Phytophthora capsici was first described by Leon H. Leonian at the New Mexico Agricultural Research station in Las Cruces in 1922 (65). In his report, he described a novel species of Phytophthora that caused considerable damage to chili pepper plants in the fall of 1918. A year later, the disease reappeared at the same site and also affected surrounding farms. During the late 1930s and early 1940s, recurrent problems with P. capsici in the Arkansas River Valley of Colorado were described on several vegetable hosts (51–55, 103). The first reported occurrence of P. capsici on a cucurbit crop occurred in 1937, when a 3.2-ha field of cucumbers became diseased resulting in 100% of the fruit rotting (51). By 1940, P. capsici had also been described on eggplant, honeydew melon fruit, summer squash, and tomato fruit (52, 103). The disease on tomatoes was reportedly so severe that the viability of the processing tomato industry in the region was threatened.

These early reports mirror the situation throughout the eastern United States, where large-scale production of several vegetables has been lost to disease. Individuals producers have experienced devastating losses. When a farm in southern Michigan was unable to harvest 121.4 ha of diseased pickling cucumbers, an estimated $300,000 was lost, along with a $40,000 loss on approximately 40.5 ha of processing tomatoes. Due to the impact of P. capsici on this farm’s ability to meet contractual obligations for cucumbers, production of this crop was discontinued (57). While ranked nationally as the number one producer and processor of cucumbers for pickling, Michigan also is a major midwestern supplier of several vegetables for fresh consumption and for processing (49). In the north-central region of the United States, P. capsici also is a reported problem on cucumber in Wisconsin (95, 96), on pumpkin in Illinois (5), and on pepper and cucurbit crops in Ohio (72). The occurrence of P. capsici throughout many vegetable growing regions in the United States has prompted recent research in Virginia (100), New York (70), Florida (69), Arizona (68), North Carolina (66), and Georgia (91).

P. capsici affects a wide range of solanaceous and cucurbit hosts worldwide (17, 27, 43). In 1967, Satour and Butler (87) reported that 45 species of cultivated plants and weeds, representing 14 families of flowering plants, were susceptible to P. capsici. They found 19 species in 8 families that were highly susceptible, with the roots and crowns completely rotted 7 to 10 days after inoculation. This was the widest host range study conducted to date. Beans, lima beans, and soybeans were reported (87) to be “immune” to P. capsici infection under greenhouse conditions highly favorable to infection. It is significant, therefore, that in the summers of 2000 and 2001, P. capsici was isolated from five commercial cultivars of lima bean in Delaware, Maryland, and New Jersey (21). Also, P. capsici has recently been isolated from commercial snap bean fields in northern Michigan, adding this crop to the long list of susceptible crops (35). These snap bean fields had a history of zucchini cropping and P. capsici infestation. All isolates from snap bean were pathogenic to cucumber fruit, and select isolates were pathogenic to soybean plants under laboratory conditions (36).

Disease caused by P. capsici may initially occur in the low areas of a field where water accumulates. Growers often assume that stunting or death of plants in such areas is due to the “waterlogging” of the roots, but infection by P. capsici may be to blame. Under warm (25 to 30°C),

### Host Range and Disease Symptoms

In Michigan, there are 32,356 ha of vegetables (currently valued at approximately $134 million) that are highly susceptible to crown, root, and fruit rot caused by P. capsici (Table 1). It is estimated that when weather favors P. capsici, up to 25% of the state’s value of these vulnerable vegetables has been lost to disease. Individual producers have experienced devastating losses. When a farm in southern Michigan was unable to harvest 121.4 ha of diseased pickling cucumbers, an estimated $300,000 was lost, along with a $40,000 loss on approximately 40.5 ha of processing tomatoes. Due to the impact of P. capsici on this farm’s ability to meet contractual obligations for cucumbers, production of this crop was discontinued (57). While ranked nationally as the number one producer and processor of cucumbers for pickling, Michigan also is a major midwestern supplier of several vegetables for fresh consumption and for processing (49). In the north-central region of the United States, P. capsici also is a reported problem on cucumber in Wisconsin (95, 96), on pumpkin in Illinois (5), and on pepper and cucurbit crops in Ohio (72). The occurrence of P. capsici throughout many vegetable growing regions in the United States has prompted recent research in Virginia (100), New York (70), Florida (69), Arizona (68), North Carolina (66), and Georgia (91).

P. capsici affects a wide range of solanaceous and cucurbit hosts worldwide (17, 27, 43). In 1967, Satour and Butler (87)

<table>
<thead>
<tr>
<th>Cucurbitaceae</th>
<th>Solanaceae</th>
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<tr>
<td>Cantaloupe</td>
<td>Bell pepper</td>
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<td>Cucumber</td>
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<td>Winter squash</td>
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wet conditions, root and crown infection of pepper, zucchini, squash, and pumpkin typically causes permanent wilt and plant death (Fig. 1D–F,L). Plants often have brown to black discolored roots and/or crowns. In contrast, infected cucumber and tomato plants may be relatively asymptomatic or exhibit limited root rot and plant stunting (Fig. 1A,B,M,N). However, when a rainstorm splashed *P. capsici*-infested soil onto the cotyledons of emerging cucumbers, the entire 24.3-ha planting was killed. Similarly, extremely rainy weather that saturates soil for extended periods can prompt a severe root and crown rot that kills even established tomato plants. Disease symptoms on snap beans include water-soaking on the leaves, stem necrosis (Fig. 1O), and overall decline. Disease symptoms were most severe on bean plants located along the surface water drainage pattern. *P. capsici* was recovered from crown, stem, and leaf tissue (35).

