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Ecologically Based Approaches to Management of Phytophthora Blight on Bell Pepper

Phytophthora blight, caused by the oomycete pathogen, *Phytophthora capsici*, is a devastating disease on bell pepper and cucurbit crops in the United States and worldwide (29,40). *P. capsici* causes a root and crown rot, as well as an aerial blight of leaves, fruit, and stems, on bell pepper (*Capsicum annuum*), tomatoes, cucumber, watermelon, squash, and pumpkin (29,35, 40,57,73). The disease was first described on bell pepper in New Mexico in 1922 (40). In recent years, epidemics have been severe in areas of North Carolina, Florida, Georgia, Michigan, and New Jersey. Oospores are believed to provide the initial source of inoculum in the field, and the disease is polycyclic within seasons (1,7,59,60,67). In this article, we discuss the biology and epidemiology of Phytophthora blight on bell pepper and also describe management strategies that can be implemented based on existing knowledge of the ecology of this devastating pathogen.

The objectives of ecologically based pest management (EBPM) are the safe, profitable, and durable management of pests that includes a total systems approach (25). EBPM relies primarily on biological input of knowledge concerning a pathogen life cycle, and secondarily, when necessary, on physical, chemical, and biological supplements for disease management. An understanding of the ecological processes that are suppressive to plant diseases is emphasized rather than secondary inputs (25). Fortunately, we have a considerable amount of information available on the biology and ecology of *P. capsici*, which can now be integrated to improve our ability to manage the disease using ecologically based approaches. Strategies recommended for management of Phytophthora blight involve integrated approaches that focus first on cultural practices that reduce high soil moisture conditions, but also include monitoring and reduction of propagules of *P. capsici* that persist in the soil, utilization of cultivars with resistance to the disease, and when necessary, judicious fungicide applications.

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Fig. 1. Root and crown rot on bell pepper caused by *Phytophthora capsici*.

Symptoms and Life Cycle

P. capsici can infect virtually every part of the pepper plant. The pathogen causes a root and crown rot on pepper (Fig. 1) and also forms distinctive black lesions on the stem (Fig. 2). *P. capsici* can also infect the leaves and causes lesions that are circular, grayish brown, and water-soaked (Fig. 3). Leaf lesions and stem lesions are common when inoculum is splash dispersed from the soil to lower portions of the plant. The pathogen can also infect fruit and causes lesions that are typically covered with white sporangia, a sign of the pathogen (Fig. 4). *P. capsici* typically causes a fruit rot or stem rot on cucumbers and squash (Fig. 5).

P. capsici reproduces by both sexual and asexual means (Fig. 6). The pathogen produces two mating types, known as the A1 and A2. These are actually compatibility types and do not correspond to dimorphic forms. Each mating type produces hormones that are responsible for gametangia differentiation in the opposite mating type. Both A1 and A2 mating types are common in fields in North Carolina and have also been identified within the same plant (59). *P. capsici* produces a male gametangium, called the antheridium, and a female gametangium, called the oogonium. The antheridium is amphigynous in this species. Meiosis occurs within the gametangia, and plasmogamy and karyogamy result

Fig. 2. Black stem lesion caused by *Phytophthora capsici* on bell pepper.

in the formation of oospores, which are the sexual spores that serve as the overwintering inoculum of the pathogen (Fig. 7). The diploid nature of the oomycetes was documented in early studies on the genetics of *P. capsici* (66). Oospores can germinate either directly via formation of a germ tube or indirectly via sporangium formation (Fig. 6).

The pathogen also reproduces asexually via sporangia that are borne on branched sporangiophores (40,69). Sporangia are generally ovoid and have a prominent papillum at their apex (Fig. 8). Sporangia are easily dislodged from the sporangiophore and can be dispersed within fields by wind, rain, and irrigation water (8,11,61). Sporangia germinate indirectly and release motile, biflagellate zoospores under conditions of free moisture on plant surfaces or in saturated soil (3). Zoospores can move readily under saturated conditions and infect roots or aboveground portions of plants (18,19).

