homogeneity			2·4661 n.s.	5·8465 n.s.	
		(<i>a-f</i>)	(<i>g-l</i>)	378·7275**	431·7207 ($\frac{n.s.}{**}$)	365·4804**	40·4100
		(<i>g-l</i>)	(<i>a-f</i>)	378·7275**	259·9044 ($\frac{n.s.}{**}$)	408·4332**	40·4100
		(<i>m-r</i>)	(<i>s-z</i>)	298·5885**	481·0812 ($\frac{n.s.}{**}$)	252·9651**	39·3900
		(<i>s-z</i>)	(<i>m-r</i>)	298·5885**	43·1184 ($\frac{n.s.}{n.s.}$)	362·4558**	39·3900
		χ^2 homogeneity			5·9975 n.s.	1·2039 n.s.	
	30°C	(<i>a-f</i>)	(<i>g-l</i>)	378·7275**	431·7207 ($\frac{n.s.}{**}$)	365·4804**	40·4100
		(<i>g-l</i>)	(<i>a-f</i>)	378·7275**	259·9044 ($\frac{n.s.}{**}$)	408·4332**	40·4100
		(<i>m-r</i>)	(<i>s-z</i>)	298·5885**	481·0812 ($\frac{n.s.}{**}$)	252·9651**	39·3900
		(<i>s-z</i>)	(<i>m-r</i>)	298·5885**	43·1184 ($\frac{n.s.}{n.s.}$)	362·4558**	39·3900
		χ^2 homogeneity			5·9975 n.s.	1·2039 n.s.	
		(<i>a-f</i>)	(<i>g-l</i>)	378·7275**	431·7207 ($\frac{n.s.}{**}$)	365·4804**	40·4100
		(<i>g-l</i>)	(<i>a-f</i>)	378·7275**	259·9044 ($\frac{n.s.}{**}$)	408·4332**	40·4100
		(<i>m-r</i>)	(<i>s-z</i>)	298·5885**	481·0812 ($\frac{n.s.}{**}$)	252·9651**	39·3900

Degrees of freedom are given in parentheses. Heterogeneity between regressions M.S. has been tested against remainder M.S. and error M.S. (upper and lower probabilities respectively). n.s. = not significant.

the heterogeneity between regressions component was not significant when tested against the error variance in three out of four cases and in all cases when tested against the remainder. However, at 30°C, this linear component became significant in all the four cases when tested against the error. The linear and the non-linear components of the interaction were statistically of the same magnitude. For isolate 26, the linear component was highly significant at both the temperatures when tested against the error variance but was not significant in seven out of eight cases when tested against the

remainder which was itself highly significant (except in one case). Statistically, these two components were of the same magnitude.

(ii) *Non-additive component*

The nature of the non-additive or non-linear component was further investigated by plotting the variances within arrays against covariances between crosses within each array and the array means of the non-common parents. The slopes of the $W'r/Vr$ graphs were calculated and are presented in table 6.

TABLE 6
Regression slopes of $W'r/Vr$ analysis in duplicate series of two isolates for growth rate under normal and high temperature

Isolate	Temperature	$bW'r.Vr$				
		(a-f)	(g-l)	(m-r)	(s-z)	Pooled
25	20°C	0.2601**	0.3549*	0.3170***	0.4392**	0.5321**
	30°C	0.4751*	0.2207	0.2797***	0.1116	0.3179***
26	20°C	0.4917*	0.3185*	0.2442**	0.3544*	0.4087**
	30°C	0.4383*	0.3001***	0.1267+	0.0575	0.4391**

*, ** Regression coefficient significantly different from zero ($P < 0.05$ and 0.01 respectively).

+ Regression coefficient significantly different from 0.5 ($P < 0.05$).

At 20°C the regression coefficient was statistically different from zero for both the isolates but it deviated from the expected value of 0.5 in three out of eight cases. However, at 30°C the regression coefficient did not differ from zero in half of the cases in respect of both the isolates and there was poor agreement between the duplicate series within an isolate. The pooled estimates over series within each isolate revealed that the simple additive-dominance model explained the total variation for growth rate of the dikaryons at 20°C for both the isolates and for isolate 26 at 30°C as well. For isolate 25, the significant departure of the regression coefficient from the expected value of 0.5 at 30°C may be due either to the presence of non-allelic interactions, or unequal gene frequencies at the loci controlling growth rate arising from small sample size.

