Identification of Strains and Inheritance of Pathogenicity in Phytophthora capsici

F. J. Polach and R. K. Webster

Department of Plant Pathology, University of California, Davis 95616. Present address of senior author: Department of Plant Pathology, New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456.

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ABSTRACT

Fourteen distinct pathogenic strains were identified among 23 diverse isolates of *Phytophthora capsici* when tested on tomato, eggplant, squash, watermelon, sugar pumpkin, and selected lines of pepper. No correlations between pathogenicity to a specific host and the mating reaction of a given isolate were found.

Factors controlling pathogenicity were further characterized by genetic studies on 391 single oospore progeny. Recombination between factors conditioning pathogenicity and mating group occurred, indicating that pathogenicity to the various hosts is controlled by a separate gene or gene system for each host. Pathogenicity to pepper is controlled by at least two genes. Genetic ratios obtained did not allow a determination of ploidy of *P. capsici* because of the low percentage of oospore germination and the possibility that some of the progeny were derived from selfed oospores of one or the other of the parent isolates.

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Additional key words: germination of oospores, mating types.

Leonian (12) described *Phytophthora capsici* Leonian and regarded it as distinct from *P. parasitica* [on the basis of pathogenicity to stems and fruits of mature pepper plants (*Capsicum annuum* L.) and the absence of chlamydospores in culture]. Later, Sarejanni (17) proposed that isolates exhibiting the morphology attributed to *P. capsici* and distinct from *P. parasitica* in the ability to attack pepper should be considered a variety of *P. parasitica* (=*P. parasitica* var. *capsici* [Leonian] Sarejanni). Satour & Butler (18) considered *P. capsici* a convenient name, but suggested that *P. capsici* probably represents a race of *P. parasitica*.

No mention of pathogenicity to hosts other than pepper is included in Leonian's concept of *P. capsici*, although isolates of *Phytophthora* identified as *P. capsici* by various workers have been reported as pathogens on tomato (*Lycopersicon esculentum* Mill.) (11), eggplant (*Solanum melongena* L.) (3), cucumber (*Cucumis sativus* L.) (9), honeydew melon (*Cucumis melo* L. var. *inodorus* Naud.) (22), pumpkin (*Cucurbita pepo* L.) (23), squash (*Cucurbita maxima* Duc.) (11), and watermelon (*Citrullus vulgaris* Schrad.) (24). Regardless of the question of taxonomic position, isolates considered as *P. capsici* constitute a taxon more complex than a single race based on pathogenicity to pepper. Even so, no extensive studies of cross inoculation tests on these hosts have been reported.

Smith et al. (20) found that resistance in pepper to *P. capsici* appears to be governed by two distinct, dominant genes that are inherited independently without additive effects. Since a number of genes (7) has been identified as conferring resistance in potato to *P. infestans* with corresponding genes postulated in the fungus to overcome this resistance, a similar situation may exist between pepper and isolates of *P. capsici* pathogenic to pepper. The success of Satour & Butler (18), Galindo & Zentmyer (6), and Timmer et al. (21) in germinating oospores from matings between isolates pathogenic to pepper and the availability of differential hosts suggested that *P. capsici* might lend itself to a study of the genetics of pathogenicity.

In the present study, isolates of *P. capsici* and the oospore progeny from certain matings were studied on different hosts to determine (i) the possibility of the existence in nature of distinct pathogenic strains; (ii) the nature of the gene pool controlling pathogenicity to this host range; and (iii) the inheritance of factors for pathogenicity.

MATERIALS AND METHODS. —*Source of isolates and maintenance of cultures.*—Isolates obtained from E. E. Butler (plant pathology stock culture collection at the University of California, Davis) were considered *P. capsici* because of amphigynous antheridia, papillate sporangia, absence of chlamydospores, and ability to grow in culture at 35 C. They were from different hosts and geographic areas (Table 1). Also included were isolate 28 (originally described by L. H. Leonian, obtained from the Central Bureau for Fungus Culture, Baarn, The Netherlands), and isolate 29 (the type culture of *P. capsici*, obtained from the British Commonwealth collection of microorganisms, London, England). The stock cultures were maintained on V-8 juice agar (200 ml Campbell's Soup Company V-8 juice, 2.5 g $CaCO_3$, 15 g agar, and 800 ml distilled water, autoclaved at 121 C for 15 min).