Detection and Quantification

Traditionally, *P. capsici* has been recovered by isolation of the pathogen from infected tissue and plating onto a semiselective medium (32,41). The pathogen can also be isolated from soil following soil dilution plating in dilute water agar onto a semiselective medium such as Masago's medium (Fig. 9) (41). No single assay method is suitable for the accurate detection and quantification of all propagule types of *P. capsici* in soil (38). A leaf disk baiting assay in which circular disks of pepper leaves are floated on saturated soil provides high levels of detection of all propagule types from soil, but it is not sufficiently quantitative to estimate inoculum densities (38). Infected leaf disks are plated onto semiselective media, and the presence of colonies of the pathogen allows qualitative determination of the presence of the pathogen in the soil or water sample. Soil dilution plating directly onto semiselective media without prior sample incubation is useful for the quantification of zoospores and sporangia in soil, whereas soil dilution plating after sample saturation and incubation allows recovery of oospores from soil (38). The incubation period provides an opportunity for oospores to germinate and produce sporangia and zoospores that are then detected by the dilution plate assay. Many of the traditional soil assays are laborious and time-consuming and require replication to reduce sampling variation.

Traditionally, accurate identification of the pathogen required morphological observations of sporangiophores, sporangia, zoospore release, and oospores (69). Identification using classical taxonomic methods is time-consuming and requires expertise. Isozyme analysis, serological assays, DNA probes, restriction fragment length polymorphism (RFLP), and polymerase chain reaction (PCR) methods have been used to identify and evaluate the genetic variation among *Phytophthora* species (16,20,28,39,45,46,50). The nuclear small subunit rDNA sequences evolve relatively slowly and are useful for studying distantly related organisms, whereas the internal transcribed spacer (ITS) regions and intergenic region of the nuclear rRNA repeat units vary among species and populations (74). Sequencing studies with small subunit ribosomal RNA sequences (20) have elucidated the evolutionary lineage of the oomycetes. *Phytophthora* species are actually more closely related to nonphoto-

Fig. 3. Grayish brown water-soaked lesions on leaves of bell pepper caused by *Phytophthora capsici.*

Fig. 4. Lesion caused by *Phytophthora capsici* with white mycelium and sporangia of the pathogen on the bell pepper fruit.

Fig. 5. Phytophthora blight lesions on fruit of cucumbers and squash.

synthetic algae than to true fungi or land plants and have been placed in the phylogenetic assemblage, stramenopile (14,24).

The nuclear small subunit rDNA and ITS sequences have been used to develop rapid tools for identification of the economically important species within the genus *Phytophthora* (39,64). A primer called PCAP was developed based on sequence data published previously for a *P. capsici*-specific DNA probe (39,64). PCAP is used with ITS 1 in PCR reactions and amplifies an approximately 172-bp fragment of DNA in all isolates of *P. capsici* tested from a range of hosts (Fig. 10, lanes 2 to 9 and 12). Isolates of *P. citrophthora* (Fig. 10, lane 10) are also amplified by the PCAP primer, but the amplified product size is larger than that of *P. capsici* (Fig. 10, lanes 2 to 9 and 12) or *P. citricola* (Fig. 10, lane 11). Digestions of the 172-bp fragment with *Msp*I allows differentiation of *P. capsici* from *P. citrophthora* and *P. citricola,* which are not digested by this enzyme. None of the other major species of *Phytophthora,* including *P. cactorum*, *P. palmivora*, *P. nicotianae*, *P. infestans*, *P. mirabilis*, *P. fragariae*, *P. sojae*, *P. megasperma*, *P. cinnamomi*, *P. cryptogea*, and *P. erythroseptica*, are amplified with the PCAP primer (64). *P. capsici* (Fig. 11, lane 5) can also be differentiated from *P. citricola* (Fig. 11, lane 6) by restriction digest of ITS DNA with *Msp*I. Four fragments, approximately 290 bp, 219 bp, 194 bp, and 140 bp, are present in *P. capsici* after digestion with *Msp*I (Fig. 11, lanes 5). *P. capsici* can be differentiated from *P. citrophthora* by restriction digest of ITS DNA with *Rsa*I (64).

