Genetics of Certain Morphological Characteristics in *Gibberella baccata*

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ABSTRACT

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Variation in colony morphology is common in the genus *Fusarium*. The most commonly encountered cultural mutants in *Gibberella baccata* (*Fusarium lateritium*) are pionnotal; they produce conidia in pionnotes rather than in sporodochia. Sporodochial and pionnotal isolates of *F. lateritium* were crossed in all possible combinations and the progeny were rated for colony morphology. Both random ascospores and unordered tetrads were studied. Production of pionnotes versus sporodochia was controlled by two linked genes. Only one arrangement of alleles resulted in sporodochial formation. Genes controlling growth rate, color, and degree of aerial mycelium development were on the same linkage group as those controlling pionnote formation. Epistasis was evident between genes controlling pionnote formation and aerial mycelium production; pionnotal isolates had reduced amounts of aerial mycelium. The unlinked genes for mating type and sexual expression were inherited independently from the genes controlling pionnote versus sporodochial production. Production of mycelial mutants was controlled by one gene.

The genus *Fusarium* consists of several species, ubiquitous in nature, which are of great importance to man as plant and animal pathogens and as producers of mycotoxins. Cultural variation in the Fungi Imperfecti is a widespread phenomenon that is especially prevalent in the genus *Fusarium*. This wide range of cultural variability has been a factor in the confusing taxonomy of this genus; over 1,000 species, varieties, and forms have been named, in many cases on the basis of superficial observations (24). Even today, not all workers agree on which criteria are the most constant and important in defining a species, as many of the characteristics used exhibit a range of variability.

Nectria haematococca (*F. solani*) has been the subject of the most extensive genetic work on colony morphology. Hansen and Snyder (12) showed that the "C" or "M" types are controlled by two

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alternative alleles at one locus. The "C" or conidial type produces colored sporodochia with large numbers of macroconidia, relatively scant mycelium and is hermaphroditic. The "M" or mycelial type, which is female-deficient, does not form sporodochia or many macroconidia, lacks pigmentation, has abundant aerial mycelium, and produces relatively numerous microconidia. Both the woolly and the slow-growing "button" mutants are the result of one gene mutation (21). Inheritance of perithecial and ascospore colors is also controlled by two alleles at a single locus (10). The inheritance of cultural characteristics for *Gibberella fujikuroi* has also been studied. Mating type, colony color (white or orange), growth rate, and mycelial type have all been shown to be controlled by single genes (19). Kuhlman (14) examined the inheritance of the presence of simple phialides or polyphialides, the manner in which microconidia are borne, and perithecial size.

Cultural mutants are important not only to the taxonomist, but also to the pathologist. There has long been concern about whether cultural mutants have reduced virulence. Some consider that a change in colony morphology indicates a concomitant reduction in virulence (7). Burgess et al (6) list, as their first guideline in choosing isolates for pathogenicity tests, the use of 'wild type' isolates since mutants are often less virulent or avirulent. Other reports indicate that the degree of virulence changes independently of morphological alterations; virulence of cultural mutants was found to decrease, or stay the same as the original strain (1,5,18). Some workers (16) report the recovery of mutants that exhibit increased virulence.

Gibberella baccata (Wallr.) Sacc. (imperfect state: *Fusarium lateritium* Nees) possesses a wide host range, and is distributed worldwide (3). This species is heterothallic and its sexual stage is easily induced in culture (15). The pionnotal mutant is most frequently encountered in *F. lateritium*, and in many other *Fusarium* species. Isolates, when first recovered from nature, most often produce abundant aerial mycelium and form conidia on branched monophialides in sporodochia. In the pionnotal mutant, aerial mycelium is greatly reduced or absent, and conidia are formed on monophialides in pionnotes.

This study was undertaken primarily to determine the genetics of the production of pionnotes versus sporodochia by means of both random ascospore and unordered tetrad analysis. The inheritance of other morphological traits was also examined.