While plant death is always a concern for vegetable producers, fruit rot seems to be especially insidious on cucurbits. In general, infected cucurbit fruit initially exhibit dark, water-soaked lesions (Fig. 1C,J), followed by a distinctive white “powdered-sugar” layer of spores on the surface. Disease symptoms include dark, water-soaked lesions on the leaves and stem necrosis. *P. capsici* was recovered from crown, stem, and leaf tissue (35).

Fig. 1. Symptoms of disease caused by *Phytophthora capsici* on: A to C, cucumber; D and E, yellow squash; F, hard squash; G, zucchini; H, immature pumpkin; I, spaghetti squash; J, bell pepper; K and L, banana pepper; M and N, tomato; and O, snap bean.
surface of the fruit 2 to 3 days later (Fig. 1A,G,H). While *P. capsici* regularly causes a blight of pepper fruit in other growing regions (84), this is not a common occurrence in Michigan and has been observed only occasionally in the last several years (Fig. 1J,K). Cucumber plants appear to tolerate root infection by *P. capsici*, yet the fruit are especially susceptible. In Michigan, fields of healthy-appearing cucumber vines with mature fruit have been abandoned in the field at harvest, or semi-truck loads of fruit rejected at the processing facility, due to rot. In our studies, we routinely observe a delay of at least 48 hours in symptom expression in cucumber following successful penetration by *P. capsici* (K. H. Lamour and M. K. Hausbeck, unpublished results). A similar 3- to 6-day lag prior to symptom expression for *P. capsici* infecting peppers has been described previously by Schlub (89). This delay explains why producers in Michigan who harvest seemingly healthy fruit have had entire loads rejected; fruit become infected while in the field but the disease progresses during storage and transit, with symptoms and/or signs becoming evident after delivery to the processor or retailer. The increased temperatures during harvest, storage, and transit may be an important factor.

### The Pathogen

Early investigators recognized that the genus *Phytophthora* exhibited striking dissimilarities to many other fungal organisms, but a full resolution of its taxonomic and evolutionary standing would not be made until DNA sequence analysis was completed by Forster et al. in 1990. They found that oomycetes are more closely related to heterokont photosynthetic algae than to members of the kingdom Fungi (29). The modern description of *P. capsici* as a species falls into Waterhouse’s Group II (101) and is characterized by sporangia that are conspicuously papillate with amphigynous oospores generally forming only when A1 and A2 mating types are paired. Information concerning the different spore types produced by members of the genus *Phytophthora* accumulated slowly between 1940 and 1970. In 1970, Waterhouse (101) provided a useful, and still used, key for identifying isolates to species based on the morphology of sporangia and oospores and whether or not an isolate could produce oospores in single culture. Research with other *Phytophthora* species established much of what is known about the three dominant spore types produced by *P. capsici* (27). The thallus is composed of coenocytic mycelium which may give rise to lemon-shaped sporangia borne on long caducous pedicels (1). When sporangia are immersed in free water, they differentiate to produce 20 to 40 bi-motile swimming zoospores (Fig. 2) (8). Long-term survival outside of host tissue is accomplished by the oospore (2,3,10,42,58–60), which has a thick, multilayered wall containing β-glucan and cellulose (27). Oospores require a dormancy period of at least a month (27,88) before germinating directly or by forming sporangia (Fig. 2).

### Sexual Reproduction and Oospores

Approximately half of the 60 recognized species in the genus *Phytophthora* are homothallic (self-fertile), and for these species, a single isolate is able to complete the sexual stage and form oospores (27). The remaining species, including *P. capsici*, are heterothallic and require two compatibility types (=mating types), designated A1 and A2, to complete the sexual stage (27). Oospores are formed when A1 and A2 compatibility types come into close association (Fig. 2) (50). Each of the parent isolates makes both male (antheridium) and female (oogonium) gametangia once

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**Fig. 2.** Disease cycle of *Phytophthora capsici* on cucumber. A, Dormant oospores germinate during wet conditions to produce lemon-shaped sporangia, which may germinate directly or release swimming zoospores. Sporangia are produced on the roots, crowns, and fruit of infected plants. B, In a cucumber field, sporangia and zoospores are disseminated by rain, irrigation, and drainage water, which can saturate soils and contribute to multiple cycles of inoculum that drive the disease during a single growing season. C, Oospores are formed when A1 and A2 compatibility types come into close proximity; oospores are able to survive for years in the soil.
the sexual stage has been initiated, and self-fertilization is possible in obligate outcrossing species (50).

