Genetics of Phytophthora

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In his 1931 monograph, Tucker (33) presented a comprehensive review of the evidence for heterothallism and hybridization in the genus Phytophthora. His conclusion was, “The tendency of mixed cultures of various species to produce oospores does not seem to warrant attaching much importance to this character as a taxonomic criterion pending further investigations on the actual occurrence of heterothallism or hybridism”. Tucker noted Narasimhan’s (22) work, however, which employed the microscopic tracing of gametangial hyphae to show that one thallus formed antheridia, and another the oogonia in paired cultures of P. arecae, and stated that if further studies confirmed Narasimhan, then heterothallism and hybridism exists in the genus. A few months after Tucker’s monograph appeared, Leonian (20) reported heterothallism in species of Phytophthora. Thus, Tucker was aware of the possibility of heterothallism in Phytophthora, but left his mind open for the future to determine whether or not it existed.

This paper reviews some of the studies which have confirmed that homothallism, heterothallism, and interspecific hybridization occur, and have provided a beginning toward understanding the genetics of species of Phytophthora. Since the background literature has been reviewed recently by Erwin et al. (7), Savage et al. (30), and Gallegly (11), only that which bears on the current status will be presented here.

Sexual patterns.—Prior to the recent studies of Savage et al. (30), much confusion and controversy still existed in regard to the nature of sexuality in species of Phytophthora. Several investigators, including Tucker (33), noted that some isolates of most species formed at least a few oospores in single culture, whereas other workers indicated that some isolates produced oospores only when paired with certain other isolates (1, 2, 8, 20). The former would indicate homothallism, and the latter heterothallism. Although Waterhouse (34) recognized that dual cultures were sometimes necessary to obtain oospores of some species, heterothallism was not a major consideration in her key to the species of Phytophthora.

The discovery of mating types in P. infestans by Smoot et al. (32) initiated studies leading to the cur-
rent understanding of sexual patterns in the genus. Galindo & Gallegy (9) showed that the mating types in P. infestans were compatibility types, with each isolate being bissexual but self-incompatible under usual cultural conditions. The compatibility factor present in isolates from the USA was designated A\(^1\), and the opposite factor in three isolates from Mexico was designated A\(^2\). They assumed that A\(^1\) and A\(^2\) were allelomorphs. Oosporas were formed in abundance at the juncture of colonies of A\(^1\) × A\(^2\) pairings on natural media such as lima bean agar. In addition to observations of gametangial fusions between A\(^1\) and A\(^2\) types, Galindo & Gallegy (9) also observed that relative strength of maleness or femaleness varied with each isolate and was not associated with compatibility type. Some isolates acted as strong males, some as strong females, and some were intermediate in sexual strength. In pairings of a strong male A\(^1\) × a strong female A\(^2\), the former always acted as a male and the latter as a female; in pairings of a strong male A\(^1\) × a strong male A\(^2\), or a strong female A\(^1\) × a strong female A\(^2\), each isolate formed antheridia and oogonia in equal numbers.

The above discoveries led Savage et al. (30) to a study of the sexual phenomena in 30 species and varieties of the genus. Species which formed oospores in abundance, and showed no evidence of mating with A\(^1\) and A\(^2\) types of other species, were considered to be homothallic. Although there is still some question of the true sexual pattern of a few species (e.g., P. fragariae), they presented the following groupings for 29 species:

Homothallic with predominantly paragamous antheridia: P. cactorum, P. citricola, P. lateralis, P. megasperma, P. porri, P. sojae, P. syringae.


Homothallic with compatibility types A\(^1\) and A\(^2\) and amphigynous antheridia: P. arecae, P. cambivora, P. capsici, P. cinnamomi, P. citrophthora, P. colocasiae, P. cryptogea, P. drenchleri, P. infestans, P. meadii, P. mexicana, P. palivora, P. parasitica, P. parasitica var. nicotianae.

Perhaps the most interesting discovery was that the compatibility types A\(^1\) and A\(^2\) previously described in P. infestans were present in 13 species and one variety of the genus. There was no evidence of additional compatibility factors among the isolates studied.

Equally interesting was the simultaneous discovery of relatively free interspecific mating between the heterothallic species, but only when an A\(^1\) isolate was paired with an A\(^2\) isolate on a natural medium such as lima bean or hemp seed agar, or a chemically defined medium containing a 3-β-hydroxy sterol such as β-sitosterol. Proof of true interspecific hybridization awaits the establishment of single zoospore cultures from single oospores obtained from interspecific pairings. The fusion of gametangia of P. capsici and P. infestans, however, observed by Savage et al. (30), with the formation of mature oospores, is strong indication that interspecific hybridization occurs, at least between some species.