TABLE 1. Descriptions of the morphological traits of *Gibberella baccata* used in this study of the genetics of their inheritance

Trait	Description
sp	Sporodochial
pi	Pionnotal
myc	Mycelial
red	Predominant colony color—red
or	Predominant colony color—orange
fast	Average growth rate of most isolates
slow	Growth rate about half that of average
mat+	Plus mating type
mat−	Minus mating type
amn	None to a trace of aerial mycelium
aml	Light aerial mycelium
amm	Moderate aerial mycelium
ama	Abundant aerial mycelium
her	Hermaphrodite
fem−	Female sterile (male only)

MATERIALS AND METHODS

Crossing of isolates and isolation of ascospores. Procedures for crosses were as outlined by Lawrence et al (15). Isolates used as the maternal parent in the crosses were initiated from single conidia (25) and grown on carrot puree agar (15) under a mixture of cool-white and black-light fluorescent lamps. Paternal parent isolates were also initiated from single conidia and grown on carnation leaf agar (15).

Random ascospores were obtained from 17 crosses of isolates exhibiting either the same or different colony morphologies according to the procedure of Lawrence et al (15). All progeny from a cross were placed on potato-dextrose agar (PDA) (25) slants which had been prepared at the same time and sealed with cigarette paper (22). Cultures were grown under cool-white fluorescent lamps on a 12-hr alternating light/dark period at a constant temperature of 23 C. After 2 wk, the progeny were rated for colony morphology phenotypes. The markers, analyzed genetically, are listed in Table 1.

The source and colony morphology phenotypes of the isolates used as parents in the crosses are summarized in Table 2. Isolate L90-OP is a spontaneous mutant obtained from a single conidium of isolate L90. It is the only mutant obtained from this isolate. Stability of the mutant was ascertained by placing a single conidium of L90-OP in each of 100 tubes of PDA, then checking for revertants after 2 weeks of growth.

Asci of *G. baccata* contain a maximum of eight unordered two- to four-celled ascospores. Since all asci did not contain eight ascospores at maturity, some asci with fewer than eight ascospores were used for analysis.

Unordered tetrads were isolated from the crosses L88 × L90-OP and L87 × L90-OP. Mature perithecia were removed from the tubes and placed in water-filled petri dishes 18–24 days after spermatization. Asci from perithecia of this age contained the maximum number of mature ascospores and the minimum number of germinated ascospores. All water used was sterilized by

TABLE 2. Source and cultural characteristics of isolates of *Gibberella baccata* used[a] in this study of the inheritance of morphological traits

Isolate	Description[b]	Source
L70	pi, red, fast, mat−, amn, her	Field isolate
L85	sp, red, fast, mat−, amm, her	Field isolate
L86	sp, red, fast, mat+, amm, fem−	Field isolate
L87	pi, red, fast, mat+, aml, her	Field isolate
L88	pi, red, fast, mat+, aml, her	Field isolate
L90	sp, red, fast, mat−, amm, her	Field isolate
L107	pi, red, fast, mat+, aml, her	Field isolate
L90-OP	pi, or, slow, mat−, amn, her	Spontaneous Mutant from single spore
LF103 (progeny of L88 × L90)	pi, red, fast, mat−, aml, her	Progeny
LF107 (progeny of L88 × L90)	pi, red, fast, mat−, aml, her	Progeny
LF120 (progeny of L88 × L90)	pi, or, fast, mat+, amn, her	Progeny
LF122 (progeny of L88 × L90)	sp, red, fast, mat+, aml, her	Progeny
LF399 (progeny of L90 × L87)	myc, or, fast, mat−, amm, fem−	Progeny
LF469 (progeny of L90 × L88)	myc, or, fast, mat+, amm, fem−	Progeny
LF473 (progeny of L90 × L88)	pi, red, slow, mat−, amn, her	Progeny
LF526 (progeny of L90 × L88)	pi, or, slow, mat−, amn, her	Progeny

[a] Source and genetic control of sex and mating type are discussed in Lawrence et al (15).

[b] See Table 1 for descriptions of abbreviated progeny phenotype traits.

autoclaving and all equipment was sterilized by autoclaving or treatment in 70% ethyl alcohol. The perithecia were cleaned of debris, conidia, and loose mycelium by means of two sharp dissecting needles.