PCR assays should make diagnosis of *P. capsici* in infected plant material, soil, or water samples more accurate. PCR is more rapid and efficient than traditional isolation methods in identification of *P. capsici* in infected plant samples. We tested the PCR assay and found that 92% of infected pepper plants with visible lesions that were positive by traditional isolation on media were also positive by PCR using the PCAP and ITS 1 primers (64). PCR with these primers also detected infection in 32% of the samples where the pathogen was not identified previously by traditional isolation on agar media (64). This indicates that the PCR technique was able to detect false negatives and could be useful for detection of the pathogen in lesions during the incubation period, when symptoms and signs of the pathogen are not obvious. PCR methods are not useful in detection of the pathogen in severely decayed tissue, since inhibition of PCR by decomposing plant products or bacteria can occur. Further research needs to be done to develop in-field, quick PCR assays that can be used with fluorescent detection methods for assays of the pathogen directly from plant, soil, or water samples using miniaturized thermocycling devices. Quantitative PCR studies are also needed to relate levels of propagules of the pathogen to levels of DNA recovered from soil.

Impact of Soil Water

Soil moisture, especially the matric component of soil water potential (ψ_m), plays an important role in the life cycle of *Phytophthora* spp. that cause root rots, including *P. capsici* (18,19). Sporangia of *P. capsici* form abundantly in saturated soil within 24 h on mycelial disks that are first incubated at drier ψ_m of –20.0 to –30.0 J/kg (1 J/kg = 10 millibars; a ψ_m value of 0 is fully saturated soil) (3). Release of zoospores from sporangia in *Phytophthora* species is extremely sensitive to small changes in ψ_m and occurs predominantly at high ψ_m values between 0 and –1.0 J/kg (19). Zoospores are released from sporangia of *P. capsici* previously formed at soil water ψ_m of –30.0 J/kg within 4 h of soil saturation (3).

P. capsici produces oospores, which are considered to be primary survival structures in soil (1,7,56). Factors affecting the germination of oospores of *P. capsici* have been well documented and include light, temperature, and soil water matric potential (6,7,26,27). Oospores have been reported in naturally infected pepper plants and germinate predominantly by formation of sporangia in distilled water, root extract, and soil extract (26,52,56,59). Oospore germination in root and soil extract is