Gough (15) and Smoot et al. (32) showed that oospores and oosporelike bodies sometimes occurred in low numbers in single cultures of P. infestans, particularly when the nutrients were low. Savage et al. (30) also observed this tendency with a number of isolates of other heterothallic species. Such isolates always acted as A\(^2\) or A\(^2\) compatibility types in paired cultures. Thus, it appears that all species of Phytophthora are either homothallic or potentially homothallic but functionally heterothallic. The tendency of the heterothallic species to sometimes form a few selfed oospores was the reason for Tucker's hesitancy of immediate acceptance of heterothallism in the genus.

In considering the implications of interspecific hybridization, it must be remembered that these fungi do not exist for long periods as saprophytes in the soil. Thus, there probably would be little chance for mating to occur, other than in the infected host tissue. Host-specific pathogenicity among species would further limit interspecific hybridization, as would the type of tissue normally invaded (e.g., foliage vs. roots); however, the root and other tissues of some hosts are susceptible to several species. For instance, buckeye rot of tomato may be caused by P. parasitica, P. capsici, and P. drechsleri; isolations from citrus roots have yielded P. citrophthora and P. parasitica. Similarly, P. palivora and P. meadii or P. acerai frequently occur on the same host. Simultaneous infections of the same host by two or more species of opposite compatibility types could provide a means for variation through interspecific sexual recombination. Perhaps taxonomic difficulties encountered among certain species could be attributed to such hybridization.

Sexual mechanisms.—Both paragynous and amphigynous occur among species of Phytophthora. When paragynous occurs, the fertilization tube from the antheridium enters the oogonium directly through the oogonial wall. In species with amphigynous antheridia, the oogonial hypha first penetrates the antheridium and then passes through to form the oogonium. A fertilization tube penetrates the part of the oogonial stalk within the antheridium, or, as suggested by Galindo & Zentnay (10), the antheridal contents are discharged into the oogonium through a pore in the oogonial stalk. Gallegy (11) has described the fertilization process for Phytophthora infestans. Following fertilization, the protoplasm in the oogonium rounds into an oospore which becomes thick-walled.

Light stimulates oospore germination (3) which may occur in situ in agar cultures at 20°C. Upon germination, there is first a swelling of the oospore (rehydration) and the emergence of a germ tube from the oospore wall. Usually the germ tube is terminated by a single germ sporangium, but branching of the germ tube and continued hyphal growth sometimes occur. The wrinkled remains of the oospore wall usually can be seen within the oogonium. The terminal sporangium (germ sporangium) usually liberates zoospores when held in water at low temp (12°C for P. infestans). In P. infestans, 16 zoospores are usually produced, but as many as 38 have been liberated by a single germ sporangium (18).
The current controversial question concerning the sexual mechanism is where meiosis occurs. It has generally been assumed that meiosis occurs in the oospore following fertilization, and that the single nucletate zoospores in the germ sporangium are haploid. The cytological studies of Sansome (28) and Galindo & Zentmyer (10) suggest that meiosis occurs in the gametangia prior to fertilization, and that upon germination the zoospores in the germ sporangium are diploid.

Cytology.—Sansome (25, 26, 27, 28) has provided information concerning the cytology of the sexual stages of certain members of the Oomycetes, including species of Pythium and Phytophthora. She has reviewed (26, 27) some of the earlier studies on the cytology of these species. Galindo & Zentmyer (10) presented information on the cytology of the sexual stages of Phytophthora drechsleri, and Marks (21) has studied the cytology of the asexual stages of Phytophthora infestans.

Sansome (26) observed an association of four chromosomes in dividing nuclei in the antheridium and oogonium of Pythium debaryanum. This observation, coupled with simultaneous division of the nuclei in one oogonium, the occurrence of a distinct metaphase stage in dividing oogonial nuclei, and the absence of metaphases in the vegetative hyphae and sporangia, indicated that meiosis occurs in the gametangia prior to fertilization, and that the vegetative stages were diploid.

Sansome (27) reached similar conclusions in studies with Phytophthora cactorum and P. erythroseptica. Two nuclear divisions occurred in the gametangia with the first division having a long prophase. The nuclei were about half the size of vegetative nuclei following the second division. A bridge and fragment were observed at anaphase in P. cactorum, and multivalents were observed in nuclei considered to be polyplid following treatment of gametangia of P. cactorum and P. erythroseptica, with camphor. These observations were considered as critical evidence that the divisions in the gametangia were meiotic. Sansome (27) has suggested that Phytophthora species (n = about 9) and Pythium species (n = about 18) belong to a polyplid series.