To our knowledge, *P. capsici* is the only heterothallic *Phytophthora* species that has been shown to regularly complete the sexual stage (outcross) in the United States (37,56,58–62). The A1 and A2 mating types both occur within natural field populations of *P. capsici*. The presence of A1 and A2 isolates of *P. capsici* in single fields was reported in New Jersey in 1981 (76) and in North Carolina in 1990 (81). Both mating types have been recovered from farms surveyed in other states when at least 15 isolates were collected from diverse locations within a field (Table 2). During 1997 and 1998, 14 Michigan farms were sampled, with 473 isolates recovered from cucurbit hosts and 30 from bell pepper (58). The A1 and A2 compatibility types were recovered in roughly a 1:1 ratio for eight farms. In 2001, we collected isolates of *P. capsici* from fields in New York, Connecticut, Pennsylvania, Ohio, North Carolina, and California; similar trends were revealed. When 429 isolates from these states were screened for mating type, 53% (227) were A1 and 47% (202) were A2 mating types. Both mating types were recovered from every location, and the A1/A2 ratio was close to 1:1 within locations (Table 2).

To determine if both mating types are present in a field, the timing and spatial scale of sampling are important. Multiple cycles of infection and spore production allow *P. capsici* to spread rapidly throughout fields during warm, wet weather, and samples collected from a few plants at the height of an epidemic may erroneously suggest that only a single mating type is present (76,82). Samples collected every 2 weeks over a 3-month period from a single field of squash in Michigan illustrated how the percentage of unique genotypes fell from 100% at the beginning of the epidemic to less than 30% by the end of the growing season (39).

Papavizas et al. (76) provided the first report of naturally occurring *P. capsici* oospores in diseased host tissue in North America. In Michigan, amphigynous oospores typical of *P. capsici* have been found in infected pumpkin, cucumber (Fig. 3C), and butternut squash fruit and in the stems of *P. capsici*-infected yellow squash seedlings. Interestingly, fungal gnat larvae (*Sciaridae*) feeding on pumpkin fruit infected with *P. capsici* had numerous oospores in the digestive tracts of three specimens (Fig. 3A,B). No attempt to determine the viability of the excreted oospores was made, but a study conducted with oospores of *Pythium* spp. and fungal gnat larvae indicates that oospores remain viable and suggests that the gnat’s larval stage may serve as a vector (33).

Although oospores have been considered the primary source of inoculum in the field, little is known about the influence of soil physical factors on infection of host crops in oospore-infested soils. In vitro treatment with chemicals and physical factors that may interact with oospores in the soil can provide information on germination and viability (44,48). Although information about oospore germination in situ is limited and reportedly difficult to observe and definitively assay (44,64), it is important to monitor oospore germination in a simulated, complex soil setting (76). Oospore survival has been successfully studied in situ with *P. infestans* (23). Thus, an important precedent for research on *P. capsici* is in place.

The main impediment to detailed studies of oospores and the inherent genetics therein was primarily the difficulty in separating and germinating oospores (65,92). In 1968, Satour and Butler provided crucial information concerning the generation and germination of *P. capsici* oospores (88). They reported that relatively young oospores produced in paired cultures of *P. capsici* germinated to produce recombinant progeny after 30 days incubation. Prior to this, it was generally thought that 6- to 9-month incubation periods were necessary for oospore germination. The progeny from their crosses were shown to differ from the parental types in both morphology and pathogenicity. For example, one progeny isolate exhibited increased virulence on pepper compared with either of the parents, which suggests that sexual reproduction could lead to increased virulence in the field. A number of important milestones were reached in this investigation. A simple method for the production, germination, and harvesting of oospore progeny for *P. capsici* was formally presented, and the authors convincingly argued that proper media containing ample nutrients as well as genetically compatible parent isolates are required for successful crosses. In addition, this work provided convincing evidence for the potential role of oospores in generating genetic variation (88). In 1971, Polach and Webster (80) corroborated this finding using the oospore incubation and germination techniques of Satour and Butler (88). Polach and Webster (80) investigated 391 single oospore

### Table 2. Phenotypic diversity of *Phytophthora capsici* isolates recovered from cucurbit and solanaceous hosts at diverse locations in the United States during 2001

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<tr>
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<td>9</td>
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<tr>
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<td>1</td>
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<td>11</td>
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<td>0</td>
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<tr>
<td>New York (upstate)</td>
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<td>10</td>
<td>9</td>
<td>2</td>
<td>10</td>
<td>11</td>
<td>2</td>
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<tr>
<td>New York (Long Island)</td>
<td>95</td>
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<td>1</td>
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<td>47</td>
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<tr>
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<td>1</td>
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<td>0</td>
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<tr>
<td>North Carolina 2</td>
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<td>53</td>
<td>4</td>
<td>0</td>
<td>25</td>
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<tr>
<td>North Carolina 3</td>
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<td>6</td>
<td>26</td>
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<tr>
<td>North Carolina 4</td>
<td>27</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>9</td>
<td>3</td>
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<tr>
<td>Total</td>
<td>429</td>
<td>164</td>
<td>31</td>
<td>32</td>
<td>137</td>
<td>44</td>
<td>21</td>
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a Isolates originated from single fields within a state except for New York and North Carolina, which had 2 and 4 fields sampled, respectively.

b Mefenoxam sensitivity determined by in vitro screening on 100 ppm AI amended media, with S (sensitive) = <30% growth of control (GC), IS (intermediately sensitive) = between 30 and 90% GC, and I (insensitive) = >90% GC.
progeny from four mating reactions and reported that the parent isolates differed in their pathogenicity to cucurbit and solanaceous hosts and that segregation and recombination were observed for all the characters studied.