Selection of host range.—The hosts studied were pepper (*Capsicum annuum* L. 'Yolo Wonder'), tomato (*Lycopersicon esculentum* Mill. 'Improved Pearson'), eggplant (*Solanum melongena* L. 'Black Beauty'), squash (*Cucurbita maxima* Duc. 'Early White Bush'), pumpkin (*Cucurbita pepo* L. 'Small Sugar'), and watermelon (*Citrullus vulgaris* Schrad. 'Charleston Gray'). Pepper lines developed by Smith et al. (20) were also tested: 493-2 with two dominant genes for resistance to *P. capsici* and 235-1-1, 493-4-1-2, and C62PM7-2-1, each with one dominant gene and one recessive gene for resistance. In

TABLE 1. Source of *Phytophthora capsici* isolates

Isolate	Source	Location
2	Pepper (*Capsicum annuum* L.)	California
3	Soil[a]	California
4	Pepper (*Capsicum annuum* L.)	California
5	Pepper (*Capsicum annuum* L.)	Peru
6	Soil	California
7	Tomato (*Lycopersicon esculentum* Mill.)	California
8	Pepper (*Capsicum annuum* L.)	California
9	Eggplant (*Solanum melongena* L.)	Japan
12	Squash (*Cucurbita maxima* Duc.)	North Carolina
13	Pepper (*Capsicum annuum* L.)	California
14	Pepper (*Capsicum annuum* L.)	California
16	Pepper (*Capsicum annuum* L.)	California
17	Tomato (*Lycopersicon esculentum* Mill.)	California
18	Pepper (*Capsicum annuum* L.)	North Carolina
19	Soil	California
20	Pepper (*Capsicum annuum* L.)	Argentina
21	Pepper (*Capsicum annuum* L.)	Argentina
22	Pepper (*Capsicum annuum* L.)	California
24	Pepper (*Capsicum annuum* L.)	West Virginia
27	Pepper (*Capsicum annuum* L.)	Mexico
28	Pepper (*Capsicum annuum* L.)	New Mexico
29	Unknown	England
30	Pepper (*Capsicum annuum* L.)	New Mexico

[a] Soil from fields planted to tomato.

addition, plants of *Capsicum annuum* L. 'Anaheim Chili', with no genes for resistance, were tested.

Preparation of inoculum and inoculation of plants.—Cultures were grown on V-8 juice agar at room temperature (24 ± 2 C) for 7-10 days. Inoculum was prepared by placing 200 ml distilled water and a culture of the isolate in a Waring Blendor for 5-10 sec. Ten ml of the fungus and agar mixture were pipetted into pots containing plants in the two- to four-leaf stage. The pots were watered heavily immediately after inoculation, and daily thereafter. Disease readings were made at 3, 7, 14, and 21 days. Plants were considered diseased when wilted and/or visible lesions occurred on the stem at the soil level. Infected plants usually collapsed, due to disintegration of the stem within 14 days; although with some isolates, complete collapse occurred within 3 days. Similar results were obtained when oospore suspensions were used as inoculum.

Matings between isolates.—Matings between isolates were attempted by placing small blocks of agar containing mycelium of each test isolate 2.5 cm apart on V-8 juice agar in a petri dish. The inoculated dishes were placed in the dark at room temperature for 10 days, at which time they were examined for the presence of oospores. In a compatible mating, oospores were formed in abundance in the area where the isolates met.

Germination of oospores.—Oospores were produced as previously described for determination of mating types. Cultures of matings were placed in the dark at room temperature for 2 months or longer, after which the agar containing oospores was removed and blended in 200 ml sterile distilled water for 5 min. This mixture was filtered successively through a double layer of cheesecloth and a double layer of Kimwipes (Kimberly-Clark Corporation, type 900-S). The filtrate containing the oospores was poured into petri dishes. To observe germination, a quantity of this oospore suspension was pipetted onto a plate of 2% water agar and observed with the aid of a stereo dissecting microscope. Oospores germinating either directly or by germ sporangia were removed from the water agar plate with a glass needle and transferred to antibiotic medium (100 ppm each of penicillin, polymyxin, and pimaricin in 1.7% Difco cornmeal agar autoclaved at 121 C for 15 min). Hyphal tips from the surviving colonies were transferred to V-8 juice agar dishes.