The observations by Marks (21) in cytological studies of the asexual stages of Phytophthora infestans, a heterothallic species, do not support Sansome's conclusions for homothallic species. Marks noted that mitotic stages in the hyphal tips of P. infestans resembled those in the oogonia and antheridia of Pythium debaryanum considered by Sansome as meiotic stages. Gallely speculated (11) that perhaps the heterothallic species are haploid and the homothallic ones diploid. However, the cytological observations by Galindo & Zentmyer (10) with Phytophthora drechsleri, a heterothallic species, were similar to those of Sansome. Additional cytological studies are needed to resolve the question of ploidy in species of Phytophthora.

Inheritance of pathogenicity and other characters.—The first evidence that genetic recombination occurs via the sexual stage was presented by Gough (15) and Smoot et al. (32) with P. infestans, but only two single oospore cultures were established. Savage & Gallegy (31) established two additional oospore cultures which also were recombinants. More recently, Galindo & Zentmyer (10) with Phytophthora drechsleri, Satour & Butler (29) with P. capsici, Romero (23) with P. infestans, and Laviola (18) with P. infestans, have studied progenies with larger numbers of individuals.

Phytophthora drechsleri.—Among 173 single-oospore colonies established by Galindo & Zentmyer (10) from oospores which germinated by producing germ mycelia, and single-zoosporium cultures established from the germ sporangia of six oospores, recombination was observed for compatibility type and several other genetic markers. Only one phenotype was obtained from each oospore, however, even in the six cases where colonies were established from different zoospores from the same germ sporangium. Phenotypic ratios among 100 single-oospore cultures derived from one cross were: A1 to A2 compatibility type, 1:1; repulsion to stimulation, 2:1; and white to gray colonies, 2:1. Ratios among 17 single-oospore cultures from one backcross were: A1 to A2 type, 1:1; arbucular to thread branching of mycelia, 1:1; and brown-pigmented to colorless colony, 1:1.

Phytophthora capsici.—Satour & Butler (29) observed recombination for several genetic markers in the F1 of A1 x A2 crosses of P. capsici. In one cross, the parent A1 isolate produced star-pattern colonies, its sporangia liberated zoospores, and it was pathogenic to tomato and pepper. The parent A2 isolate was nonster in colony appearance, its sporangia also liberated zoospores, and it was pathogenic to tomato and pepper. Thus, the parent isolates differed only in compatibility type and colony appearance. However, some of the isolates in the F1 were nonpathogenic to tomato and pepper, and the sporangia of some failed to liberate zoospores. Similarly, star patterns different from the pattern in the parent appeared in the F1. Segregation ratios among 51 single-oospore cultures from one cross were as follows: star to nonstar colonies, 2:1; zoospore to nonzoospore formation, 2:1; A1 to A2 compatibility type, 2:1; pathogenic to nonpathogenic to tomato, 2:1; and pathogenic to nonpathogenic to pepper, 1:2. Only one phenotype was detected in each oospore culture; cultures from single zoospores liberated by germ sporangia were not established, but single-zoospore and hyphal-tip cultures obtained from previously established single-oospore cultures were phenotypically the same.

Phytophthora infestans.—In potato, nine R-genes (R1, R2, R3, etc.) have been identified (11), and each is inherited in a monogenic dominant manner to confer resistance expressed as a hypersensitive reaction following inoculation with an apathogenic race of P. infestans. In the fungus, pathogenic races have been identified and labeled according to the R-gene hosts which they will attack. For example, race 0 is pathogenic only on plants without R-genes (recessive), race 1 is pathogenic only on recessive and R1 plants, race 2 is pathogenic only on the recessive and R2 plants, race 3 is pathogenic on recessive, R1, R2, and R1R2.
plants, and races 1,2,3,4, are pathogenic on the 16 host
genotypes possible with genes \( R_1, R_2, R_3, \) and \( R_4. \)