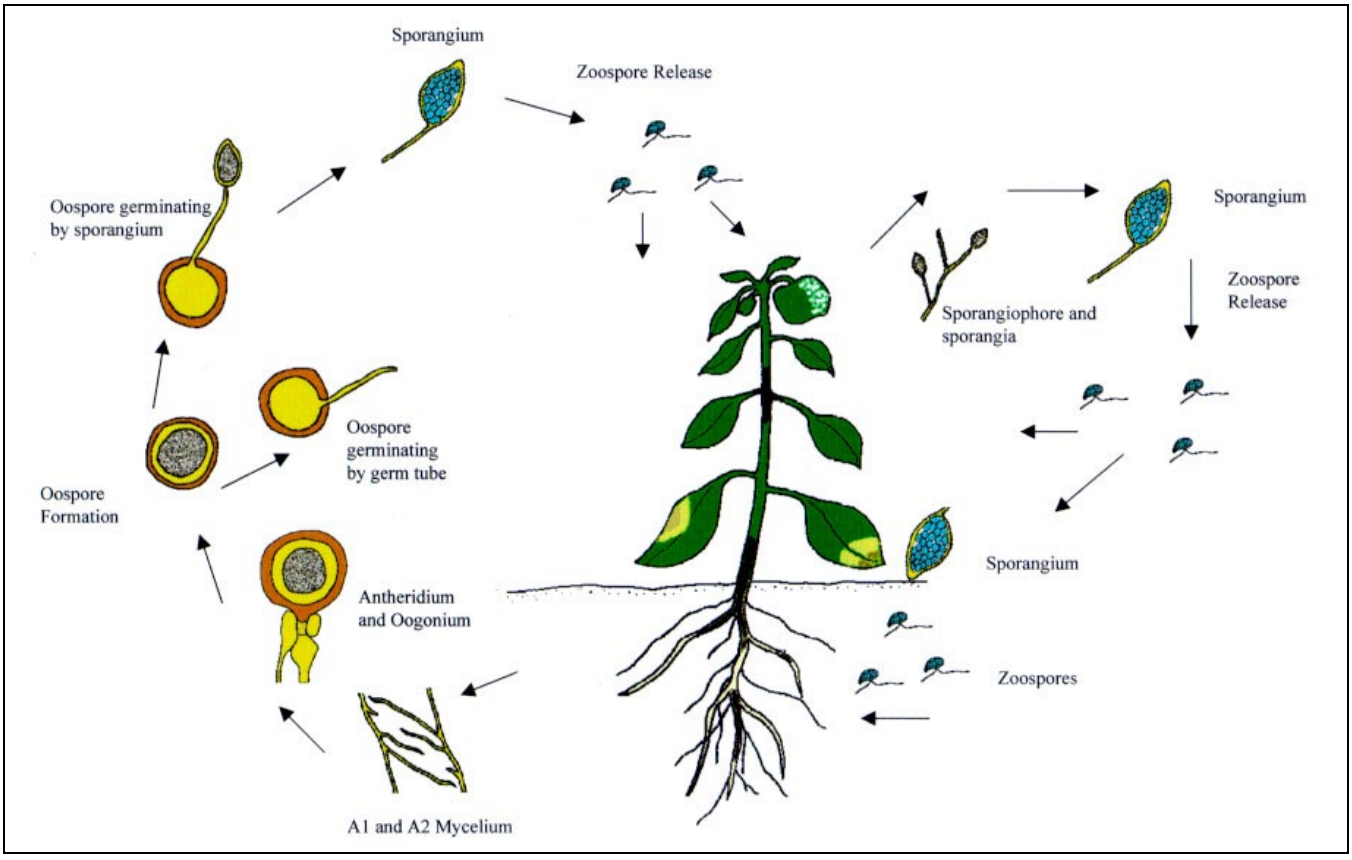

Fig. 6. Life cycle of *Phytophthora capsici,* causal agent of Phytophthora blight on bell pepper.

asynchronous and increases with time of incubation (26). Germination of oospores is initiated when oospores are first incubated in drier soils at ψ_m of –2.5 to –10.0 J/kg prior to saturation (27).

Experiments have been conducted under controlled conditions of ψ_m to determine the effect of cyclical changes in ψ_m on disease caused by oospores in soil (6,27). Final incidence of disease was higher in plants held at ψ_m of –2.5, –5.0, or –10 J/kg for 10 days than for 5 days prior to saturation, and disease increased with decreasing ψ_m (27). Periods of continuous soil saturation are not conducive to oospore germination or disease, and in fact, disease development was less than 10% in plants grown in oospore-infested soil maintained under constant saturation (27). These results serve to illustrate that it is the cyclical changes in ψ_m that stimulate oospore germination in soil and infection in this pathosystem. Even brief periods of soil saturation after oospores have germinated in drier soils can result in high levels of disease. Periods of constant soil saturation inhibit oospore germination and disease. Further experiments are needed in the field in regions where pepper is grown under irrigated conditions to determine whether disease due to primary inoculum from oospores can be reduced by maintaining more constant soil moisture throughout the growing season.

Dispersal of *P. capsici* and Disease Development

Virtually every part of the plant can become infected by *P. capsici*, and the pathogen can spread by several distinct mechanisms, including primary inoculum movement from root to root down rows via (i) root growth to inoculum, (ii) inoculum movement to roots, or (iii) root-to-root contact. Inoculum can also spread in surface water, or inoculum can be splash dispersed from soil to leaves, stems, or fruit. Local aerial dispersal from sporulating lesions on leaves, stems, or fruit may also occur in this pathosystem.

Components of the primary inoculum dispersal of *P. capsici* have been evaluated in field soils (63,72). Primary inoculum of *P. capsici* in the soil causes root infections that progress to crown infections (63). Wilting almost always precedes crown lesion development in naturally infested fields, suggesting the importance of root infections and the soilborne phase of the disease (63). In controlled field tests, an infected plant containing sporangia and zoospore inoculum was placed in PVC tubes on the soil surface, and rainfall events spread inoculum to roots in soil. Infection of the crowns and roots of adjacent plants in the plot was more rapid when inoculum moved to roots than when spread of inoculum of the pathogen in soil occurred via growth of healthy roots to inoculum buried in soil or root-to-root contact in soil (72). Management strategies that minimize inoculum dispersal in and on the soil surface have great potential for disease reduction in this pathosystem.