Role of Sporangia and Zoospores in Field Epidemics

Like many species in the genus *Phytophthora*, *P. capsici* has the potential for rapid polycyclic disease development from a limited amount of inoculum (82). The asexual sporangia and zoospores proved to be much easier to manipulate and study than the oospore, and it is not surprising that the salient features of these spore types were outlined relatively early (40,73). *P. capsici* grows optimally between 25 and 28°C and can produce copious amounts of deciduous sporangia on the surface of infected tissue (1,17,99,102). When cucumber fruit were inoculated and incubated at 60, 80, and 98% relative humidity (RH) for 5 days, more sporangia were produced at 60 and 80% RH than at >90% RH (Fig. 4) (K. H. Lamour and M. K. Hausbeck, unpublished results). Mature sporangia are easily dislodged by rain and irrigation and can directly germinate or, when immersed in water, release 20 to 40 motile zoospores (40) that travel with water in fields (89). Zoospores exhibit negative geotropism and chemotactically follow nutrient gradients while swimming (27). Once zoospores contact the plant surface, they encyst and germinate to produce germ tubes (40). Scanning electron microscopy illustrates that zoospores are able to directly penetrate the intact cuticle within an hour (K. H. Lamour and M. K. Hausbeck, unpublished data). Penetration of leaf surfaces by *P. capsici* occurs directly and through natural openings such as stomata (47). *P. capsici* produces an extra-cellular macerating enzyme that likely plays a significant role in breaching the host epidermis and ramifying through susceptible host tissue (104).

In general, sporangia and zoospores are thought to be relatively ephemeral structures contributing to the spread of *P. capsici* within a single growing season but unlikely to survive the harsh conditions typical of nonhost periods in North America (2,3,11,58,59,61,62). Results from investigations with *P. capsici* in Michigan suggest that overwintering of clonal inoculum is rare but that reproduction of clonal populations within a single season is significant (58). Tracking a single population of *P. capsici* over the course of the growing season in 1999 using molecular markers indicated that asexual spread increased dramatically as the season progressed and that a single clone accounted for approximately 50% of the isolates recovered in the final one-third of the growing season (59).

Thus, the infection and subsequent sporulation on host tissue and fruit likely play a key role in driving the polycyclic phase of disease development in the field. The number of sporangia on a single naturally infected spaghetti squash fruit was estimated to be 44 million with the potential to release 840 million zoospores (K. H. Lamour and M. K. Hausbeck, unpublished results).

In addition to the epidemiological advantage provided by a large aboveground reservoir of inoculum, there may be an additional evolutionary advantage conferred by the large number of hyaline sporangia exposed to UV irradiation on the surface of infected fruit. Fungicide insensitivity was easily induced in *P. capsici* using UV irradiation (14), and it seems reasonable that the thousands of sporangia present on an infected cucurbit fruit represent a significant substrate for the effects of UV-mediated mutation. Dekker (22) suggests that the UV-sensitive pathogen population will occur faster in a heavily sporulating population on aerial plant parts than in a slowly spreading, soilborne pathogen, and cites as an example that the buildup of metalaxyl resistance in the aerially sporulating *P. infestans* was much faster than occurred with *P. cinamomi* causing avocado root disease.

Sexual Reproduction and Adaptation to PAFs

Historically, growers have relied on a limited number of fungicides for control of *Phytophthora* root, crown, and fruit rot. The phenylamide class of fungicides (PAF), specifically metalaxyl and the newest fungicide mefenoxam (Ridomil Gold EC), has been used by many growers to combat *P. capsici*. Mefenoxam is the active enantiomer contained in the racemic fungicide metalaxyl (77,78). Both compounds are strongly fungidal to sensitive isolates (20,75), and isolates recovered from farms without a history of PAF use are highly sensitive to both mefenoxam and metalaxyl (58,78).

Metalaxyl has been shown to specifically inhibit the incorporation of uridine into RNA in sensitive oomycetes (20). The mode of action of metalaxyl is postulated to be site specific, and it was not surprising when resistance surfaced in populations of susceptible plant pathogens after PAFs were introduced during the late 1970s (20). As early as 1981, researchers working with *P. capsici* demonstrated that insensitivity to metalaxyl was readily selected for by using sublethally amended media (12,13). Insensitivity soon developed in natural populations of oomycetous organisms where metalaxyl was heavily relied upon (18,34,46). Adaptation to PAFs is common throughout the oomycetes (19,34) and is generally accepted as inevitable due to the specificity of this group of fungicides (20). Studies characterizing the inheritance of mefenoxam insensitivity in *P. capsici* suggest that insensitivity is conferred by a single incompletely dominant locus (58).