Romero & Erwin (24) found recombinations of
pathogenic race characters and compatibility types
among the progenies from three crosses of different
races of \( P. \) *infestans*. Among the \( F_1 \) of cross \( 473 \times 445
(1,2,3,4 A^1 \times 0 A^2) \), segregation ratios for the presence
to absence of the four race characters were 10:10 for
race 1, 3:17 for race 2, 9:11 for race 3, and 10:10 for
the race 4 character. The segregation ratio for \( A^1 \) to
\( A^2 \) compatibility types was 16:4. Cultures from single
zoospores liberated by germ sporangia were not analyzed
by Romero & Erwin (24) to determine whether segre-
gation occurred during oospore germination. However,
analysis of single-ozoospore cultures from previously
established single-oospore cultures showed that each
germinating oospore gave rise to only one phenotype.
Romero (23) also noted that four cultures established
from bodies considered to be parthenogenetic oospores,
which occasionally appeared in single culture of their
isolate 445, were of the same phenotype as the parent
445.

Laviola (18) studied the pathogenic race and com-
patibility type characteristics of individuals in the \( F_1
\) from four crosses of \( P. \) *infestans*. Twenty-nine cultures
were established from single oospores producing germ
tubes directly from germ sporangia, and 194 cultures
were established from single zoospores liberated by the
germ sporangia of 59 oospores.

The ten single-oospore cultures established from
cross 63B \( \times 60A \) (race 3, compatibility type \( A^1 \times 1,2
A^2 \) were nonpathogenic on all the differential hosts
including recessive plants. Similarly, all but one of the
cultures from single zoospores picked directly from
among those liberated by the germ sporangia of three
dozen oospores were nonpathogenic; a single-ozoospore culture
from one oospore was pathogenic race 4. All cultures
obtained from this cross were of compatibility type
\( A^1. \) Both parent isolates were weakly pathogenic when
the crosses were made. The predominance of non-
pathogenicity among the offspring was attributed to a
predominance of nonpathogenic nuclei in the hetero-
caryotic mycelium. The appearance of race 4 in one
isolate was not unexpected, since Gallegly & Eichen-
muller (12) observed that this character frequently
appeared spontaneously.

Cultures established from cross 63B \( \times 445 \) (3 \( A^1 \times 0
A^2 \) included eight from single oospores, and 30 from
single zoospores from the germ sporangia of 24 oospores.
One single-oospore and six single-ozoospore cultures
were nonpathogenic. Except in one instance not yet
fully studied, the cultures were either race 3 or race 0;
the race 4 character appeared in a few isolates. Re-
combination for compatibility type and pathogenic race
was evident among the progeny. Segregation for com-
patibility type was in a ratio slightly less than 3:1.

From cross 473 \( \times 60A \) (1,2,3,4 A^1 \times 1,2 A^2), three
single-oospore and 14 single-ozoospore cultures were
established; the latter were from the germ sporangia
of five oospores. All these cultures were of compat-
itability type \( A^1 \), and all but one carried the pathogenic
race characters 1 and 2 which were present in both
parents. Segregation for the race 3 and 4 characters
occurred, with recombination for compatibility type
and pathogenic race being evident among the offspri-
g; e.g., race 1,2 and type \( A^1. \)

The cultures established from cross 473 \( \times 445
(1,2,3,4 A^1 \times 0 A^2) \) included 140 from single zoospores
liberated by the germ sporangia of 26 oospores, and 7
from oospores producing only germ tubes. Segregation
for the pathogenic race characters and compatibility
type occurred, with all but three of the possible 16
races appearing among the \( F_1 \}; races 2, 2,4, and 1,2,4
were not detected. The ratio for \( A^1: A^2 \) compatibility
type was approximately 3:1. Among the phenotypes
in the progeny, segregation ratios for the presence to
absence of race characters 1, 3, and 4 were about 1:1;
for the race 2 character the ratio was 6:31.

In six instances, Laviola (18) found more than one
phenotype among the cultures established from zoo-
spores liberated by the germ sporangium produced by a
single oospore. From crosses 473 \( \times 60A \) (race 1,2,3,4 \( \times
race 1,2 A^2) \) two single-ozoospore cultures were estab-
lished from the germ sporangium of oospore No. 35.
One was pathogenic race 1,2,4 and the other race
1,2,5,4; both were of compatibility type \( A^1. \) Thus, re-
combination for pathogenic race was evident among
the individuals of a single oospore. Five oospores from
cross 473 \( \times 445 \) (1,2,3,4 \( A^1 \times 0 A^2) \) yielded more than
one phenotype per oospore among the individual cul-
tures established from the zoosporangia of oospore
No. 35. Oospore No. 40 yielded race 1,3, type \( A^2 \) and
race 1,4, type \( A^1; \) No. 44 yielded race 1,3,4, type \( A^1
\) and 1,2,3,4, type \( A^1; \) and No. 53 yielded races 1,1,2,
and 3,4, all of type \( A^1. \) Among 11 single-ozoospore cul-
tures obtained from the germ sporangium of oospore
No. 58, nine were race 1,3,4 and type \( A^2 \), and two
were race 1,3,4 and type \( A^1. \) The germ sporangia of
oospore No. 56 and 57 liberated zoosporangia simulta-
nearly in the same water droplet. Among the cultures
established from 12 zoospores, the phenotypes ob-
tained were race 3,4, type \( A^2 \), race 3,4, type \( A^1 \), race 4
type \( A^1 \), and race 2,3,4 which produced oospores so
abundantly in single culture that compatibility type
could not be determined.

