Etiology

# Intraspecific Variation Among Isolates of *Phytophthora capsici* from Pepper and Cucurbit Fields in North Carolina

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## ABSTRACT

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*Phytophthora capsici* was isolated from seven pepper and seven cucurbit fields in North Carolina. The relative virulence of the isolates was tested on pepper (*Capsicum annuum*), morphological characteristics of sporangia and oospores were evaluated, and mating type and growth response to temperature were determined. All pepper and some cucurbit isolates of *P. capsici* were highly virulent on pepper, whereas other cucurbit isolates were less virulent on pepper. Sporangia of cucurbit isolates were greater than 55 $\mu$m in length and were less variable in length than sporangia of pepper isolates. Pedicel lengths of sporangia ranged from 31 to 99 $\mu$m and were highly variable among isolates from both hosts. Oospore diameters ranged from 24 to 35 $\mu$m among isolates. The potential exists for sexual recombination and oospore formation to occur in some fields in the state, because both mating types were present in two of 14 fields sampled. None of the isolates produced chlamydospores in culture. A culture from the ATCC and other isolates grew slowly or not at all at 36 C; therefore, growth at temperatures greater than 35 C was not a definitive character for identification of isolates of *P. capsici*. Continuous rather than discrete variation was observed in sizes of sporangia, pedicels, and oospores based on host.

Additional keyword: taxonomy.

Phytophthora blight of pepper caused by *Phytophthora capsici* Leonian (19) is a widespread and destructive disease of peppers (*Capsicum annuum* L.) in many areas of the United States and worldwide. The pathogen can also infect tomato, eggplant, cucumber, watermelon, pumpkin, squash, cocoa, and macadamia (16–18,26,35). Symptoms of the disease on solanaceous and cucurbit hosts include damping-off, foliar blight, stem lesions, fruit rots, and a root and crown rot. *P. capsici* has been reported

to cause a fruit rot on squash in North Carolina (7). In recent years, the incidence of root and crown rot on pepper and fruit rots on cucurbits has increased (J. B. Ristaino, *unpublished data*). Although Phytophthora blight currently is not limiting pepper and cucurbit production in the state, an increase in the use of overhead and drip irrigation in vegetable production areas could exacerbate disease problems.

Isolates of *P. capsici* from cucurbits are pathogenic on both pepper and cucurbits (7,17,29); however, evaluations of the relative virulence of cucurbit isolates on pepper have not been reported. Because the major cultivars of pepper and cucurbits grown are susceptible to the pathogen and vegetable growers rotate from cucurbits to pepper, the potential exists for Phytophthora blight to cause severe epidemics.

*P. capsici* is a heterothallic fungus (10). Pairings between opposite mating types result in oospore formation and genetic variation (24,26). Oospores are believed to be the primary overwintering propagules in the field (23). Little is known about the occurrence of mating types of *P. capsici* within and among fields of pepper and cucurbits in North Carolina. Both mating types were isolated from pepper field soils in New Jersey, whereas either A1 or A2 mating types were isolated from squash field soils (23).

My objectives were to evaluate intraspecific variation among many isolates of *P. capsici* obtained from pepper and cucurbit fields in North Carolina. Specifically, the relative virulence of the isolates was tested on pepper, and mating type was determined; morphological characteristics of sporangia and oospores were evaluated; and chlamydospore production and growth response to temperature were measured. A preliminary report of a portion of the work has been published (4).

## MATERIALS AND METHODS

*P. capsici* was isolated consistently from diseased roots, stems, or fruit of pepper (bell, Hungarian wax, and cayenne types), squash (*Cucurbita maxima* Duc. and *C. pepo* L., acorn, spaghetti, butternut, and pattypan types), and cucumber (*Cucumis sativus* L.) when tissue was surface-disinfested in 0.5% NaOCl for 3 min, rinsed in sterile distilled water, and plated on selective media (PARP) containing pimaricin, ampicillin, rifampicin, and PCNB at 10,250, 10, and 100 ppm, respectively (14). In some cases, soil adjacent to infected plants was diluted (1:10 w/v) in 0.25% water agar and spread onto PARP medium. A total of 60 isolates (27 cucurbit, 29 pepper, and 4 soil) were obtained from the 14 fields sampled. All the isolates were tested for mating type, whereas only selected isolates were used in other experiments. Two additional isolates of *P. capsici* (ATCC 15399 and PcW3a), obtained from J. Bowers and D. Mitchell, University of Florida, Gainesville, were also evaluated. Cultures were maintained on cornmeal agar (17 g/L) slants (Difco Laboratories, Detroit, MI) or V-8 juice agar in petri dishes (800 ml water, 200 ml V-8 juice, 2 g CaCO₃, 15 g agar) at room temperature.