Characterization of progeny.—All of the progeny obtained from germinated oospores were characterized with respect to mating reaction (production of oospores within 10 days when mated with the parent isolates) and pathogenicity to Yolo Wonder pepper, Improved Pearson tomato, Black Beauty eggplant, and Smith's resistant line 493-2. Additional pathogenicity tests on squash, watermelon, and pumpkin were made with 123 of the oospore progeny.

RESULTS.—*Cross inoculation tests and identification of strains.*—Fourteen pathogenic strains were distinguished among the 23 isolates tested on tomato, eggplant, squash, watermelon, and 6 lines of pepper (Table 2). Isolates 3, 14, and 28 were nonpathogenic on all hosts tested; isolate 30 from pepper in New Mexico was pathogenic on all hosts tested, including the resistant pepper lines developed by Smith et al. (20). Two isolates (17 from tomato and 12 from squash) were nonpathogenic on the hosts from which they were originally isolated.

In addition to demonstrating the existence of a number of pathogenic strains in *P. capsici*, the results

TABLE 2. Pathogenicity of 23 isolates of *Phytophthora capsici* on 10 possible suscepts[a] 3 weeks after inoculation

Isolate	Tomato	Eggplant	Squash	Watermelon	Pepper					
					YW	P-101	P-106	P-107	P-111	P-113
30	+[b]	+	+	+	+	+	+	+	+	+
4	+	+	+	+	+	−	−	+	+	+
27	+	+	+	+	+	−	−	+	+	+
22		+	+	+	+	−	−	+	−	+
2	+	+	+	+	+	−	−	−	−	+
9	+	+	+	+	+	−	−	−	−	+
20	+	+	+	+	+	−	−	−	−	+
21	+	+	+	+	+	−	−	−	−	+
6	−	+	+	+	+	−	−	−	−	+
24	+	−	+	+	+	−	−	−	−	+
16	+	+	−	−	+	−	−	+	−	+
5	+	−	+	−	+	−	−	−	−	+
8	−	−	+	+	+	−	−	−	−	+
19	+	+	+	+	−	−	−	−	−	−
7	+	+	−	−	−	−	−	−	−	−
12	−	−	−	−	+	−	−	−	−	+
13	−	−	−	−	+	−	−	−	−	+
17	−	−	−	−	+	−	−	−	−	+
29	−	−	−	−	+	−	−	−	−	+
18	−	−	−	+	−	−	−	−	−	−
3	−	−	−	−	−	−	−	−	−	−
14	−	−	−	−	−	−	−	−	−	−
28	−	−	−	−	−	−	−	−	−	−

[a] YW = Yolo Wonder pepper; TOM = Improved Pearson Tomato; EP = Black Beauty eggplant; SQ = Early White Bush squash; WM = Charleston gray watermelon. The remainder of plants were Smith's pepper lines. The numbers correspond to his designations (20) as follows: P-101 = 493-2 (two dominant genes for resistance), P-106 = 493-4-1-2, P-107 = 235-1-1, P-111 = C62PM7-2-1 (each with one dominant gene and one recessive gene for resistance), and P-113 = Anaheim chili (no genes for resistance).

[b] + = pathogenic; − = nonpathogenic

in Table 2 provide an insight into the complexity of the gene pool governing pathogenicity to the various hosts tested. For example, isolate 30 attacked all the hosts tested, whereas isolate 16 attacked tomato, eggplant, and three pepper lines, but not squash or watermelon. One can conclude from this that the ability to attack a given host is conditioned by specific genes in the isolate. Since the ability to attack tomato does not necessarily mean that it will also attack squash or watermelon, a specific factor or set of factors conditions pathogenicity to each of the separate hosts tested. Further comparisons substantiating this are seen between isolates 18, 16, 5, and 24, where pathogenicity to squash and watermelon are shown to be controlled by different genes. The validity of this interpretation is further substantiated in the inheritance studies.