Abundant oospores were produced in single culture
by two single-ozoospore isolates and 28 single-ozoospore
isolates established by Laviola (18). Only three iso-
lates lost this selfing ability upon serial transfer. Further
studies are necessary to determine whether any of
these are true homothallic isolates, whether they con-
sist of intermingled hyphae of \( A^1 \) and \( A^2 \) types, or
whether the \( A^1 \) and \( A^2 \) characters are present in the
same hypha in a heterocaryotic condition.

**Asexual variation.**—Asexual variation in the fungi
is generally attributed to mutation, heterocaryosis,
parasexuality, physiological adaption, and cytoplasmic
control. The extent of variation in the genus *Phytoph-
thora* has been reviewed thoroughly by Erwin et al.
(7), and will not be repeated here. An excellent discus-
sion of the above mechanisms of asexual variation as
they relate to cultural variations among single-ozoospore
isolates of *Phytophthora infestans* has been presented
by Caten & Jinks (6). Asexual variation in regard to
pathogenicity of *P. infestans* has been reviewed recently by Gallegly (11).

It has been assumed that new pathogenic-race characters of *P. infestans* arise through mutation (11, 14). One argument in favor of this assumption is that the new *R*-gene-specific races are stable and do not revert to race 0 when cultured on a recessive host. Another is that such races first appear in nature only under severe epiphytotic conditions when the inoculum level is high. However, in the laboratory, new pathogenic races appear regularly after serial passage of an apathogenic race through senescent or juvenile leaf tissue of resistant potato hosts (16). In contrast, efforts to induce pathogenic race mutants artificially through the use of conventional mutagenic agents have met with little success (35). The relative ease in securing new races through host passage raises questions regarding the mechanism of variation involved. Whether the host passage technique simply provides a method of working with large populations of the pathogen on resistant tissue where a specific mutant will grow when it appears, or whether some other mechanism is involved, is an unanswered question.

Heterocaryosis is a possible mechanism for asexual variation in species of *Phytophthora*. However, anastomosis seems to be rare among them, even though Wilde (35) illustrated anastomosis in *P. infestans*. It is possible for heterokaryons to originate from zoospore fusions (17), but the most logical method would be from mutations in certain nuclei which would be perpetuated along with the original nuclei. Gallegly & Eichemuller (12) explained the frequent appearance of the race 4 character in almost any isolate of *P. infestans* on this basis.

It is questionable whether or not paragameus occurs in species of *Phytophthora*. Leach & Rich (19) suggested paragameus as an explanation for the recombinations of pathogenic race characters observed in their study of *P. infestans*. However, Sansome (28) suggested that the asexual stages may be diploid. If so, then mitotic crossing over and nondisjunction might be involved in variation in these organisms. Sansome (27) suggested that the continuous variation observed by Buddenhagen (4) in single-zoospore cultures of *Phytophthora cactorum* could be explained by the diploid hypothesis.

Caten & Jinks (6) concluded that the continuous variation in cultural characteristics among single-zoospore cultures of *P. infestans* could be explained best on the basis of cytoplasmic control. Variation in rate of growth and sporangium production continued to occur after several successive single-zoospore propagations. Leach & Rich (19) indicated that cytoplasmic effects may have been responsible for the appearance of a new pathogenic race character in certain mixed cultures of *P. infestans*. Perhaps the results of Buddenhagen (4) also can be explained on the basis of cytoplasmic control. Examination of the inheritance data presented above suggests the possibility that control of compatibility type may be cytoplasmic. Gallegly & Gallegly (9) pointed out that isolates of *P. infestans* varied in relative sexual strength. Some isolates were strong males, others strong females, and others intermediate in relative sexual strength. If a strong female A1 were paired with a strong male A2, the A3 isolate would always produce the oogonium. Lavilla (18) found that all individuals in the F1 from crosses involving isolate 60A as the A2 parent were of the A1 compatibility type. When isolate 445 was used as the A2 parent, the ratio of segregation in the F1 for A1:A2 was about 3:1. Perhaps isolates 60A and 445 are relatively strong males. If so, all or the majority of the oogonia would have been produced by the A1 parent. If compatibility type is under cytoplasmic control, presumably the cytoplasm of the oogonium, rather than that contributed by the antheridium during fertilization, would determine the type of cultures established from single oospores. Ratios of segregation for compatibility type would then be determined by the relative sexual strength of the parent isolates.