Recovering insensitive *P. capsici* isolates from farms with a history of PAF use is increasingly common in the United States. Data from North Carolina, Michigan, and New Jersey indicate that a significant proportion of *P. capsici* populations under PAF selection pressure may be intermediate or fully insensitive to mefenoxam (28,58,77,78). Insensitivity to mefenoxam, which also conferred insensitivity to metalaxyl, was reported from field populations of *P. capsici* on bell pepper (77). The inheritance of mefenoxam sensitivity was assessed in naturally occurring populations of *P. capsici* in Michigan. In Michigan, greater than half (55%) of the 498 isolates sampled were sensitive, 32% were intermediate, and 13% were fully insensitive to mefenoxam (58). Three farms, two in North Carolina and one in New York, had a history of mefenoxam use, and insensitive isolates were recovered from each (Table 2). Overall, 70% (301) of the isolates were fully sensitive, 17% (75) were intermediate sensitive, and 13% (53) were insensitive to mefenoxam. The majority (40%) of the fully insensitive isolates were recovered from a single bell pepper field in North Carolina with a history of mefenoxam use. In North Carolina, the process of adaptation to mefenoxam appears to have occurred rapidly (78).

Because only sensitive isolates of *P. capsici* are controlled by the mefenoxam fungicide (63), the observed control failure in some Michigan fields during the last few years is likely due to the development and increasing incidence of *P. capsici* isolates insensitive to this fungicide. Sexual recombination appears to play an important role in adaptation by generating fully insensitive isolates (e.g., mating between intermediate sensitive isolates) (Fig. 5). A Michigan population of *P. capsici* comprised of intermediate and fully insensitive isolates tracked for 3 years (1999 to 2001) in the absence of PAF use showed no evi-
dence of reversion back to the wild-type, PAF-sensitive, state (62).

Effective fungicides that act on a single enzyme or molecular pathway exert significant selection pressure favoring isolates able to withstand the activity of the fungicide. In the case of mefenoxam, there appears to be a low level of isolates harboring a mutation responsible for insensitivity to mefenoxam. Application of mefenoxam favors these isolates, and sexual reproduction results in numerous genetically unique progeny carrying what was previously a rare trait. Because of sexual reproduction, the process of incorporating a novel advantageous trait into numerous genetic backgrounds makes it less likely that insensitive isolates will be less fit than their fungicide-sensitive wild-type counterparts. It is reasonable to suspect that sexual recombination may play a similar role in the adaptation of P. capsici to other fungicidal compounds whether they are applied manually or generated by resistant varieties of plants.

Genetic Diversity

Significant molecular investigations into the genetics of P. capsici do not appear in the literature until the late 1980s and early 1990s, when isozyme and restriction fragment length polymorphism (RFLP) analysis of both mitochondrial and nuclear DNA were conducted on isolates from widely different geographical locations, years, and hosts located in a worldwide Phytophthora culture collection at the University of California at Riverside (30,71,74). Results from an isozyme study involving 113 P. capsici isolates were interpreted as revealing two subgroups within the P. capsici species (71). Subgroups are defined as being significantly different based on sporangial morphology and ontogeny. RFLP investigation of mitochondrial DNA revealed no patterns of similarity based on host or geographical location (30). RFLP analysis of nuclear DNA using low copy number probes of 15 P. capsici isolates indicated nuclear DNA diversity was high (30). These early studies highlighted the diversity of P. capsici on a worldwide scale. In the United States, this genetic diversity has been exploited to better understand how natural populations of P. capsici are distributed in space and time.

Almost 15 years ago, J. B. Ristaino (81) showed that morphological characters varied widely in natural populations and that variation in pathogenicity among solanaceous and cucurbit hosts existed in field populations. This work corroborated earlier laboratory studies showing that pathogenicity and virulence to tomato and pepper segregate during sexual recombination and that sex can generate strains more virulent than either parent (88). Mating type and sensitivity to mefenoxam provide a limited level of resolution, and choosing among the many techniques available for measuring variation at the DNA level can be difficult due to the advantages and limitations inherent in each. Because P. capsici has the potential for significant polycyclic reproduction, one of our primary goals was to differentiate uniparental (clonal) lineages. This is an important consideration to accurately determine how far P. capsici is dispersed and if clonal lineages are able to survive outside of hosts. The amplified fragment length polymorphism (AFLP) technique is useful for this type of differentiation because it allows numerous markers to be resolved simultaneously and provides a robust sample across individual genomes. The AFLP technique results in the selective amplification of restriction fragments from a digest of total genomic DNA using the polymerase chain reaction (PCR). The DNA fragments, called AFLP markers, are resolved using a polyacrylamide gel or, if the PCR primers are labeled with a fluorescent dye, a DNA sequencing machine. An example of AFLP analysis by automated DNA sequencing is shown in Figure 6. The advantages to this technique are its reproducibility and sensitivity (e.g., between 50 and 70 AFLP markers are resolved per reaction per isolate) (9). Characterization of 107 oospore progeny from a laboratory cross between parents with differing AFLP genotypes indicated that the progeny were all recombinant and that the AFLP markers segregated as Mendelian characters (59).