Inoculum movement down rows with surface water is also an important mechanism of dispersal for many polycyclic *Phytophthora* diseases, and this is the predominant mechanism of dispersal of *P. capsici* in naturally infested fields (8,11–13,48,62,63). Soilborne members of the genus *Phytophthora* are disseminated considerable distances in the direction of water flow in furrows during irrigation events (11,13,48). For example, inoculum of *P. capsici* can be dispersed up to 70 m from point sources of inoculum with furrow irrigations (13). Movement of inoculum down rows with surface rain water or furrow irrigation can result in rapid increases in disease (13,63). *P. capsici* can spread from plant to plant within rows from initial inoculum sources and across rows from primary foci of disease (8,65). Spread of inoculum may be detected unidirectionally within many rows for long distances, and disease foci increase in size over time (Fig. 12A and B) (8,11,60,65).

Splash dispersal of inoculum from the soil to aboveground parts of plants with rainfall, wind, or overhead irrigation water can also occur, resulting in rapid pathogen

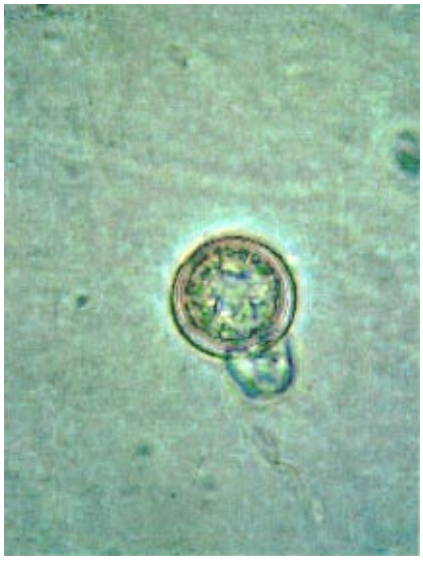

Fig. 7. Thick-walled oospore of *Phytophthora capsici*. An amphigynous antheridium is attached at the base of the oospore.

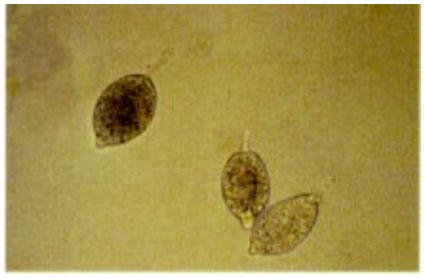

Fig. 8. Sporangia of *Phytophthora capsici* are asexual structures that release zoospores under saturated conditions. They have a medium pedicel and are easily dislodged from the sporangiophore.

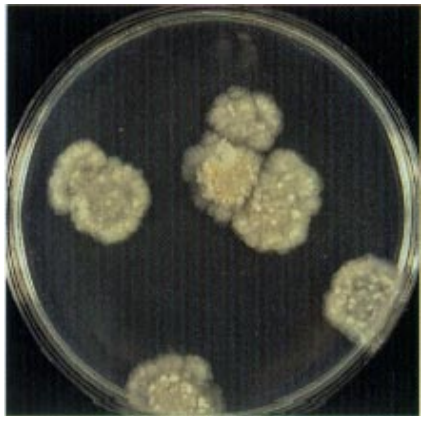

Fig. 9. Petri dish containing semiselective Masago's medium and colonies of *Phytophthora capsici* isolated from soil.

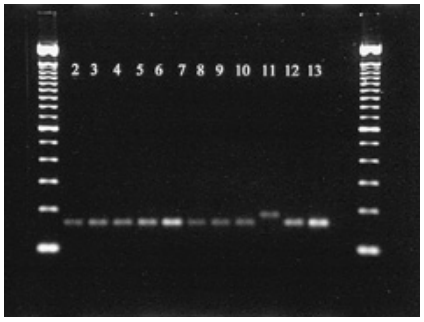

Fig. 10. DNA amplified with the primers PCAP and ITS 1 from isolates of *Phytophthora capsici* (lanes 2 to 9, 13). The primer also amplifies *P. citrophthora* (lane 10) and *P. citricola* (lane 11). Digestion with *Msp*I differentiates *P. capsici* from the other two species. Lanes 1 and 14 contain 100-bp ladders, and lane 13 contains a no-template control.