Determination of mating group and its relationship to pathogenicity.—Although there are conflicting reports as to whether *P. capsici* is homothallic (8) or heterothallic (10, 12, 19, 21), oospores are readily formed in matings between certain isolates within 10 days after mating; whereas in selfed cultures, no oospores are present within this time. Kreutzer et al. (10) considered *P. capsici* to be heterothallic. In their study, isolates from pepper would mate only with isolates from cucumber. Apple (1) reported in *P. parasitica* var. *nicotianae* that isolates from flue-cured tobacco mated only with isolates from Burley tobacco. To determine if similar correlations between mating type and pathogenicity to specific hosts existed in our isolates, the 23 isolates (Table 1) were mated in all possible combinations. Results of these matings showed that the isolates can be divided into two distinct mating groups on the basis of oospore formation. One group (I) contained isolates 7, 12, 13, 14, 16, 18, 24, and 27; the other (II) contained isolates 2, 3, 4, 5, 6, 8, 9, 17, 19, 20, 21, 22, 28, 29, and 30. All intergroup matings were fertile with the exception of that between isolates 24 (I) and 9 (II). Although some of the isolates produced a few oospores in selfed cultures after 3 months, no isolate formed oospores when mated with itself or isolates of the same mating group (intragroup matings) within 10 days (the time required for fertile intergroup matings). When mating group and pathogenicity of individual isolates were compared, no correlations between pathogenicity to a specific host and the mating reaction of an isolate were found.

Inheritance of pathogenicity.—A study of oospore progeny produced from matings between isolates differing in pathogenicity and mating group would allow a determination of the inheritance and nature of the genetic systems governing pathogenicity. Oospores from a number of the possible crosses

TABLE 3. Mating type of oospore progeny from four separate matings between *Phytophthora capsici* isolates 4 and 13 and their pathogenicity to Yolo Wonder pepper, Improved Pearson tomato, and Black Beauty eggplant

Oospore Isolation Group[a]	Per cent Oospore Germination	Mating Type		Pathogenicity: Pepper		Tomato		Eggplant	
1	7.0	a[b]	= 18	p	= 22	t	= 19	e	= 13
		A	= 8	P	= 4	T	= 7	E	= 13
2	5.5	a	= 71	p	= 92	t	= 80	e	= 67
		A	= 50	P	= 29	T	= 41	E	= 54
3	6.0	a	= 89	p	= 148	t	= 84	e	= 58
		A	= 73	P	= 14	T	= 78	E	= 104
4	8.0	a	= 33	p	= 66	t	= 52	e	− 44
		A	− 49	P	= 16	T	= 30	E	= 38
Total		a	= 211	p	= 328	t	− 235	e	= 182
		A	= 180	P	= 63	T	= 156	E	− 209

[a] Isolation groups 1, 2, 3, and 4 represent separate occasions when germination and isolation of oospores was successful.
[b] a = mating group 1; A = mating group 2; p = pathogenicity to pepper; P = nonpathogenicity to pepper; t = pathogenicity to tomato; T = nonpathogenicity to tomato; e = pathogenicity to eggplant; E = nonpathogenicity to eggplant.

TABLE 4. Proposed genotypes and pathogenicity reactions of oospore progeny obtained in crosses of *Phytophthora capsici* isolates 4 and 13

Oospore isolation group[a]	ATE	ATe	AtE	Ate	aTE	aTe	atE	ate
1	3	1	1	3	3	0	5	10
2	20	2	6	22	19	1	6	45
3	34	1	13	25	43	2	15	29
4	15	2	7	25	8	4	7	14
Total	72	6	27	75	73	7	33	98

[a] Isolation groups 1, 2, 3, and 4 represent separate occasions when germination and isolation of oospores was successful. A = mating group 1; a = mating group 2; T = nonpathogenic on tomato; t = pathogenic on tomato; E = nonpathogenic on eggplant; e = pathogenic on eggplant.

between isolates showing differential pathogenicity to selected hosts were tested for germination. Of the matings that formed oospores, the 4 X 13 cross was the only one in which oospores germinated, and then only on four occasions. Progeny obtained from the 4 X 13 cross were characterized for mating group and pathogenicity to Yolo Wonder pepper, tomato, eggplant, and Smith's resistant pepper line 493-2. The pathogenicity of the parents can be seen in Fig. 1. The pathogenic reactions of 391 oospore progeny from the 4 X 13 cross are shown in Table 3, and are further analyzed with suggested genotypes in Table 4. Recombination between factors controlling pathogenicity and mating group occurred (Table 3). Tables 3 and 4 also show that genes conditioning pathogenicity in *P. capsici* to one host are not the same as those conditioning pathogenicity to another, as recombination between factors for pathogenicity to separate hosts and mating group is evident in the various classes of progeny.