(iii) *Directional dominance*

Directional dominance is indicated by the significant correlation between the $W'r + Vr$ values of the arrays and the corresponding array mean (mean of the dikaryotic progeny in the array) and the sign of the correlation is determined by whether the increasing or the decreasing alleles are more frequently dominant. At 20°C, this correlation was consistently negative in all the four independent samples in isolate 25 but positive (except one case) in isolate 26 (table 7). Individually, these correlations were statistically non-significant (each based on 4 d.f.). However, these correlations were found to be homogeneous for each isolate and the average correlations (-0.6126 for isolate 25 and $+0.5908$ for isolate 26) were significant. The upper and

lower 99 per cent confidence limits of these average correlations had negative and positive signs for isolates 25 and 26 respectively and there was no overlapping of these confidence limits. This suggests that on a net balance, there is a directional element to the dominance in both the isolates at 20°C and it is in opposite directions in the two isolates. In the slow growing isolate 25, dominance tends to increase the growth rate at the lower temperature whereas in the fast-growing isolate 26, it tends to decrease the growth rate. Under high temperature conditions, this directional dominance not only disappears but also appears to be reversed. However, the degree of reversal was not sufficient to be detected at a significant level. It has, therefore, to be regarded as ambi-directional dominance.

4. DISCUSSION

Under natural conditions, the monokaryotic and the dikaryotic stages coexist in the same habitat at the same time in the life cycle of *S. commune*. The monokaryotic stage while capable of prolonged vegetative growth is a temporary one in the sense that it terminates as soon as the two compatible monokaryons meet. On the other hand, the dikaryon has to produce a certain minimum growth before the formation of fruiting bodies. A very

TABLE 7

Directional dominance as indicated by the correlation between $W'r + Vr$ and array mean of dikaryotic descendants

Isolate	Temperature	$r (W'r + Vr)$. Array mean					Average	99% confidence limits of average
		(a-f)	(g-l)	(m-r)	(s-z)	χ^2 for homogeneity		
25	20°C	-0.5214	-0.7268	-0.7320	-0.3961	0.75 < P > 0.09	-0.6126*	-0.069 to -0.875
	30°C	0.4936	0.1701	0.3072	0.2498	0.95 < P > 0.975	0.3107	-0.312 to 0.747
26	20°C	0.6639	0.5973	0.8418	-0.0004	0.50 < P > 0.75	0.5908*	0.035 to 0.867
	30°C	0.2635	-0.1027	-0.7551	-0.5330	0.25 < P > 0.50	-0.3391	0.283 to -0.760

fast-growing dikaryon is expected to cover a large area and is likely to produce more fruiting bodies provided the food resources are not limiting. In the event of limited resources due to competition with the other dikaryons and monokaryons in the population, a very fast-growing dikaryon may utilise the available nutrients for its growth leaving little for the formation of fruiting bodies. So natural selection is likely to favour mediocre genotypes at the expense of extremes. This type of natural selection has been referred to as stabilising selection (Mather, 1953).

The two isolates with extreme growth rate exhibited large differences in

TABLE 8

Relative distribution of dikaryons in relation to parental monokaryons

Isolate	Temperature	Number of dikaryons		
		Faster than both parents	Intermediate	Slower than both parents
25	20°C	7	32	33
26	20°C	43	21	8
25	30°C	43	21	8
26	30°C	54	16	2

growth rate under both temperature conditions. There was a considerable genetic variation for growth rate within each isolate which suggested that growth rate is not a neutral character but has adaptive significance. At the lower temperature which is nearer to that found in the natural environment, the two isolates also differed in the rate of growth of the dikaryons in relation to the parental monokaryons. The relative frequency of the faster-growing, intermediates and the slower-growing dikaryons (table 8) was not the same in the two isolates ($\chi^2 = 43.45$ for 2 d.f.). This distribution remained constant for isolate 26 at both the temperatures ($\chi^2 = 5.52$ for 2 d.f.) but it differed for isolate 25 ($\chi^2 = 28.61$ for 2 d.f.). The dikaryons of isolate 25

TABLE 9
Correlations between deviations from linear regression at 20°C and 30°C

Series	Isolates	
	25	26
(<i>a-f</i>)	-0.3040	-0.6514
(<i>g-l</i>)	-0.6784	-0.4525
(<i>m-r</i>)	-0.2662	-0.3165
(<i>s-z</i>)	-0.2252	-0.3626
Average	-0.3889	-0.4568

TABLE 10
Regression analysis of growth rate of dikaryons on mid-parental value of monokaryons