Cleaned perithecia were placed in a depression slide half filled with distilled water on a dissecting microscope stage. Perithecia were crushed with fine needles, the rosettes of asci were separated, and the perithecial walls and debris were removed. Using fine glass or metal needles, asci with mature ascospores were singled out by gently teasing apart the rosettes of asci. Individual asci were transferred with a micropipette to 6% water agar in a petri dish and the position of each ascus on the plate was marked with a dissecting needle. Both micropipettes and microneedles were prepared from 1 mm (OD) capillary tubing in a microburner, as outlined in the Leitz micromanipulator instruction manual. Microburners consisted of syringe needles attached to a small Bunsen burner base by means of a short piece of rubber tubing; needles were pulled by hand.

After several asci were placed on the water agar in the petri dish, the petri dish was set aside to dry for 1 hr. It was then placed on the stage of a Leitz microscope for use in conjunction with the Leitz micromanipulator. Ascospores were removed by holding the base of the ascus down with one needle and pushing the spores out of the ascal sack with a second needle. Spores were then separated under the dissecting microscope (cut out as in the regular method for obtaining single conidia) and the ascospores were placed on PDA slants. Tubes were handled and rated in the same manner as described above for the random ascospores. Asci from each cross were given letter designations.

RESULTS

The phenotypes of the random ascospore progeny are presented in Tables 3 and 4. Tables 5 and 6 contain the results of the unordered tetrad analyses.

Genetics of predominant culture color. The predominant colors in cultures of *F. lateritium* grown on PDA were red and orange. Colors did not diffuse into the agar, but were present where the mycelium grew over the agar surface. Several variant types of orange coloration were noted—orange which remained orange, orange with red tints, and orange in which brown or red tints developed after 4 wk. The red colors observed were either deep red, red with some degree of secondary orange tints, or red with brown and orange tints.

There did not appear to be any lethal combinations of color and colony morphologies. Both red and orange pionnotal progeny were recovered from cross L90 × L87 (Table 4). Seven red sporodochial progeny and six orange sporodochial progeny were recovered from the cross L90 × LF469 (Table 4). Two orange mycelial types were also observed: LF399 from cross L90 × L87 and LF469 from cross L90 × L88 (Table 4).

In several crosses, L90 × LF120, LF473 × L88, L90 × LF469, L88 × L90-OP, L87 × L90-OP, and LF107 × L90-OP, progeny segregated for parental colors. In the remainder of the crosses, some progeny with different color combinations were recovered. These combinations often involved different shadings of the predominant color.

TABLE 3. Segregation of certain cultural characteristics among random ascospore progeny from crosses of *Gibberella baccata* in which the parents exhibit the same colony morphology

Parents		Progeny phenotypes[a]													No test cross
Female	Male	sp	pi	red	or	χ^{2b}	fast	slow	χ^{2b}	amn	aml	amm	ama	mat+	mat−	
Pionnotal × pionnotal																
L88	× LF107	0	75	75	0		75	0		0	46	29	0			
LF103	× L88	0	67	66	1		67	0		0	67	0	0			
LF526	× L88	0	82	48	32	2.061	48	34	2.061	34	48	0	0			
LF473	× L88	0	84	84	0		46	38	0.583	38	46	0	0			
L107	× L90-OP	10	17	16	11	0.593	16	11	0.593	21	6	0	0			
L88	× L90-OP	18	101	60	59	0.009	60	59	0.009	59	42	18	0			
L87	× L90-OP	10	56	35	31	0.136	35	31	0.136	31	25	10	0			
Sporodochial × sporodochial																
LF122	× L90	53	0	53	0		53	0		0	←53→		0			
L90	× L86	161	8	169	0		169	0		0	38	106	25	87	35	47

[a] See Table 1 for descriptions of abbreviated progeny phenotype traits and Table 2 for cultural characteristics of parental isolates.
[b] χ^2 for 1:1 ratio is 3.84 at $P = 0.05$ according to Yates' correction factor (20).