Any further conclusions regarding inheritance of specific factors in the present data must consider the random nature of the samples and the ploidy of *P. capsici*. These results are explainable whether meiosis occurs in the gametangia or the oospores, and do not allow a distinction as to whether the somatic nuclei are haploid or diploid. However, the low percentage of germination of oospores as seen in Table 3 and the possibility of selfs in the progeny (16) indicate the strong possibility that the germinated oospores do not represent a random sample of the population and that emphasis on the inheritance ratios is not justified, or at best should be viewed with caution. One only need compare the two interpretations as summarized in Table 5 to better appreciate this conclusion.

Inheritance of pathogenicity to Yolo Wonder pepper.—Both parents (isolates 4 and 13) were pathogenic on Yolo Wonder pepper, but 63 of the 391 progeny were not. The nonpathogenic recombinant progeny can be accounted for by assuming that pathogenicity to Yolo Wonder pepper is controlled by either of two gene loci, and that (i) isolates are pathogenic when either of the two alleles at the two loci are recessive; (ii) when homozygous dominant is nonpathogenic; and (iii) when the parent isolates 4 and 13 are heterozygous in the *trans* arrangement. This conclusion is supported by the fact that Yolo Wonder pepper does not possess either of the dominant genes identified by Smith for resistance.

Inheritance of pathogenicity to tomato, eggplant,

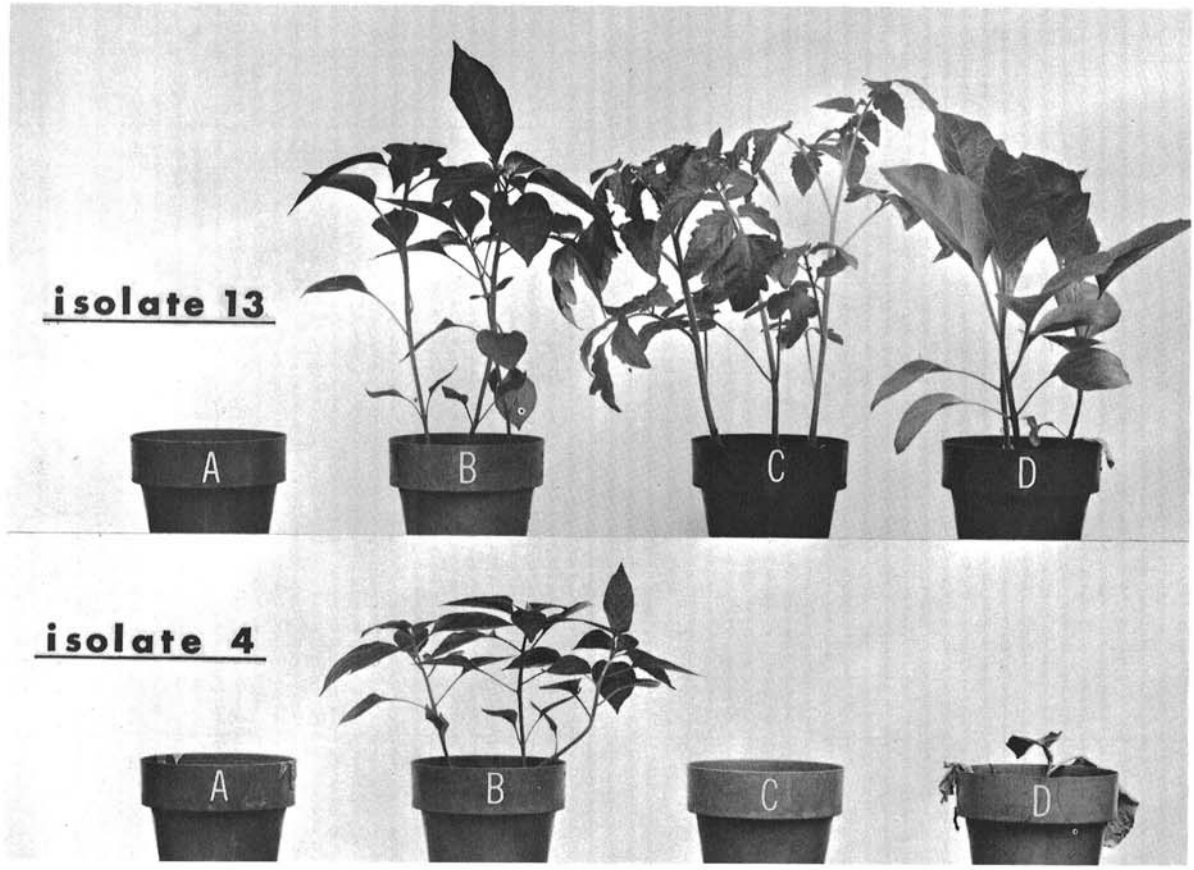

Fig. 1. Pathogenic reactions of *Phytophthora capsici* isolates 4 and 13 on Yolo Wonder pepper (A), Smith's resistant pepper line 493-2 (B), Improved Pearson tomato (C), and Black Beauty eggplant (D) 21 days after inoculation.

and cucurbit hosts.—The recombination and segregation of factors controlling pathogenicity and mating type (Tables 3, 4, 5) indicate that pathogenicity to each host is controlled by a separate gene or gene system. This verifies the occurrence of pathogenic strains in *P. capsici*. Interpretation of the independence or linkage relationships between factors controlling pathogenicity to each of the hosts is not attempted here because of the limitations expressed previously.

Inheritance of mating group type.—Segregation among the progeny for mating group approaches a 1:1 ratio (211:180, Table 5), indicating that mating type is controlled by either a single pair of alleles at one locus or by more than one closely linked loci inherited as a single factor in the present study. A detailed analysis of the nature and inheritance of sexuality in *P. capsici* will be given elsewhere.