Inoculum used in pathogenicity tests was produced by incubating isolates of *P. capsici* on V-8 juice agar for 1 wk at room temperature. Sporangia were obtained by cutting agar cultures into pieces and incubating the pieces in a shallow layer of sterile distilled water in petri dishes at room temperature for 72 hr. Sporangia were induced to release zoospores by chilling dishes at 6 C for 1 hr and rewarming to room temperature for 1 hr. Zoospores were filtered through cheesecloth, quantified with the aid of a hemacytometer, and diluted to appropriate concentrations for each experiment. Both encysted and motile zoospores were present in the suspension.

Isolates of *P. capsici* were tested for pathogenicity on seedlings of bell pepper cultivar Keystone Resistant Giant in the greenhouse. A randomized complete block design was used, and each experiment was repeated at least twice. Pepper seed were planted in Metro Mix (W. R. Grace and Co., Cambridge, MA) and fertilized once with half-strength Hoagland's solution (12) after emergence. Each pot (10 cm in diameter) was considered an experimental unit, and at least eight replicates were used. Six-week-old seedlings were inoculated by placing 25 ml of a $10^4$/ml suspension of

zoospores on the surface of the Metro Mix in each pot. The Metro Mix was flushed with 50 ml of distilled water to move inoculum into the root zone. After inoculation, all seedlings were given a 3-hr saturation period by placing pots in containers of water and saturating from below until the soil surface was wet. Beginning 2 days after inoculation, the incidence and severity of disease were evaluated for 13 successive days. Disease severity was evaluated on a scale of 0–4, where 0 = no symptoms; 1 = wilting of plant, without a stem lesion; 2 = wilting and stem lesion without girdling; 3 = girdled plant stem; 4 = dead plant. After harvest, roots were surface-disinfested and plated on PARP medium to reisolate the pathogen.

Morphological characteristics of sporangia were observed after incubation of V-8 juice agar disks in sterile distilled water in the light for 72 hr. Length and width of 20 sporangia were measured from each isolate with the aid of an optical micrometer on a compound microscope, and length-breadth (LB) ratios were calculated. Sporangia were also obtained from isolates grown on clarified V-8 juice (CV8) agar (200 ml of V-8 clarified juice, 2 g CaCO₃, 15 g agar, 800 ml water) for 3 days in the dark and 1 wk under lights (two General Electric cool-white fluorescent lights, 74 μmoles m⁻²s⁻¹). Agar disks containing sporangia were removed from the CV8 dishes, placed in 4 ml of sterile distilled water, and stirred with a glass rod to dislodge the sporangia (1). Caducity (deciduousness) of 20 sporangia of each isolate was determined, and pedicel lengths of sporangia were measured.

Mating types were analyzed by pairing isolates with known mating types of *P. capsici*. Agar plugs were placed 2 cm apart on CV8 agar with either an A1 isolate (PcW3a) or an A2 isolate (ATCC 15399), or isolates were paired with themselves. Cultures were incubated in the dark at 25 C for up to 2 wk. Twenty oospores, oogonia, and antheridia were observed and measured with an optical micrometer. Isolates were also evaluated to determine whether oospores were produced in single culture on modified CV8 agar (36). Pepper or cucurbit plants sampled in the field were not examined microscopically for the presence of oospores in infected tissue before isolations were made on PARP medium.

To determine whether the isolates produced chlamydospores in liquid medium, bottles containing 25 ml of CV8 broth were seeded with inoculum plugs from V-8 juice agar cultures (30). Cultures were incubated vertically at 25 C in the dark for 24 hr, shaken to fragment hyphae, and incubated horizontally at 25 C in the dark for 6 days. Sterile distilled water (100 ml) was added to the bottles, and cultures were incubated vertically at 18 C in the dark for 3 wk. Four samples were removed from each bottle and observed for chlamydospore production with a compound microscope.

The effect of temperature on linear growth of the isolates was evaluated over the range of temperatures from 16 to 36 C (±1 C at 2-degree intervals) in controlled-temperature incubators. Cornmeal agar in each of five plates was seeded with an agar plug of each isolate, and cultures were incubated in the dark for 3–7 days in a completely randomized design at each temperature. Colony diameters were measured, and data were converted to radial growth in millimeters per day.

All experiments were repeated at least twice. Data are shown for a single experiment. Data were tested for normality and homogeneity of variance before analysis of variance with the Statistical Analysis Systems (SAS Institute, Inc., Cary, NC). Repeated-measures analysis of variance was conducted on disease progress data. Area under the disease progress curve (AUDPC) was calculated for each isolate (28). AUDPCs were standardized for each experiment by dividing the mean AUDPC by the number of days in each experiment that disease was evaluated. Results were compared, and mean AUDPCs are reported. Means from significant treatment effects were separated with either Duncan's multiple range test or a least significant difference test.