TABLE 4. Segregation of certain cultural characteristics among random ascospore progeny from crosses of *Gibberella baccata* in which the parents exhibit different colony morphologies

Parents		Progeny phenotypes[a]														No test cross
Female	Male	myc	sp	pi	χ^{2b}	red	or	χ^{2b}	fast	slow	amn	alm	amm	ama	mat+	mat−	
Pionnotal × sporodochial																	
L88	× L85		16	18	0.029	34	0		34	0	0	18	16	0			
L70	× L86		49	56	0.343	105	0		105	0	56	10	21	18			
L88	× L90		66	80	1.34	141	5		146	0	2	80	64	0	28	32	86
Sporodochial × pionnotal																	
L90	× L88	1	49	63	1.509	99	14		113	0	0	63	50	0			
L90	× L87	1	14	20	0.735	31	4		35	0	0	20	15	0			
L90	× LF120		35	35	0.004	35	35	0.004	70	0	35	0	35	0			
Sporodochial × mycelial																	
L90	× LF469	13	13		0.038	7	19	2.807	26	0	0	6	20	0			
Pionnotal × mycelial																	
L87	× LF399	26		24	0.02	24	26	0.02	50	0	0	24	←26→				

[a] See Table 1 for descriptions of abbreviated progeny phenotype traits and Table 2 for cultural characteristics of parental isolates.
[b] χ^2 for 1:1 ratio is 3.84 at $P = 0.05$ according to Yates' correction factor (20).

An examination of the inheritance of the predominant colors—red and orange—suggested their production may be controlled by two alternative alleles at the single locus. The ratio of red:orange in segregating progeny was 1:1. A chi-square test of the inheritance of red and orange progeny for the random ascospores of appropriate crosses was performed (see Tables 3 and 4). The null hypothesis examined was that the production of these colors was controlled by one gene with two alleles. In all cases, the level of significance was less than 0.05, indicating the null hypothesis could not be rejected. Only one ascus, L87 × L90-OP G (Table 6), contained 5:2 red:orange progeny.

Genetics of growth rate. Growth rate was uniform for most of the isolates and progeny. However, three isolates, L90-OP, LF473, and LF526, exhibited a growth rate approximately half that of the other isolates. L90-OP and LF526 were orange and LF473 was red. Fast- and slow-growing progeny appeared in a 1:1 ratio from random ascospores of crosses LF473 × L88, LF526 × L88, L88 × L90-OP, L107 × L90-OP, and L87 × L90-OP (Table 3). Again, a chi-square test was performed for the above crosses based on the null hypothesis that fast and slow growth rate was determined by two alleles at a single locus. At the 0.05 level of significance, the null hypothesis could not be rejected for any case.

Relationship between predominant color and growth rate. The last four crosses mentioned above involved a slow-growing orange parent and a fast-growing red parent. Orange progeny were also slow growing in all four crosses. Linkage between the genes for growth rate and color could be determined by a chi-square contingency table. The chi-square values ranged from 31.65 to 120 with $P < 0.005$. The genes for growth rate and the predominant color seem to be linked.

Genetics of the production of pionnotes and sporodochia. The genetics of the production of pionnotes or sporodochia were examined initially by random ascospore analysis of three pionnotal × sporodochial crosses and three sporodochial × pionnotal crosses (Table 4). The pionnotal:sporodochial progeny ratio for all six crosses fit a 1:1 ratio, indicating a single-gene segregation.

To further test whether a single Mendelian gene was involved, pionnotal × pionnotal and sporodochial × sporodochial crosses were made (Table 3). Of the two sporodochial × sporodochial crosses, 100% of the progeny of LF122 × L90 were sporodochial and 95.3% of L90 × L86 were sporodochial. However, the three pionnotal × pionnotal crosses that involved L90-OP all yielded some sporodochial progeny.

L90-OP was considered a stable mutant since all 100 of the cultures that were started from single conidia and grown on PDA slants looked exactly like the original L90-OP isolate. To ascertain whether the sporodochial progeny from the crosses involving L90-OP were stable and not the result of accidental mixtures of more than one ascospore, 50 single-conidial cultures of two of the sporodochial progeny from L88 × L90-OP and L87 × L90-OP were initiated on PDA. In each case, all 50 cultures on PDA slants were sporodochial and identical to the original progeny isolate. These results indicated that more than one gene was involved in the production of pionnotes and sporodochia. For this reason, unordered tetrad analysis was undertaken to obtain more precise data.

