# 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 & Gallegly (9) showed that the mating types in *P. infestans* were compatibility types, with each isolate being bisexual 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 allelomorphic. Oospores were formed in abundance at the juncture of colonies of $A^1 \times A^2$ pairings on natural media such as lima bean agar. In addition to observations of gametangial fusions between $A^1$ and $A^2$ types, Galindo & Gallegly (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 $A^1 \times$ a strong female $A^2$, the former always acted as a male and the latter as a female; in pairings of a strong male $A^1 \times$ a strong male $A^2$, or a strong female $A^1 \times$ 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 paragynous antheridia: *P. cactorum, P. citricola, P. lateralis, P. megasperma, P. porri, P. sojae, P. syringae.*

Homothallic with amphigynous antheridia: *P. boehmeriae, P. erythroseptica, P. fragariae, P. heveae, P. hibernalis, P. ilicis, P. phaseoli, P. richardiae.*

Heterothallic 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. drechsleri, P. infestans, P. meadii, P. mexicana, P. palmivora, 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 matings. 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 $A^1$ 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. palmivora* and *P. meadii* or *P. arecae* 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 paragyny and amphigyny occur among species of *Phytophthora.* When paragyny 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 & Zentmyer (10), the antheridial contents are discharged into the oogonium through a pore in the oogonial stalk. Gallegly (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 nucleate 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 polyploid 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 polyploid 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. Gallegly 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 & Gallegly (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-zoospore 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 over 100 single-oospore cultures derived from one cross were: $A^1$ to $A^2$ 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: $A^1$ to $A^2$ type, 1:1; arbuscular 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 $F_1$ of $A^1 \times A^2$ crosses of *P. capsici.* In one cross, the parent $A^1$ isolate produced star-pattern colonies, its sporangia liberated zoospores, and it was pathogenic to tomato and pepper. The parent $A^2$ isolate was nonstar 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 $F_1$ 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 $F_1$. 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; $A^1$ to $A^2$ 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 ($R_1$, $R_2$, $R_3$, 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 $R_1$ plants, race 2 is pathogenic only on the recessive and $R_2$ plants, race 1,3 is pathogenic on recessive, $R_1$, $R_3$, and $R_1R_3$

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 × 445 (1,2,3,4 $A^1$ × 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 segregation occurred during oospore germination. However, analysis of single-zoospore 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 parthenogenic 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 compatibility 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 × 60A (race 3, compatibility type $A^1$ × 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 oospores were nonpathogenic; a single-zoospore 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 nonpathogenicity among the offspring was attributed to a predominance of nonpathogenic nuclei in the heterocaryotic mycelium. The appearance of race 4 in one isolate was not unexpected, since Gallegly & Eichenmuller (12) observed that this character frequently appeared spontaneously.

Cultures established from cross 63B × 445 (3 $A^1$ × 0 $A^2$) included eight from single oospores, and 36 from single zoospores from the germ sporangia of 24 oospores. One single-oospore and six single-zoospore 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. Recombination for compatibility type and pathogenic race was evident among the progeny. Segregation for compatibility type was in a ratio slightly less than 3:1.

From cross 473 × 60A (1,2,3,4 $A^1$ × 1,2 $A^2$), three single-oospore and 14 single-zoospore cultures were established; the latter were from the germ sporangia of five oospores. All these cultures were of compatibility 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 offspring; e.g., race 1,2 and type $A^1$.

The cultures established from cross 473 × 445 (1,2,3,4 $A^1$ × 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 zoospores liberated by the germ sporangium produced by a single oospore. From crosses 473 × 60A (race 1,2,3,4 × race 1,2 $A^2$) two single-zoospore cultures were established from the germ sporangium of oospore No. 35. One was pathogenic race 1,2,4 and the other race 1,2,3,4; both were of compatibility type $A^1$. Thus, recombination for pathogenic race was evident among the individuals of a single oospore. Five oospores from cross 473 × 445 (1,2,3,4 $A^1$ × 0 $A^2$) yielded more than one phenotype per oospore among the individual cultures established from the zoospores of a germ sporangium. 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-zoospore cultures 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 zoospores simultaneously in the same water droplet. Among the cultures established from 12 zoospores, the phenotypes obtained 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-oospore isolates and 28 single-zoospore isolates established by Laviola (18). Only three isolates lost this selfing ability upon serial transfer. Further studies are necessary to determine whether any of these are true homothallic isolates, whether they consist 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 *Phytophthora* has been reviewed thoroughly by Erwin et al. (7), and will not be repeated here. An excellent discussion of the above mechanisms of asexual variation as they relate to cultural variations among single-zoospore 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 heterocaryons 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 & Eichenmuller (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 parasexuality occurs in species of *Phytophthora*. Leach & Rich (19) suggested parasexuality as an explanation for the recombinations of pathogenic race characters observed in his 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. Galindo & 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 $A^1$ were paired with a strong male $A^2$, the $A^1$ isolate would always produce the oogonium. Laviola (18) found that all individuals in the $F_1$ from crosses involving isolate 60A as the $A^2$ parent were of the $A^1$ compatibility type. When isolate 445 was used as the $A^2$ parent, the ratio of segregation in the $F_1$ for $A^1:A^2$ 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 $A^1$ 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 $A^1$ and $A^2$ 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 Laviola (18) with *P. infestans* showed a predominance of $A^1$ types in the progeny of $A^1 \times A^2$ 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 $A^1$ 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*; $aa \times Aa$ should yield segregation ratios of 1:1 in the $F_1$.

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 $F_1$ for every character. The data of Laviola (18) particularly support the premise that these heterothallic species are haploid in their asexual stages.

In addition to observing recombination in the $F_1$ and segregation ratios of 1:1 for the presence to absence of pathogenic race characters, Laviola (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). Laviola's

(18) 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) cytological 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 genotype 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 genotype 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 genotype 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 620 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).

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