## RESULTS

Pepper and cucurbit plants with symptoms of infection by *P. capsici* were observed in 14 fields in North Carolina between

1987 and 1989. Diseased pepper plants exhibited typical root, crown, and stem infections. Brown, water-soaked lesions and sporulation on the fruit surface and stem were common on infected cucumber and squash. Lesions on cucurbit fruits were not always present on the fruits in contact with the soil surface; therefore, splash-dispersed sporangia may have been responsible for infections on fruit. *P. capsici* was isolated consistently from infected fruit, stems, or roots of plants from the fields sampled.

Isolates from both pepper and cucurbits were pathogenic on pepper; however, the severity of disease among isolates differed over time in a given experiment (Fig. 1). Repeated-measures analysis of variance of the data revealed a significant ($P < .0001$) isolate $\times$ time interaction, in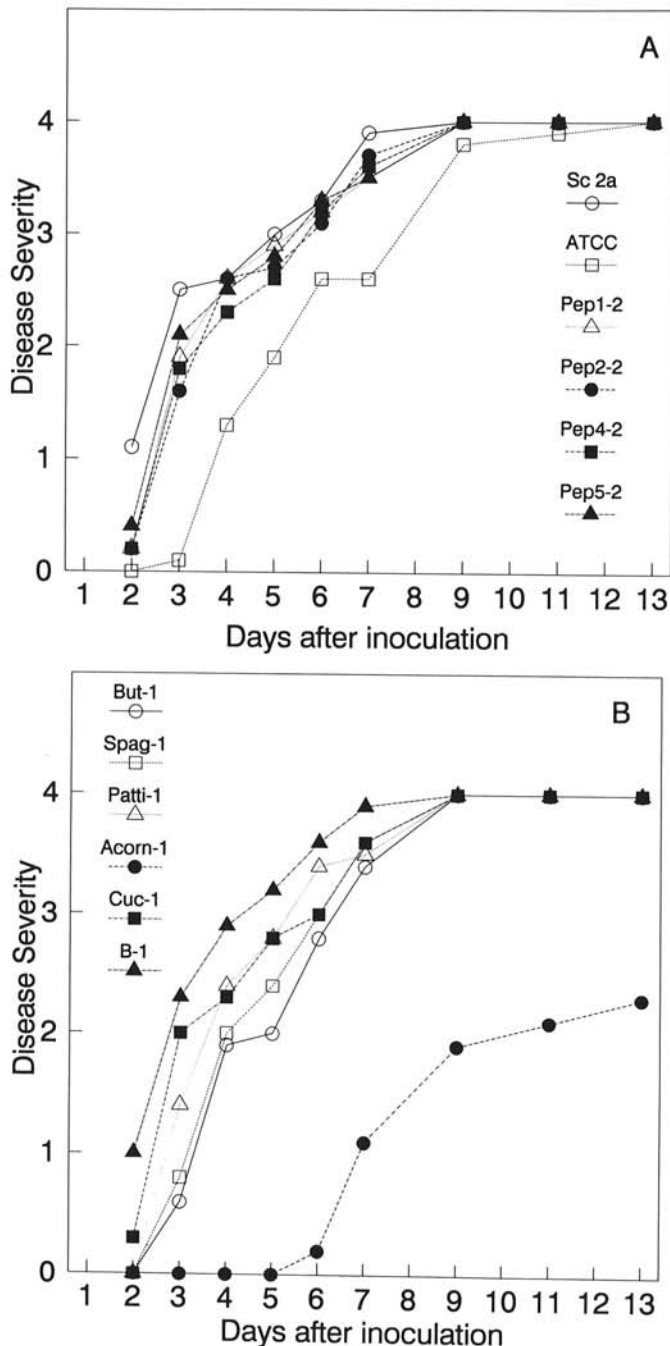dicating that disease increase over time differed among isolates. Isolate ATCC 15399 caused significantly less disease between days 3 and 7 after inoculation than the other pepper isolates, even though final disease severity was high (Fig. 1A). Mean AUDPC was significantly less in plants inoculated with isolate ATCC 15399 than in the other pepper isolates (Table 1). The cucurbit isolates were also highly virulent on pepper (Fig 1B). There was a lag in disease onset in plants inoculated with the cucurbit isolate Acorn-1. This isolate caused significantly less disease on pepper between 6 and 13 days after inoculation than the other cucurbit isolates. Both final disease severity on pepper and the AUDPC were significantly less in plants inoculated with the Acorn-1 isolate compared with the other isolates tested (Table 1). The AUDPC for isolate B-1 was significantly greater than the AUDPCs for isolates Spag-1, But-1, and Acorn-1.