Monogenic segregation was not an adequate explanation of the production of pionnotes and sporodochia. Another possible explanation would involve two genes, each with two alleles. Most isolates mutate from sporodochial to pionnotal form. This indicates a change from the sporodochial gene and the following designations were assigned: *AB* for sporodochia produced, and *Ab*, *aB*, or *ab* for pionnotes produced. It was reasonable to assume that the original L90 was *AB* and mutated to L90-OP which was *aB* or *Ab*. Isolates L88, L87, and L107 were *Ab* or *aB*, but differed from L90-OP since recombinant types were formed in crosses.

To determine whether genes *A* and *B* were linked, the random ascospore data from L88 × L90-OP and L87 × L90-OP were examined. If two unlinked genes were involved, with only one combination of alleles producing sporodochia, progeny ratios should have been three pionnotals to one sporodochial with a maximum of two sporodochial progeny produced per ascus. Chi-square values were calculated for the progeny of the above two crosses. The hypothesis stated above was rejected at $P = 0.05$. This observation, combined with the fact that four asci from the two crosses contained more than two sporodochial progeny (Table 7) indicate that genes *A* and *B* are linked.

If two linked genes were involved, the data in Table 7 would be expected. The total number of asci with one or two sporodochial ascospores representing a two-strand single or three-strand double crossover should be greater than the number of asci that produced three sporodochial progeny (a four-strand double crossover).

Ascus B from cross L88 × L90-OP (Table 5) is probably a tetratype ascus. Of the four slow-growing, orange, pionnotal cultures, two were parental types like L90-OP and two were pionnotal recombinants (with genes *ab*). Of the four red cultures, two were parental types like L88 (fast-growing, red, and pionnotal) and two cultures are sporodochial recombinants (with genes *AB*).

Relationship between genes for the production of pionnotes and sporodochia and other morphology genes. The linkage relationship between genes controlling mating type and the production of pionnotes and sporodochia was determined from a contingency chi-square calculation of the cross L88 × L90 (Table 4). Of the 21 sporodochial progeny used in a test cross, eight were mat+ and 13 mat−; of the 39 pionnotal progeny used in a test cross, 20 were mat+ and 19 were mat−. A $\chi^2 = 1.17$ led to the acceptance of the hypothesis that the mating type gene and the genes that control production of pionnotes and sporodochia are not linked.

TABLE 5. Segregation of relative growth rate, predominant color, and pionnotes/sporodochia production from unordered tetrads of the cross of L88 × L90-OP of *Gibberella baccata*

	Ascospores (no.) giving rise to colonies that were:		
Ascus	Slow-growing, orange, pionnotal	Fast-growing, red, pionnotal	Fast-growing, red, sporodochial
A	2		2
B	4	2	2
C	3		3
E	3	1	1
F	1	3	
G	2	1	
H	2	1	1
I	2		3
J	2		3
K	3	3	
L	1		2
M	1	4	
N	2	1	2

TABLE 6. Segregation of relative growth rate, predominant color, and production of pionnotes and sporodochia from unordered tetrads of the cross L87 × L90-OP of *Gibberella baccata*

	Ascospores (no.) giving rise to colonies that were:		
Ascus	Slow-growing, orange, pionnotal	Fast-growing, red, pionnotal	Fast-growing, red, sporodochial
A	2	4	
B			2
C	1	3	
D	1	2	
E		4	
F	1		2
G	2	4	1
H	2	4	
I	2	1	2
J	2	2	
K	1	4	
L	3		2
M	3		3
N	2		2
O	1	2	1

Linkage has been established between genes controlling growth rate and the predominant color (red/orange)-controlling genes. An examination of the data from the unordered tetrads (Tables 5 and 6) reveals the relationship between these genes and genes *A* and *B*. Of the 34 sporodochial recombinants recovered, all were red and fast growing. The same was true of all the sporodochial recombinants recovered as random progeny from pionnotal × pionnotal crosses (Table 3). If the set of linked genes for growth rate and predominant color were inherited independently of genes *A* and *B*, equal numbers of slow-growing orange and fast-growing red sporodochial recombinants should have been present. Since this was not the case, it was concluded that genes *A* and *B* and the genes for growth rate and predominant color are linked.