**Discussion of inheritance studies.—** Galindo & Gallegly (9) assumed that *P. infestans* was haploid in its vegetative stages and therefore considered the compatibility types A1 and A2 to be allelic. The occurrence of the two types in Mexico (13) in a ratio of 1:1 was cited as supportive evidence, since the expected ratio of segregation in haploid organisms of monogenically controlled characters is 1:1. However, the data of Romero (23) and Lavilla (18) with *P. infestans* showed a predominance of A1 types in the progeny of A1 × A2 crosses. Galindo & Zentmyer (10) obtained the expected 1:1 ratio in progeny from crosses of *P. capsici*. It is possible that compatibility type may be cytoplasmically controlled with individuals among the progeny having the same type as that of the parent which produced the oogonium. If compatibility type is under intranuclear control, another explanation for the predominance of the A1 type must be found.

If species of *Phytophthora* prove to be diploid in their vegetative stages, as suggested by the cytological studies of Sansome (27) and Galindo & Zentmyer (10), a different interpretation of genetic control of compatibility type would be needed. If intranuclear and monogenically controlled, perhaps dominance and recessiveness might be involved. One type could be Aa and the other Aa; Aa × Aa should yield segregation ratios of 1:1 in the F1.

Whereas the cytological studies indicate that species of *Phytophthora* may be diploid, the results from the inheritance studies are more indicative of haploidy in these species. If they were diploid, it seems only logical that one of the parents would be homozygous for at least one of the genetic markers studied. However, the segregation data showed recombination in the F1 for every character. The data of Lavilla (18) particularly support the premise that these heterothallic species are haploid in their asexual stages.

In addition to observing recombination in the F1 and segregation ratios of 1:1 for the presence to absence of pathogenic race characters, Lavilla (18) obtained more than one phenotype from one oospore in six cases. His data strongly suggest that meiosis occurs in the oospore following fertilization, and not in the gametangia before fertilization as suggested by Sansome (27). Lavilla's
data further indicate that segregation may occur in both the first and second division. However, Laviola
(18) found that a single germinated oospore most commonly gave rise to only one phenotype, as found in
every instance by previous workers who studied recombination in progeny from \(A^1 \times A^2\) crosses of species of
Phytophthora. The finding of only one phenotype per oospore has been used as evidence to support the diploid hypothesis. Although Galindo & Zentmyer's (10) cytopathological observations supported the diploid hypothesis, their genetic data did not. They proposed that all but one of the meiotic nuclei possibly degenerated during oospore germination so that only one gametocyte was present among the zoospores of the germ sporangium of an oospore. Laviola's (18) results certainly support this hypothesis as the usual behavior, but point out that in about one of ten cases more than one gametocyte can be detected among the individual cultures established from zoospores released by a germ sporangium. Thus, if degeneration occurs, it is apparent that occasionally not all of the products of meiosis degenerate, and that more than one meiotic nucleus may appear in the germ sporangium. If meiosis occurred prior to fertilization and the resulting diploid nuclei divided mitotically, an explanation of more than one gametocyte being present in a germ sporangium would involve more than one fertilized nucleus per oospore.

Backcrosses and sibcrosses would be helpful in determining the mode of inheritance of pathogenic race and the other characters studied, and in determining whether or not Phytophthora species are diploid. However, in an attempt to study the progeny from sibcrosses of the \(F_1\) of P. infestans, Castro & Zentmyer (5) found that only a few oospores formed in some crosses, and in others a high rate of mortality occurred among the germinated oospores; from 602 germinated oospores only four survived, two of which failed to produce sporangia and the sporangia of the other two failed to liberate zoospores.

Additional discussions of the inheritance studies of species of Phytophthora, and other aspects of the genetics of pathogenicity of P. infestans have been presented by Gallegly (11).

**Literature Cited**

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