All isolates produced papillate sporangia that were ellipsoid to ovoid in shape. Mean length of sporangia among pepper isolates ranged from 38.9 to 60.1 $\mu$m (Fig. 2), and mean width of sporangia ranged from 27.6 to 40.5 $\mu$m. Mean length of sporangia among cucurbit isolates ranged from 55.6 to 62.8 $\mu$m (Fig. 2), and mean width of sporangia ranged from 34.2 to 38.8 $\mu$m. Mean lengths of sporangia among cucurbit isolates were greater than 55 $\mu$m and were significantly greater than all but seven of 17 pepper isolates. The overall mean length of sporangia among pepper isolates was 49.2 $\mu$m, compared with 59.2 $\mu$m among cucurbit isolates. LB ratios of sporangia ranged from 1.4 to 1.7 among pepper isolates and from 1.5 to 1.8 among cucurbit isolates (Fig. 3). Isolate Acorn-1 had the greatest LB ratio (1.8). The most frequent LB ratio among all isolates was 1.6 (37.5%).

All the isolates were caducous (produced sporangia that were deciduous in water). Mean pedicel length of sporangia was a highly variable character among isolates, ranging from 37.5 to 98.6 $\mu$m and from 31.5 to 85.3 $\mu$m among pepper and cucurbit isolates, respectively (Fig. 4). The shortest pedicel lengths were measured among cucurbit isolates.

All isolates tested were heterothallic and produced oospores when paired with known A1 or A2 mating types on CV8 agar. Homothallic oospores were not produced on CV8. However, several pepper (Sc 1B, Sc Ban, Pep 1-2) and cucurbit (Acorn-1, But-1, Patty-1) isolates and the ATCC isolate formed a few oospores in single culture under the inoculum disk on modified CV8 agar. Eleven pepper isolates were identified as A2 mating type, whereas 18 were identified as A1 mating type (Fig 5A). Isolates from a given pepper field were usually either A1 or A2 mating type; both mating types were isolated in only one field. The A2 mating type was found in only two of seven pepper fields



Fig. 1. Progression of Phytophthora root rot on bell pepper in inoculated plants in the greenhouse. **A,** Disease severity over time on pepper inoculated with pepper isolates. **B,** Disease severity over time on pepper inoculated with cucurbit isolates. Disease severity rated on a scale of 0–4, where 0 = no symptoms, 1 = wilting of plant without a stem lesion, 2 = wilting and stem lesion without girdling, 3 = girdled plant stem, 4 = dead plant.

TABLE 1. Mean areas under the disease progress curve (AUDPC) on pepper inoculated with *Phytophthora capsici* from pepper, cucurbits, or soil

| Isolate[y] | Host or source of origin | Mean[z] AUDPC |
|---|---|---|
| SD-6 | Soil | 38.9 a |
| Sc-2A | Pepper | 37.8 a |
| Pep 5-2 | Pepper | 36.1 ab |
| Pep 1-2 | Pepper | 35.9 ab |
| Pep 2-2 | Pepper | 35.6 ab |
| Pep 4-2 | Pepper | 35.4 ab |
| ATCC 15399 | Pepper | 29.2 c |
| Cuc-1 | Cucumber | 35.6 ab |
| B-1 | Squash | 38.3 a |
| Patty-1 | Pattypan squash | 35.4 ab |
| Spag-1 | Spaghetti squash | 33.6 b |
| But-1 | Butternut squash | 32.4 bc |
| Acorn-1 | Acorn squash | 12.1 d |

[y] Isolates were obtained by either soil dilution or isolation from infected tissue onto PARP medium (14).

[z] AUDPC was calculated as $\sum_{i=1}^{n-1}[y_i + y_{i+i})/2] (t_{i+1} - t_i)$ where $y_i$ = disease severity at the $i$th observation, $t_i$ = time at the $i$th observation, and $n$ = total number of assessment times. Means in a column followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$.

sampled. Both mating types were not isolated from a single pepper plant in any field sampled. A1 and A2 mating types were obtained in equal frequencies among the isolates from cucurbit fields (Fig. 5B). Isolates from two cucurbit fields contained only the A2 mating type. The A2 mating type was found in three of seven cucurbit fields sampled. Both mating types were found in only one of seven cucurbit fields sampled and were isolated from the same squash plant in one field.

Mean diameters of oogonia among pepper isolates ranged from 24.8 to 33.4 $\mu$m, whereas mean diameters of oogonia among cucurbit isolates ranged from 25.5 to 32 $\mu$m (data not shown). Antheridia were amphigynous in all isolates. Mean diameters of oospores among pepper isolates ranged from 23.7 to 34.9 $\mu$m, whereas mean diameters of oospores among cucurbit isolates ranged from 27.8 to 34.2 $\mu$m (Fig. 6). Sixty-three and 54% of the isolates had mean oogonial and mean oospore diameters, respectively, within the range of 25–30 $\mu$m. There were no clear groups based on oospore diameter between the pepper and cucurbit isolates. However, six of eight isolates classified as the A2 mating type had mean oospore diameters greater than 31 $\mu$m. None of the isolates produced chlamydospores in liquid culture.