Considering the above linkage group, it is now possible to determine which alleles of genes *a*/*A* and *b*/*B* should be assigned to isolates L90-OP, L88, and L87. Isolate L90-OP is slow growing, orange, and either *Ab* or *aB*. Isolates L88 and L87 are fast growing, red, and either *aB* or *Ab*. An examination of Fig. 1 reveals why case A is the proper one, i.e., why isolate L90-OP is *aB* and isolates L88 and L87 are *Ab*. If case B was correct, i.e., isolate L90-OP is *Ab*, and isolates L88 and L87 are *aB*, then slow-growing, orange sporodochial isolates would have resulted from crossovers between *A* and *B*, never from fast-growing, red, sporodochial isolates. Since only fast-growing, red, sporodochial isolates were formed, it must be concluded that case A is correct.

Genetics of aerial mycelium production. Inheritance of the amount of aerial mycelium produced appears to be controlled by several genes. The 53 BC_1s of isolate LF122 (sporodochial with light aerial mycelium) × isolate L90 (sporodochial with moderate aerial mycelium) (Table 3) showed continuous variation in amount of aerial mycelium formed that ranged from less than that of LF122 to more than that of L90. Transgressive segregation for aerial mycelium production was evident for the progeny of many of the crosses as seen by the results presented in Tables 3 and 4.

While sporodochial and mycelial isolates produced from very slight to abundant aerial mycelium, the situation was somewhat different for the pionnotal isolates. Some pionnotal isolates, L90-OP, LF473, and LF526, produced no aerial mycelium. Others developed slight to moderate aerial mycelium either as the colony grew or after a period of time. However, under no conditions did pionnotal isolates develop abundant aerial mycelium. At 2 wk all 75 BC_1s of L88 × LF107 had very slight aerial mycelium. After 6 wk, 29 of these had developed slight to moderate aerial mycelium.

After L90 mutated to L90-OP, aerial mycelium was no longer produced. In all cases, however, sporodochial recombinants produced aerial mycelium; most of them produced moderate to abundant mycelium. The pionnotal progeny of the tetrads developed either no, or very slight, aerial mycelium but never moderate or abundant aerial mycelium. In every case, sporodochial recombinants produced more aerial mycelium than their pionnotal parents.

Aerial mycelium production by pionnotal isolates appears to be depressed or delayed when compared to sporodochial isolates. This indicates that a related effect exists between the genes coding for production of pionnotes and sporodochia and those coding for production of aerial mycelium. If the isolate is sporodochial (with genes *Ab*) full production of aerial mycelium is possible. Aerial mycelium production is depressed or delayed if the isolate is pionnotal (with genes *aB*, *Ab*, or *ab*).

TABLE 7. Number of sporodochial (recombinant) progeny per ascus from unordered tetrads from crosses of pionnotal isolates of *Gibberella baccata*

Sporodochial F_1 found per ascus (no.)	Asci (no.) from cross	
	L88 × L90-OP	L87 × L90-OP
0	4	7
1	2	2
2	4	5
3	3	1
4	0	0

Tetrad data indicated linkage between genes *A* and *B* and those for aerial mycelium production. No slow-growing, orange pionnotals ever developed aerial mycelium and only in two asci, L87 × L90-OP ascus C and E (Table 6), did fast-growing red pionnotals in the same ascus develop different degrees of aerial mycelium. Sporodochials in the same ascus exhibited different degrees of aerial mycelium in only two asci—L88 × L90-OP A and C (Table 5). If the genes coding for development of aerial mycelium were not linked to genes *A* and *B*, more variation in the tetrad progeny would have been expected.