A key expectation when studying outcrossing populations is the recovery of unique combinations of phenotypic and molecular characters. If outcrossing is occurring in natural populations of P. capsici, then multiple combinations of mating type, mefenoxam sensitivity, and AFLP markers should be present (Tables 2 and 3) (98). In Michigan, 70% (454) of the 646 isolates analyzed had unique AFLP profiles. In total, 94 AFLP markers were resolved but no single population had all 94 markers. Individual populations had between 68 and 80 AFLP markers, and isolates were clearly more similar based on geographic locations (60). The high number of unique AFLP profiles and high proportion of polymorphic markers suggests that populations residing at all monitored locations are sexually active (Table 3). Studies of individual populations over multiple years indicated that the pools of genetic diversity remained stable and that outcrossing among locations was limited (60–62). As expected for an organism with the potential for significant polycyclic disease development, clonal lineages were detected and were shown to play an important role in epidemic development (59–61).

Management Strategies and Challenges

As P. capsici has spread to more acreage devoted to vegetables, producing vulnerable crops has become a significant, and
for some producers, an overwhelming challenge. The future of the vegetable industry in Michigan and other regions of the United States plagued by *P. capsici* is at risk without long-term sustainable approaches such as genetic resistance and remediation of infested sites. In the short term, the economic risk of growing *P. capsici*-susceptible crops may be reduced by using several management tools. Ristaino and Johnston (84) previously provided a summary of management of this disease in bell pepper.

**Crop rotation.** While crop rotation is an important foundation of disease management, the long-term survival of oospores in absence of a host limits the effectiveness of this strategy as a stand-alone tool. The survivability of oospores has been clearly demonstrated with a number of *Phytophthora* spp., including *P. capsici* (3,11). Growers practicing even lengthy rotations (>5 years) to nonsusceptible hosts may be reduced by using several management tools. Ristaino and Johnston (84) previously provided a summary of management of this disease in bell pepper.

**Exclusion.** In Michigan, it does not appear that *P. capsici* is dispersed over long distances, and excluding the pathogen from noninfested growing areas is emphasized to producers during extension programs and farm visits. Increased attention to the routes by which *P. capsici* may be introduced is warranted. Movement of other *Phytophthora* spp. via irrigation water has been documented (27), and aboveground water sources may play a role in the long-distance movement of *P. capsici*. Runoff water from infested fields can transport the pathogen from diseased

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**Table 3. Genetic diversity of *Phytophthora capsici* isolates recovered from locations in the United States**

<table>
<thead>
<tr>
<th>Location</th>
<th>Isolates analyzed</th>
<th>Unique isolates</th>
<th>AFLP markers resolved</th>
<th>Polymorphic markers (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Connecticut</td>
<td>12</td>
<td>10</td>
<td>78</td>
<td>40 (51)</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>15</td>
<td>11</td>
<td>90</td>
<td>51 (57)</td>
</tr>
<tr>
<td>California</td>
<td>20</td>
<td>11</td>
<td>81</td>
<td>42 (52)</td>
</tr>
<tr>
<td>Ohio</td>
<td>15</td>
<td>12</td>
<td>86</td>
<td>45 (52)</td>
</tr>
<tr>
<td>New York (upstate)</td>
<td>12</td>
<td>10</td>
<td>86</td>
<td>50 (58)</td>
</tr>
<tr>
<td>New York (Long Island)</td>
<td>42</td>
<td>37</td>
<td>90</td>
<td>58 (64)</td>
</tr>
<tr>
<td>North Carolina</td>
<td>57</td>
<td>52</td>
<td>88</td>
<td>49 (56)</td>
</tr>
</tbody>
</table>

* All isolates have unique multilocus amplified fragment length polymorphism (AFLP) profiles.
plants to nearby water sources used for irrigation. We began testing aboveground water sources in Michigan for contamination with *P. capsici* during 2001 and recovered the pathogen from irrigation ponds on two farms (K. H. Lamour and M. K. Hausbeck, unpublished data). Additional irrigation water sources were monitored for *P. capsici* in 2002 and 2003, and the pathogen was frequently detected in a river, creek, and a naturally fed pond (35,36). All of these water sources were located near crops infected with *P. capsici*. Prior to this research, the presence of *P. capsici* in Michigan irrigation sources had not been reported. Another potential source of *P. capsici*–contaminated water may be from vegetable processing facilities that apply their waste water to nearby vegetable production sites. Using water that may be contaminated with *P. capsici* to irrigate healthy crops must be avoided to limit pathogen spread.

Identifying factors contributing to the spread of *P. capsici* to new locations can be challenging. Producers are warned against dumping *P. capsici*–infected produce on or near their farms. However, a survey of cultural practices in Michigan indicated that in some cases producers were spreading over- and under-size cull and diseased fruit onto fields after returning from processing stations. Historically, some processors mandated that producers haul culls and diseased fruit from the processing station for disposal in their fields even if the fruit were from other farms. A single fruit infected with both A1 and A2 mating types may contain thousands of genetically unique oospores that can establish a resident population of *P. capsici* in a field while history of *P. capsici* problems. Once *P. capsici* is established in a field, tillage and cultivation distribute diseased plant material and spread oospores throughout the field and soil profile. It is possible that *P. capsici* may be disseminated to new fields via equipment even when no remnants of diseased plant material are visible.