All isolates grew on cornmeal agar at temperatures between 16 and 36 C, but the rate of growth differed among isolates at a given temperature (data not shown). Analysis of variance revealed a significant isolate $\times$ temperature interaction. Maximal radial growth of both the pepper and cucurbit isolates occurred at temperatures between 26 and 32 C. All isolates grew at temperatures above 32 C, with the exception of pepper isolate SC Ital, which did not grow at 36 C. Cucurbit isolate Spag-1 had higher rates of growth between 26 and 36 C than the other pepper and cucurbit isolates. Isolates Pep 2-2, Pep 4-2, Pep 5-2, and most of the cucurbit isolates had higher rates of growth at 16 and 36 C than other pepper isolates. Growth of isolates ATCC 15399 and PcW3A was less than most North Carolina isolates at 36 C.
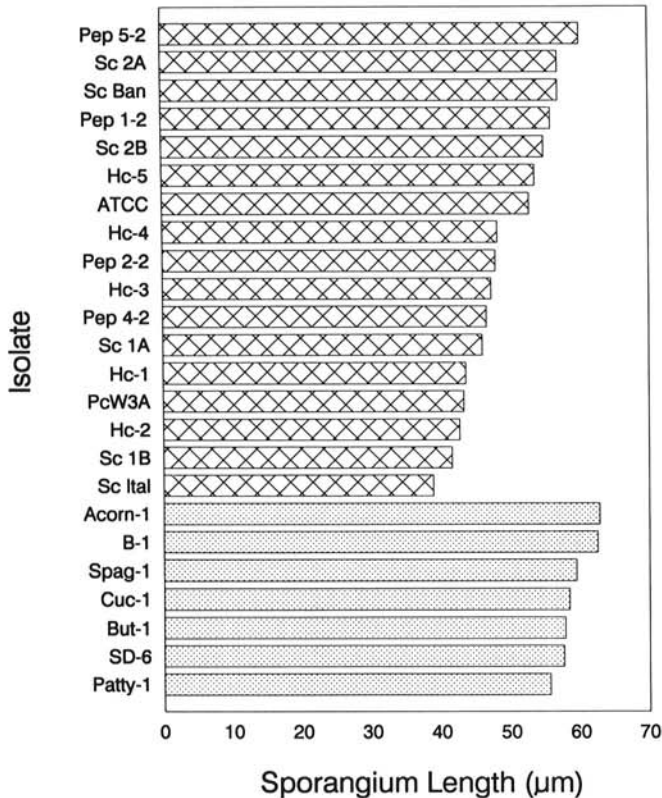
## DISCUSSION