Genetics of the mycelial variant. The inheritance of the mycelial variant was examined in the crosses L90 × LF469 and L87 × LF399 (Table 4). Chi-square tests for the BC_1s of L90 × LF469 rated for sporodochial or mycelial morphology and for L89 × LF399 (pionnotal × mycelial) indicated that the difference in morphology was controlled by two alleles at a single locus. Since mycelial mutants produce neither pionnotes nor sporodochia, it is probable that neither genes *A* or *B* are present.

A contingency chi-square was used to test for independent inheritance of mycelial mutant production and predominant color (red/orange) for L87 (red pionnotal) × LF399 (orange, mycelial) (Table 4). All pionnotal progeny were red and all mycelial progeny

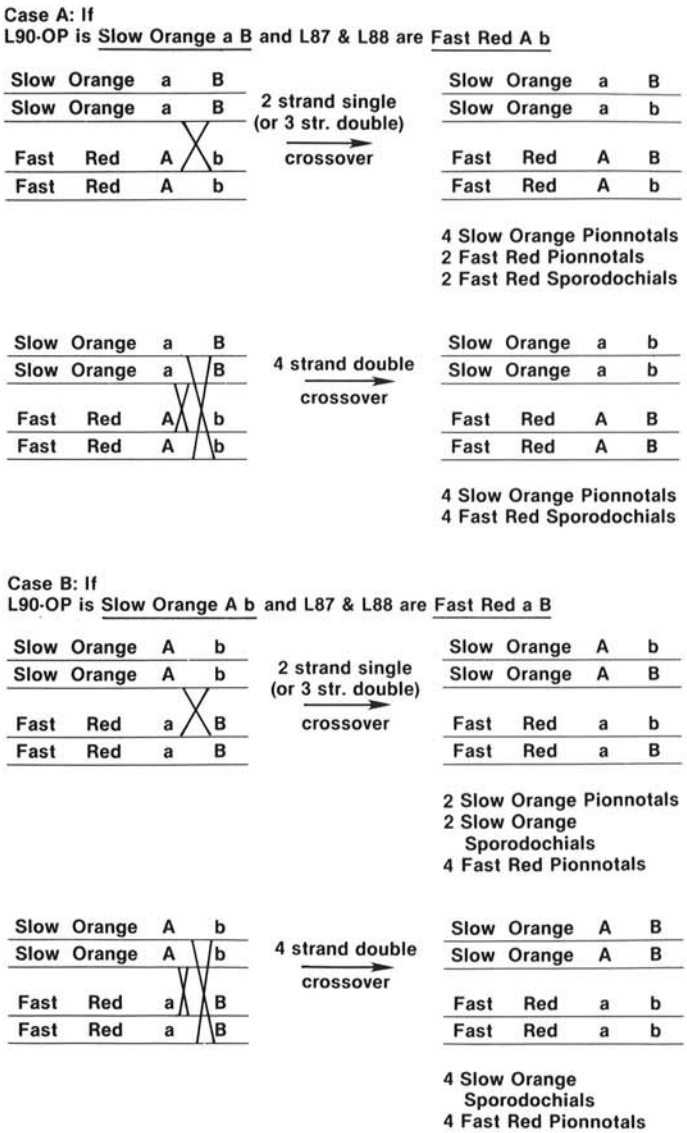

Fig. 1. Crossover diagram illustrating the two possible allele assignments (Case A, Case B) of genes *A* (*a*) and *B* (*b*) to isolates L87, L88, and L90-OP of *Gibberella baccata*, and the results of crossover events between these genes.

were orange. The probability of color and pionnote/mycelial production being independently inherited was less than 0.005. The gene coding for a mycelial mutant is most likely linked to the predominant color (red/orange) gene.

Genetics of microconidia production. Inheritance of production of microconidia was examined in the cross L90 (macroconidia only) × L88 (both macroconidia and microconidia). Chi-square values were calculated for the progeny of the above cross based on production of microconidia. While the ratio of progeny producing microconidia to those that did not produce microconidia did not fit a 1:1 ratio, it did fit a 3:1 ratio based on chi-square values. This observation indicates that two genes are involved in formation of these two types of conidia.