**Cultural control.** Commonly recommended cultural control strategies reflect our understanding of the importance of water in the epidemiology of *P. capsici* and include planting into well-drained fields and into raised beds whenever possible (84). Excess moisture is the single most important component to the initial infection and subsequent spread of *P. capsici* (10,11,82,83,85,89,94). Similar findings exist for many species in the genus *Phytophthora* and are not surprising in light of these organisms’ evolutionary ties to the algae (25,26).

Since water plays a key role in disease development (82,89), water is managed based on the crop and the water dynamics of the region. A significant problem in the eastern United States is that heavy rainstorms typically occur and provide a strong, uncontrollable force for driving disease development. In growing areas where rainfall is prevalent, growers are encouraged to choose well-drained sites and plant into raised beds and/or mowed cover crops (84,86). However, plants growing in well-drained fields on raised beds may become diseased if the rainfall is heavy (≥2.5 cm), because even a well-drained field may hold standing water long enough for zoospores to be released. Draining rain likely assists in disseminating sporangia. Strategies to limit splash dispersal such as planting into mowed cover crops and trellising of cucurbits appear promising as the fruit are kept off the ground and out of standing water (86).

Unfortunately, trellising may not be an option for large cucurbit fruit such as pumpkins. In Michigan, the dependence of many large-acreage cucumber and winter squash producers on mechanical harvesters limits the range of cultural modifications available.

In many areas of the southwestern United States, *P. capsici* has plagued vegetable growers since being described more than 80 years ago. Although water-poor farmers may not see it as such, a major advantage in these arid areas is low annual rainfall. Growers can control the amount and frequency of irrigation and thus can significantly impact the severity of disease in fields known to harbor *P. capsici* (15,16). For example, in California where rainfall is low, placing drip emitters away from the stems of pepper plants can reduce incidence of *Phytophthora* crown rot of peppers (15). Café-Filho et al. (16) showed that the incidence of root and fruit rot of squash caused by *P. capsici* in California increased with increased frequency of irrigation. They recorded almost total crop loss with an irrigation frequency of 7 days, compared with almost no disease when the field was furrow irrigated every 21 days. In the absence of the disease, irrigation intervals of 21 days did not negatively affect fruit yield compared with more frequent irrigations (16).

Similar observations were reported for *Phytophthora* root and crown rot of bell peppers in North Carolina, where disease incidence increased with increased frequency of drip irrigation (82,83). Heavy rainfall (>2.0 cm) was also directly implicated with increased disease (82). In addition to splash dispersal, a heavy rainfall causes mass flow of water on the soil surface and inoculum redistribution in the field. Reducing field wetness periods may be a useful tool in managing fruit rot. Most irrigation systems in Michigan use a travel celer that produces relatively large water droplets, thereby increasing the risk of contaminating fruit with soil that is splashed via water (67). Irrigation may be reduced to a minimum after fruit set and even completely eliminated prior to crop harvest with no yield reduction (16) and may reduce fruit rot not only in the field but also after harvest.

When a field is infested with *P. capsici*, narrow spacing enhances disease spread and development by increasing relative humidity in the microclimate and lengthening the duration of soil surface and fruit wetness after a rain or irrigation episode (16). Growers of pickling cucumbers in Michigan have historically used a narrow (27.9 cm) row spacing in a production system that was developed over 15 years ago by university and industry professionals to maximize yield through high plant densities and suppress weeds through early canopy closure. Most growers have been reluctant to alter their current production system because they anticipate a reduced yield with increased row spacing. However, Schultheis and Wehner showed that the density of cucumber plants could be reduced without significantly reducing yield (90). They evaluated densities ranging from about 34,500 to 556,000 plants per ha and observed more culls with high plant densities.

Preliminary studies have been conducted at Michigan State University to integrate cultural control methods of controlling *P. capsici* on zucchini, methods including soil amendments, protective mulches, and water management. Raised beds, flat beds, and raised beds with black plastic + 2.5 cm straw and/or 4,483.3 kg/ha compost were compared (Fig. 7B,C). Significant differences in *P. capsici* incidence occurred each year the trial was conducted (Fig. 7A) (M. K. Hausbeck and B. Cortright, unpublished data). Although the treatments with raised beds in combination with plastic, straw, and/or compost were significantly better than flat beds in stand count, numbers, and weight of healthy fruit both years (Fig. 7A), disease still occurred in these treatments. While cultural strategies offer reasonably effective protection for fresh-market zucchini or similar bush-type cucurbit varieties, these management tools are too costly and impractical for growers of cucurbits for the processing industry where the profit margin is relatively small.