Isolates of *P. capsici* from pepper and cucurbit hosts were highly virulent on pepper in repeated experiments. One pepper isolate (ATCC 15399) caused less disease early in disease progress, although the final severity of disease was high. Distinct pathogenic
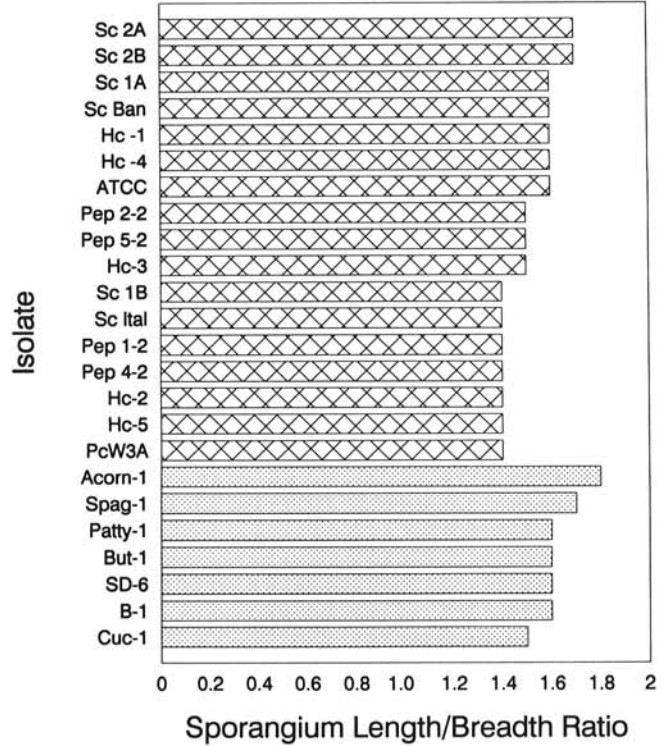
**Fig. 3.** Length-breadth ratios of sporangia of isolates of *Phytophthora capsici* from pepper (crosshatch) and cucurbit (dots) fields. LSD$_{.05}$ = 0.1 among and between pepper and cucurbit isolates.
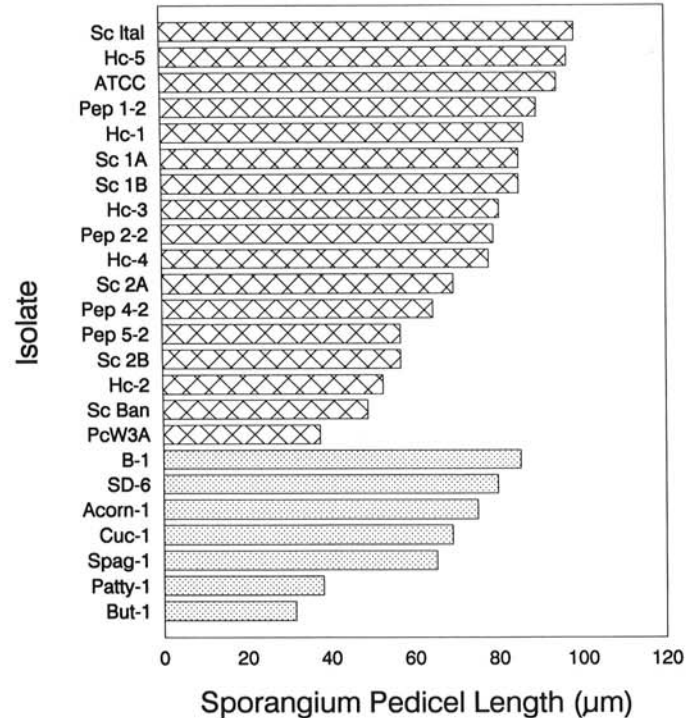
**Fig. 2.** Mean lengths of sporangia of isolates of *Phytophthora capsici* from pepper (crosshatch) and cucurbit (dots) fields. LSD$_{.05}$ = 3.9 among pepper isolates, LSD$_{.05}$ = 4.0 among cucurbit isolates, and LSD$_{.05}$ = 3.9 between pepper and cucurbit isolates.

**Fig. 4.** Pedicel lengths of sporangia of isolates of *Phytophthora capsici* from pepper (crosshatch) and cucurbit (dots) fields. LSD$_{.05}$ = 26.2 among pepper isolates, LSD$_{.05}$ = 20.2 among cucurbit isolates, and LSD$_{.05}$ = 24.6 between pepper and cucurbit isolates.

strains have been identified among diverse isolates of *P. capsici* from tomato, eggplant, squash, watermelon, pumpkin, and pepper (24). Specific pairings between isolates pathogenic to pepper have resulted in both pathogenic and nonpathogenic strains of the fungus (6,23). Therefore, specific pathogenicity to pepper is not a useful diagnostic criterion for identification of *P. capsici*. Others have demonstrated differences in virulence among pepper isolates of *P. capsici* on pepper genotypes with different levels of resistance (21,25). However, the pepper isolates from North Carolina fields did not differ markedly in virulence on the genotype of pepper examined in this study.

Disease severity among the cucurbit isolates differed early in disease progress, and one cucurbit isolate was less virulent than the other isolates tested on pepper. Cucurbit isolates of *P. capsici* are known to be pathogenic on pepper (17,24,29,35), but differences in virulence of cucurbit isolates on pepper has not been reported. Polach and Webster (24) demonstrated that pathogenicity of *P. capsici* to various hosts was controlled by a separate gene or gene system for each host. Differences in virulence on pepper occurred among cucurbit isolates of *P. capsici* in the study reported herein; however, most of the cucurbit isolates tested were highly virulent on pepper. Therefore, rotation from cucurbits to peppers in fields infested with *P. capsici* could result in severe disease.

There was considerable intraspecific variation in morphological characteristics among isolates of *P. capsici*. Sporangium lengths

among isolates of *P. capsici* have been described as variable by Waterhouse (34) and large (>75 $\mu$m) by others (20). Leonian's (19) original description of the species on pepper included sporangial sizes of 35–85 $\mu$m or even 105 × 21–56 $\mu$m, with an average of 60 × 36 $\mu$m. In our study of 24 isolates from pepper and cucurbits, only three isolates had sporangia with lengths greater than 60 $\mu$m. However, all of the cucurbit isolates produced sporangia with lengths greater than 55 $\mu$m under the conditions of these experiments, and sporangial lengths were less variable among cucurbit than among pepper isolates. This character, when used in combination with other morphological characters, may be useful for separating cucurbit isolates of *P. capsici* from pepper isolates.