DISCUSSION.—The pathogenic reactions of *P. capsici* isolates included in the present study on our host range indicate that strains for pathogenicity do exist in this collection of isolates. Nonpathogenicity to original hosts observed in isolates 17 and 12 could be due to a number of factors, such as (i) varietal differences between original host and that used here; (ii) environmental conditions; and (iii) the fact that some of these isolates have been maintained in culture for a long period of time; e.g., isolate 28 was isolated nearly 50 years ago.

Squash and watermelon were included in the host range to determine if separate genes control pathogenicity to these hosts, or if pathogenicity to cucurbits is controlled by a single gene system. The reactions of isolates 5 and 18 provide the explanation. Isolate 5 is pathogenic on squash, but not on watermelon; whereas isolate 18 is pathogenic on watermelon, but not on squash. Therefore, two different genetic systems must be in effect. Pathogenicity to pepper, eggplant, and tomato was apparently inherited independently, confirming the evidence from the host range study that separate genetic systems control pathogenicity to each of these hosts.

Segregation and recombination were observed in the progeny for all characters studied. This confirms the reports of Satour & Butler (18) and Timmer et al. (21) that the oospore is the site of sexual recombination in *P. capsici*.

Further analysis of the genetics of pathogenicity to each of the hosts studied here may reveal the genetic systems to be more complex than can be seen in the present results. For example, one might expect that additional genes for pathogenicity to pepper will

TABLE 5. Chi-square values demonstrating the goodness of fit of classes of *Phytophthora capsici* oospore progeny to mating group and pathogenicity to six different hosts

Character	Observed ratio	Expected ratio[a] 1:1 (3.84)[b]	Expected ratio[a] 3:1 (7.84)[2]
Mating group			
Group 1	211		
Group 2	180	2.64	92.12
Pathogenicity to pepper			
Pathogenic	328		
Nonpathogenic	63	179.60	3.93
Pathogenicity to tomato			
Pathogenic	235		
Nonpathogenic	156	15.96	46.20
Pathogenicity to eggplant			
Pathogenic	182		
Nonpathogenic	209	1.86	96.64
Pathogenicity to squash			
Pathogenic	101		
Nonpathogenic	22	50.74	4.56
Pathogenicity to sugar pumpkin			
Pathogenic	90		
Nonpathogenic	33	26.42	0.17
Pathogenicity to watermelon			
Pathogenic	66		
Nonpathogenic	57	0.66	31.74