**Fungicides.** While fungicides cannot be relied upon alone to prevent disease, they have provided Michigan growers with an extra degree of protection, especially when used in combination with other management practices, such as crop rotation, raised beds, and water management. A limited number of fungicides are available for combating *P. capsici*, especially when the pathogen is resistant to mefenoxam, but none have proven wholly efficacious under optimal conditions for disease (5,41,93). When resistance of *P. capsici* to mefenoxam was discovered in Michigan, we obtained a Specific Exemption in 1998 for the use of the fungicide Acrobat (dimethomorph). This product now has a full label, and its efficacy has been demonstrated in controlled, replicated large-scale
pickling cucumber field studies (Fig. 8A–C) (38,39). In 2002, the fungicide Gavel (zoxamide + mancozeb) was registered for use against *P. capsici* and has also proven to be helpful (Fig. 8A). Studies have indicated that mixing a full rate of copper hydroxide with Acrobat 50WP or Gavel 75DF may be helpful, and is recommended (Fig. 8A) (38,39). Seed treatment with either Apron XL LS (mefenoxam) or Allegiance FL (metalaxyl) may be helpful during seed germination to limit pre- and post-damping off caused by *P. capsici* (7). Growers are encouraged to alternate fungicides and avoid relying on a single fungicide to delay development of fungicide resistance in *P. capsici*.

Good coverage of the plant and fruit with fungicide is essential for maximum protection, but can be difficult to achieve when fruit are shielded by a dense foliar canopy. Plant spacing within the field has been increased by some growers to facilitate improved fungicide coverage. Early and frequent fungicide applications are required for maximum disease control, but increase the cost of production. In Michigan, a fungicide spray may be needed every 5 to 7 days when the weather is wet and rainy. However, the preharvest interval required for Gavel (≥4 days) makes it difficult to use this fungicide in some production systems. Also, mancozeb (a component of Gavel) is a B2 carcinogen, and may be impacted by the Food Quality Protection Act.

**Fumigation.** The long-term persistence of the oospore in agricultural soils poses a continual threat to the successful commercial production of host crops (11,64,89). Oospores germinate asynchronously, and detecting *P. capsici* oospores in the soil prior to an epidemic is notoriously difficult and the likelihood of obtaining a false negative is high (27,64). To reduce the risk and uncertainty of growing *P. capsici*-susceptible crops, producers of solanaceous and cucurbit crops for the fresh market rely on methyl bromide fumigation as the primary means of ensuring fruit yield and quality. Methyl bromide is used in

![Fig. 7. A, A replicated demonstration trial with a commercial grower to highlight cultural tools to manage *Phytophthora capsici*, including raised planting beds, black plastic mulch, composted chicken manure, and straw mulch. B, Zucchini grown on raised planting beds (right) were healthier than those raised on flat beds (left). C, Using a combination of cultural practices, including a raised planting bed, plastic mulch, and straw mulch over the plastic (right) kept zucchini healthy compared with growing zucchini on a flat bed (left).](image1)

![Fig. 8. A, Efficacy of fungicides in reducing fruit rot incidence compared with untreated fruit. B, Application of fungicide in a large-scale, replicated trial. C, Fungicides were applied when fruit were approximately 2.5, 7.6, and 12.7 cm in length.](image2)
conjunction with raised beds, black plastic, and fungicide applications. Because of the short plant-back interval of methyl bromide, crops can be transplanted as soon as the soil reaches an appropriate temperature in the spring, allowing access to early marketing opportunities. Critical Use Exemptions have been submitted and accepted by EPA on behalf of Michigan’s solanaceous and cucurbit producers for the extended use of methyl bromide on these crops. Given the scheduled phaseout of methyl bromide in the very near future, it is imperative that effective and cost-efficient replacements be identified and implemented.

Both registered and experimental fumigants have been tested in Michigan in conjunction with commercial producers at known *P. capsici*-infested sites. A study conducted by the authors in 2003 at a site infested with *P. capsici* showed that water-soluble sodium (Vapam), 66% methyl bromide, 33% chloropicrin (methyl bromide/chloropicrin), and 61% 1,3-dichloropropene, 35% chloropicrin (Telone C-35) all effectively limited disease when used in a raised bed, plastic mulch system.

**Genetic resistance.** Genetic resistance or tolerance is often at the core of integrated management programs and would be especially helpful in managing *P. capsici*. Screening cucumber varieties, and plant introduction accessions. Although complete fruit disease resistance has not been observed, varieties appear to have limited lesion development and sporulation have been identified (A. Gevens and M. K. Hausbeck, unpublished data). Babadoost and Islam, Johnston et al., and Driver and Louws evaluated commercial varieties and experimental breeding lines of pepper for resistance to *P. capsici* (6,24,45). ‘Paladin,’ a commercially available pepper cultivar with resistance to Phytophthora crown rot, appeared promising in these studies. In Michigan, ‘Paladin’ has been commercially grown in *P. capsici*-infested sites, although the plants have been observed to eventually succumb to disease when environmental conditions are favorable. Since neither genetic resistance nor fungicide management appears to be perfect, combining the two may provide significant control advances.

**Information dissemination.** While preventing the introduction of the pathogen is optimal, once *P. capsici* is introduced, several control measures need to be used in a comprehensive management program to reduce losses from disease (Sidebar). As techniques and tools are developed to ease the severity of crop loss due to *P. capsici*, on-farm research trials and educational workshops are emphasized to enhance grower implementation. Further, education of other crop specialists, extension personnel, and consultants is ongoing to ensure that growers receive accurate and consistent information and recommendations.

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Kurt H. Lamour

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