The length of the pedicel or stalk on which sporangia are borne is considered to be a more stable morphological character of the sporangia of species of *Phytophthora* than the degree of caducity of sporangia (1,2). All isolates of *P. capsici* examined in this study produced caducous sporangia, with mean pedicel lengths ranging from 31 to 99 $\mu$m. Al-Hedaithy and Tsao (1) categorized species of *Phytophthora* based on short (<5 $\mu$m), medium (5–20 $\mu$m), and long (>20 $\mu$m) pedicels. Pedicels under 20 $\mu$m in length are described in the Newhook, et al (20) key for *P. capsici*. Others have reported pedicel lengths of 27–120 $\mu$m among pepper isolates of *P. capsici* (3,31). The isolates examined in the study reported herein produced pedicels greater than 20 $\mu$m in length and are similar to isolates of *P. capsici* (formerly *P. palmivora* MF4) reported on black pepper, cocoa, and macadamia (3,13,16,18,31). A revised species description for *P. capsici* has been published (31). The length of the pedicel on sporangia of *P. palmivora* has been considered a stable character for separation of morphological forms (1,8,13); however, in the study reported herein, pedicel length was not uniform but was the most highly variable character examined among isolates of *P. capsici* from pepper and cucurbits.

Isolates of *P. capsici* from macadamia and cocoa have deciduous, long-pedicellate sporangia with LB ratios of 1.7 or greater (16,18,31,32). Tsao's (31) recent description of *P. capsici* reports LB ratios of 1.14–2.19 among isolates from diverse hosts. Some isolates from both solanaceous and cucurbit hosts reported herein have these characters. However, none of the pepper and cucurbit
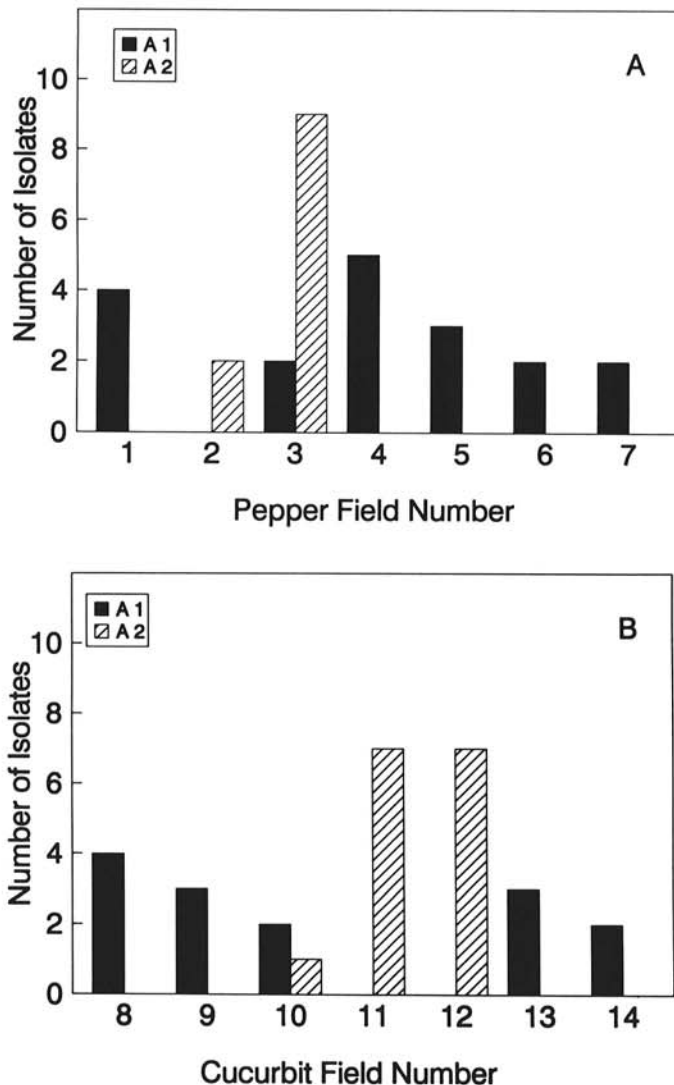