DISCUSSION

Linkage groups in *G. baccata*. Mating type is not linked to the gene(s) coding for expression of sex (15) or to the *A B* genes for the production of pionnotes and sporodochia. Growth rate is linked to the predominant color (red/orange) gene, and these genes are linked to the gene coding for mycelial mutants and to the *A B* genes for the production of pionnotes and sporodochia. The polygenes determining aerial mycelium production are also linked to the *A B* genes.

Linkage groups in *G. baccata* would therefore be as follows: I) mating type; II) growth rate, predominant color, mycelial mutant, A, B (production of pionnotes and sporodochia), aerial mycelium production genes. No attempt was made to ascertain the location of the gene(s) coding for expression of sex. Actual map distances could not be determined due to the lack of complete tetrads. This was due in part to the fact that not all asci contained eight ascospores and some ascospores were not viable. Some ascospores in such asci may have been too immature to germinate.

Secondary colors, orange, red, brown, and yellow, were noted but progeny analysis did not reveal any consistent pattern of inheritance. Snyder et al (21) determined that several genes were related to pigmentation in *Nectria haematococca* (*F. solani* f. sp. *cucurbitae*) but it was not possible to classify them due to the number of genes involved. The number and location of the secondary color genes in *F. lateritium* could not be specified.

Pigments in some *Fusarium* species are not an end in themselves, but rather are active metabolites of the organisms with definite functions (26). However, the function of the pigments in *F. lateritium* is not known at the present time. Pigmentation in the genus has been shown to depend on the carbon/nitrogen ratio. As a colony ages, if the medium has a high C/N ratio, it tends to become increasingly acidic causing some pigments to act as pH indicators (4). The secondary shadings in some of the cultures may have been the same pigment under different pH conditions. Whether a separate pigment gene was present in the isolates that changed color, or whether a pH change affected the orange pigment was not determined.

Ascus G from L87 × L90-OP had two slow-growing orange progeny and five fast-growing red progeny. This is the only ascus in which five of the ascospore isolates had the same combination of traits. The maximum number of fast-growing or red progeny expected in an ascus is four. The presence of more than four progeny with these traits may be due to gene conversion. The fact that both slow growth rate and red color were present in five progeny points to the possibility of a co-conversion event for both genes. This implies very close linkage between these genes (9).

The mycelial ("M") mutants of *N. haematococca* studied by Hansen and Snyder (12) and Tegtmeier and Van Etten (23) only acted as males in a cross. This was shown to be due to a mutation that blocks the normally constitutive female pathway (2). The gene controlling mating type was not linked to the two genes that coded for the ability to function as a male or female. The two genes coding for sexual function were linked (8,12,13). Both mycelial mutants studied here also functioned as males only. The responsible gene was linked to those coding for growth rate and predominant color as were genes *A* and *B*. The mycelial mutant gene appears to be separate from *A* and *B* since combinations of those two genes produced either pionnotes or sporodochia, neither of which were formed by the mycelial mutants. The mycelial mutant of *F. lateritium* may be functionally similar to that found in *F. solani*. If so, one would expect mycelial mutants to be female deficient.

Traits such as presence or absence of microconidia, pigmentation, amount of aerial mycelium, growth rate, and conidiophore morphology which are discussed and used by Fusarium taxonomists to separate *Fusarium* species (3,11,17) were found to vary within *F. lateritium*. If different species of *Fusarium* were accurately described by these traits, then isolates differing in colony morphology should not have been compatible in crosses. This was not the case. A fast-growing red isolate (L88) crossed with slow-growing orange isolates (LF526 and L90-OP). Isolate L88, which produced microconidia and sparse aerial mycelium, crossed with isolate L90 which did not have microconidia but produced abundant aerial mycelium. Isolate L85, which had macroconidia borne on monophialides, crossed with isolate L55, which had macroconidia borne on monophialides and microconidia borne on both monophialides and polyphialides (15). The potential variation possible in *F. lateritium* due to the number of genes controlling colony morphology and the number of alleles present is indeed impressive.

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