Temperature	Isolate	Series	Mean squares		
			Regression (1)	Remainder (34)	Error (70)
20°C	25	(<i>a-f</i>)(<i>g-l</i>)	602.4**	77.9***	4.3
		(<i>m-r</i>)(<i>s-z</i>)	97.9	81.1***	4.2
	26	(<i>a-f</i>)(<i>g-l</i>)	2149.3**	241.2***	11.0
		(<i>m-r</i>)(<i>s-z</i>)	193.3**	35.5***	13.4
30°C	25	(<i>a-f</i>)(<i>g-l</i>)	2523.6**	222.5***	63.3
		(<i>m-r</i>)(<i>s-z</i>)	47.4	1123.2***	42.5
	26	(<i>a-f</i>)(<i>g-l</i>)	3622.2	932.9***	40.4
		(<i>m-r</i>)(<i>s-z</i>)	972.5	490.9***	39.4

Degrees of freedom are given in parentheses.

were in general slower growers than the parental monokaryons. On the other hand, the dikaryons of isolate 26 were generally faster in growth, and did not differ significantly from the growth rate of their faster monokaryotic parent. However, with the abrupt change in the environment (high temperature), there was a tremendous increase in the growth rate of monokaryons as well as dikaryons of both the isolates. The dikaryons grew faster than their faster-growing parent for both isolates except for one duplicate set of isolate 25.

In the genotype-genotype interaction analysis the non-linear component was highly significant for both isolates in both temperature environments. More important, however, the direction of this component tended to be reversed between the two environments. Indeed, the correlations for this component between the two environments while non-significant were

Isolate 25, while being the slowest growing in the population sample of 77 isolates, is expected on this model to grow as fast or faster than 98 per cent (faster than 76 per cent) of all possible isolates heterozygous at the same number of randomly chosen loci while remaining homozygous for the decreasing allele at the other four loci. Similarly, isolate 26, while being one of the faster growing isolates in the population sample, is expected on this same model to grow as slow or slower than 98 per cent of all possible isolates heterozygous at the same number of randomly chosen loci while remaining homozygous for the increasing allele at the other four loci. Thus dikaryons that are more extreme in rate of growth than 25 and 26 must continually arise in the population, as a result of the compulsory outcrossing followed by segregation, at frequencies well in excess of isolates which like 25 and 26 must be heterozygous at a restricted set of loci. Indeed such segregants arise in the dikaryotic progenies derived from isolates 25 and 26. Their absence from the extreme segments of the population sample, therefore, must mean that they are selectively eliminated from the population because of their extreme phenotypes. Thus the directional dominance towards intermediate growth rates displayed by the extreme phenotypes which have survived to be represented in the sample is a predictable consequence of stabilising selection on a character displaying an overall ambi-directional dominance. The directional dominance displayed by these extreme phenotypes is in no way in conflict with the expectation that low or ambi-directional dominance is the result of a past history of stabilising selection and directional dominance of a past history of directional selection (Mather, 1953, 1960, 1973; Jinks, 1954; Breese and Mather, 1957; Jinks and Broadhurst, 1963; Lawrence, 1965; Barnes, 1966, 1968; Kearsley and Kojima, 1967; Kearsley and Barnes, 1970).

The mechanism of directional dominance operating in the two isolates seems to be temperature-dependent because ambi-directional dominance was observed in both the isolates at the higher unfamiliar temperature. In the population from which the isolates were obtained, the genetical system regulating rate of growth has been evolving at temperatures that are nearer to 20°C than 30°C and for most of the time below 20°C. Growth at 30°C, therefore, involved an abrupt change in the environment that might be expected to affect and even disrupt this regulatory system. However, although the increase in temperature had a tremendous effect on growth rate, there is no compelling evidence that the simple additive-dominance model of gene action was inadequate at this temperature. It could be argued that if directional dominance has a role in stabilising growth rate at some intermediate optimum, then at the higher temperature, uni-directional dominance favouring slow growth should appear in isolate 25 and the uni-directional dominance favouring slow growth already present in isolate 26 should become more intense. Such uni-directional dominance, however, will not manifest itself in the same generation in which the genetical system is exposed to higher temperatures unless the necessary dominance modifiers are already present and since the evolution of dominance is a long-term process, these modifiers will be present in the population only if it has been regularly exposed to high temperatures or to other environmental factors that evoke equivalent responses in the phenotype.

There is evidence that most of the genetic variation for growth rate of dikaryons is not correlated with the variation in monokaryons (Simchen and

Jinks, 1964). In this study as well, the regression analysis of growth rate of the dikaryotic descendants on their parental monokaryons revealed that the regression mean squares when tested against the remainder were significant only in some of the duplicate sets (table 10). However, a significant part of the variation in growth at 20°C can be accounted for by the variation in the monokaryotic parents but the remainder mean squares were always significant at both the temperatures in both the isolates indicating that a major part of the variation in the growth of dikaryons is not related to the variation in the monokaryons. It clearly brings out the fact that the nature of gene action is not the same in the two stages and presumably the selective forces acting on them are correspondingly different.

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