[a] See text for discussion of the relation of a 1:1 or 3:1 ratio to the ploidy of the fungus.
[b] Expected values at the 5% level of significance.

be identified as more is learned about the genetic basis for resistance in this host, and further studies with differential lines are made. This also brings another point to focus. Since progeny that are nonpathogenic to pepper can be obtained from crosses between parents which are both pathogenic to pepper, it would be unwise to continue using pathogenicity on this host as a criterion in identifying an isolate as *P. capsici*. This observation has been made previously by Satour & Butler (18).

The ploidy of the Oomycetes has been in question since Sansome (15) suggested in 1961 that *Pythium debaryanum* and Oomycetes in general, might be diploid in the vegetative state. Prior to this, these fungi were considered to be haploid, based on early cytological studies. Sansome made her prediction of a diploid vegetative state on the basis of meiotic figures in antheridia and oogonia. As she observed reduction division in the gametangia rather than the oospore, she maintained that the somatic thallus is diploid, since if the vegetative state were haploid one would expect the meiotic divisions to occur in the oospore.

From a cytological study, Marks (13) concluded that the vegetative state of *P. infestans* is haploid. He did not view the study by Sansome (15) as decisive evidence that the vegetative state of *P. infestans* is diploid. However, Barksdale (2) recently provided cytological evidence that *Achlya ambisexualis* is diploid, and Bryant & Howard (4) suggested that *Saprolengnia terrestris* is diploid on the basis of a microspectro-photometric analysis of nuclear deoxyribonucleic acid (DNA).

Genetic studies should provide evidence as to the ploidy of the Oomycetes, but to date none have done this. The genetic ratios obtained by Galindo & Zentmyer (*P. drechsleri*) (6), Satour & Butler (*P. capsici*) (18), Romero & Erwin (*P. infestans*) (14), and Timmer et al. (21) are subject to either a haploid or diploid interpretation. Sansome (16) interpreted the data of Galindo & Zentmyer (6) as being indicative of diploid somatic state, and believed that the atypical segregation ratios of characters in the progeny classes could best be explained by the possibility that selfing had occurred in one of the parent isolates. Recently DeBoccas (5) suggested that oogonial germination has contributed to the confusing ratios which have been obtained.

Segregation ratios of progeny types which we obtained are not considered to provide direct evidence for a haploid or diploid vegetative state for two reasons. Firstly, with germination percentages in the range of 6-8%, it would be invalid to assume that we had a random sample of the population. Secondly, selfing could have occurred, possibly skewing the data toward one or both of the parental types. Oospores have been observed in cultures obtained from single zoospores which were the same age as those from which oospores used for germination were obtained. As a considerable percentage of the oospore progeny are like one or the other of the parents in the characters studied, it would appear that this may have occurred.

Whether or not a 3:1 ratio indicates ploidy of the fungus is dependent on the genotype of the parents. For example, if one assumes that meiosis occurs in the gametangia (diploid), only one progeny type (one nuclear type) would be expected for each oospore. With a haploid interpretation, four progeny types/oospore are possible; however, in the past workers have assumed that only one nucleus from meiosis in the oospore survives. This line of reasoning is interesting when the interpretation by Sansome (16) of the results published by Galindo & Zentmyer (6) is considered. These workers assumed the somatic thallus of their isolate to be haploid; thus, the phenotype in fact represents the genotype of the isolate. However, Sansome considered this isolate as diploid. Without a knowledge of the genotype of the parent isolates, gene action of characters involved (i.e., dominance and recessiveness), little could be gained regarding a decision on ploidy from such a comparison. This is substantiated with the present results, since neither a 3:1 or 1:1 ratio allows a conclusion regarding ploidy of the *P. capsici* isolates studied.

Continued backcrossing of selected progeny to either of the parent isolates should provide better-defined strains from which further information on inheritance in this species could be obtained.

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