Fig. 5. Occurrence of isolates of *Phytophthora capsici* of either A1 (solid) or A2 (dots) mating type. **A**, Numbers of isolates of A1 or A2 mating type from fields of pepper. **B**, Numbers of isolates of A1 or A2 mating type from fields of cucurbits.
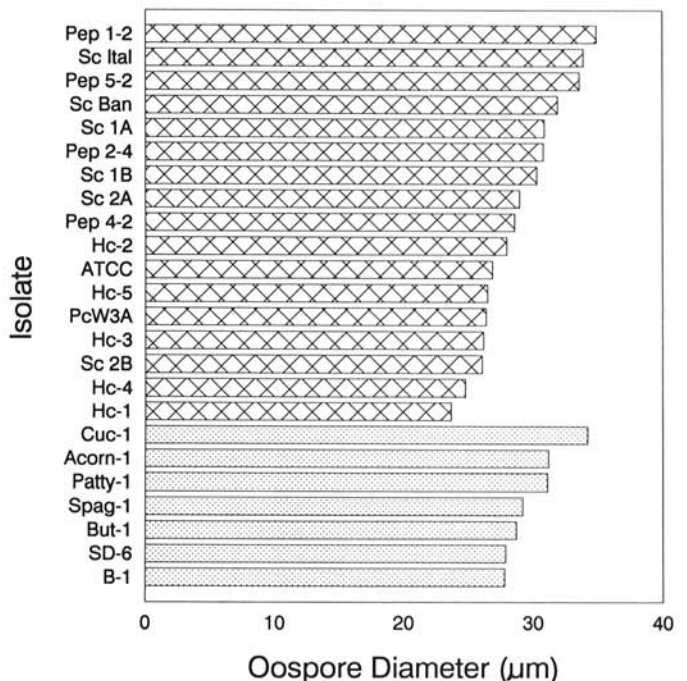


Fig. 6. Mean oospore diameters of isolates of *Phytophthora capsici* from pepper (crosshatch) and cucurbit (dots) fields. LSD$_{.05}$ = 1.7 among pepper isolates, LSD$_{.05}$ = 2.0 among cucurbit isolates, and LSD$_{.05}$ = 1.8 between pepper and cucurbit isolates.

isolates tested in this study produced chlamydospores in culture. Some isolates of *P. capsici* from macadamia produce chlamydospores and are not virulent on pepper (32,33). These characters apparently separate the macadamia isolates of *P. capsici* from the pepper and cucurbit isolates evaluated in this study.

The isolation of both A1 and A2 types from cucurbit and pepper fields in North Carolina and, in one instance, from a single squash plant, indicates that the opportunity exists for oospore formation in the field. Oospore formation in *P. capsici* can result from actual sexual recombination between opposite mating types or selfing (10). External stimuli can also induce oospore formation. The potential exists for the pathogen to overwinter as oospores in soil or plant debris in pepper and cucurbit fields and for genetic recombination to occur, because both mating types were found in some fields.

Oospores formed readily when compatible isolates of A1 and A2 types were paired in culture. Isolates producing oospores formed as a result of a pairing with A1 isolate PcW3A were considered A2 types. In six of eight isolates, large oospores (>31 μm in diameter) resulted from a pairing with isolate PcW3A. Others have reported variation in the size (8,27) and germinability (6,13) of oospores as a result of a particular pairing with an A1 or A2 type. Separation of different morphological forms or species of *Phytophthora* based on this character alone is questionable (8,13). Pepper and cucurbit isolates produced a few homothallic oospores in single culture on modified CV8 agar in this study. This phenomenon has been observed in culture with isolates of *P. capsici* from cocoa and other typically heterothallic species of *Phytophthora* (15,24,27).

Isolates of *P. capsici* have been characterized by growth at temperatures greater than 35 C (20). One isolate in this study did not grow at 36 C but conformed to the description of the species in all other respects. In addition, the ATCC culture and other pepper isolates grew slowly at 36 C. Apparently, growth at temperatures greater than 35 C is not a definitive character for identification of *P. capsici*, as noted by Tsao (31) in the latest revision of the the species.

In addition to classical taxonomic approaches, protein electrophoresis, repetitive DNA polymorphism analysis, and DNA probes have been used by others as tools for identification of *Phytophthora* spp. (5,9,11,22). Three isolates of *P. capsici* from tomato, melon, and pepper were classified into one group by restriction fragment length polymorphism (RFLP) analysis (22). The molecular approaches to identification of species of *Phytophthora* could provide the most use in rapid identification of isolates from hosts that are commonly infected by multiple species or from isolates from soils (5,11). In some studies, the grouping of isolates of *Phytophthora* spp. by either protein electrophoresis or RFLP analysis has led researchers to the same delimitation of species as classical taxonomic approaches (5,22). However, a recent study of mitochondrial DNA within several isolates of *P. capsici* indicated that the overall diversity of mitochondrial DNA was high, and that no distinct subgroups could be found based on host (9). Clearly, both molecular and classical taxonomic approaches will continue to provide valuable information on the taxonomy of the genus.

The morphological characters examined in this study, including sporangial size, pedicel length, and oospore diameter, showed continuous rather than discrete variation within populations based on host of origin. It is important to examine a range of characters from a population of naturally occurring isolates when addressing taxonomic questions in the genus *Phytophthora*, since considerable variation can occur among isolates of a given species (8). All the isolates examined in this study were pathogenic on pepper and identified as *P. capsici*. Future studies that combine molecular and classical taxonomic approaches may enable a more clear separation of isolates of *P. capsici* from solanaceous, cucurbit, and other hosts.

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