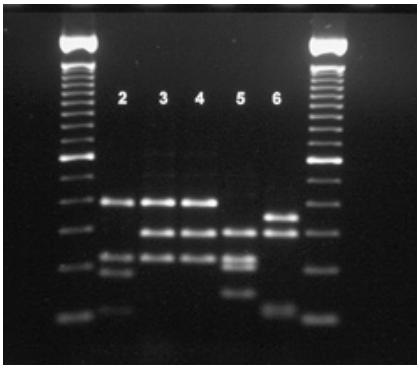

Fig. 11. Restriction digest with *Msp*I of DNA amplified with universal primers ITS 5 and ITS 4 from *Phytophthora cactorum* (lane 2), *P. infestans* (lane 3), *P. mirabilis* (lane 4), *P. capsici* (lane 5), and *P. citricola* (lane 6). *P. capsici* has a unique amplified fragment restriction fingerprint. Lanes 1 and 7 contain 100-bp ladders.

spread and disease increase (8,37,63). Sporangia can move rapidly on polyethylene mulch with rain events, resulting in rapid disease spread (8,65). In artificially infested plots, final disease became very high when surface inoculum was spread on plastic or splash dispersed on bare soil (Fig. 13). If the numbers of infected plants are minimal, these plants can be removed from fields to reduce the amount of sporangial inoculum that is dispersed in the field during rainfall events. In addition, removal of a 61- to 91-cm-wide section of polyethylene mulch between healthy and infected plants can be useful to prevent spread of the pathogen down rows.

Ecologically Based Disease Management

A great deal is known about the biology and ecology of *P. capsici* that can be used to develop ecologically based disease management strategies. Phytophthora blight poses many problems for commercial pepper production. For each problem listed below, we have developed disease management strategies based on the ecology of the pathogen.

Problem: Phytophthora blight is more severe under conditions of high soil moisture from frequent rainfalls or irrigations.

Management strategy: Use site preparation, waterway systems, bed structures, and transplanting procedures that minimize water accumulation and irrigate appropriately.

Site preparation. Fields must be well drained and must not have low-lying areas that collect water, since these areas are often the focal points for epidemic development (37) (Fig. 12A and C). Waterway systems and drainage ditches can be constructed in fields with extensive low-lying areas prior to production of peppers, and a land plane or laser level can be used to level the field as much as possible before planting to minimize areas of standing water. In addition, fields can be subsoiled or chisel plowed to improve drainage in compacted areas (22).

Transplanting procedures. Peppers should be transplanted on raised, crowned beds (>23 cm high) to avoid extensive soil moisture accumulation around the base of plants (Fig. 14). Beds should be prepared prior to transplanting. Flat bed culture and ridging by cultivation after transplanting can cause water to accumulate around the crowns of plants, thus exacerbating disease. Peppers should be transplanted on top of a small ridge or raised, crowned bed in bare ground culture (Fig. 15A). Rainfall during the season can result in bed "washout" in bare ground culture, so cultivation may be necessary to reshape beds during the growing season. Polyethylene mulch culture of pepper can result in increased yields and has become the preferred method of production in the majority of production areas in the United States (Fig. 14B and C). However, polyethylene mulch culture of pepper can result in high levels of Phytophthora blight if the proper cultural practices are not implemented (8,65) (Figs. 13 and 14A). Beds should be shaped with a crown to allow water to run off during rainfall events (Fig. 14B and C).

Transplanting equipment must also be adjusted properly to avoid making depressions in beds during transplanting that accumulate water during rainfall or irrigation events and create conditions conducive for infection by *P. capsici* around the crown of the plant (Fig. 15B). On polyethylene mulch, the transplanter must be driven slowly enough to allow the entire root ball to be buried in soil, and surrounding soil needs to be used to fill in transplant holes to create a mound at the base of each plant (Fig. 15C and D). Phytophthora blight can be severe if this procedure is not followed and a heavy rainfall occurs in a *P. capsici*–infested field.

Phytophthora blight usually develops first in fields in low-lying areas where water accumulates between beds at the ends of rows (37,62) (Figs. 12 and 14D). A 76-m-wide waterway area can be con-

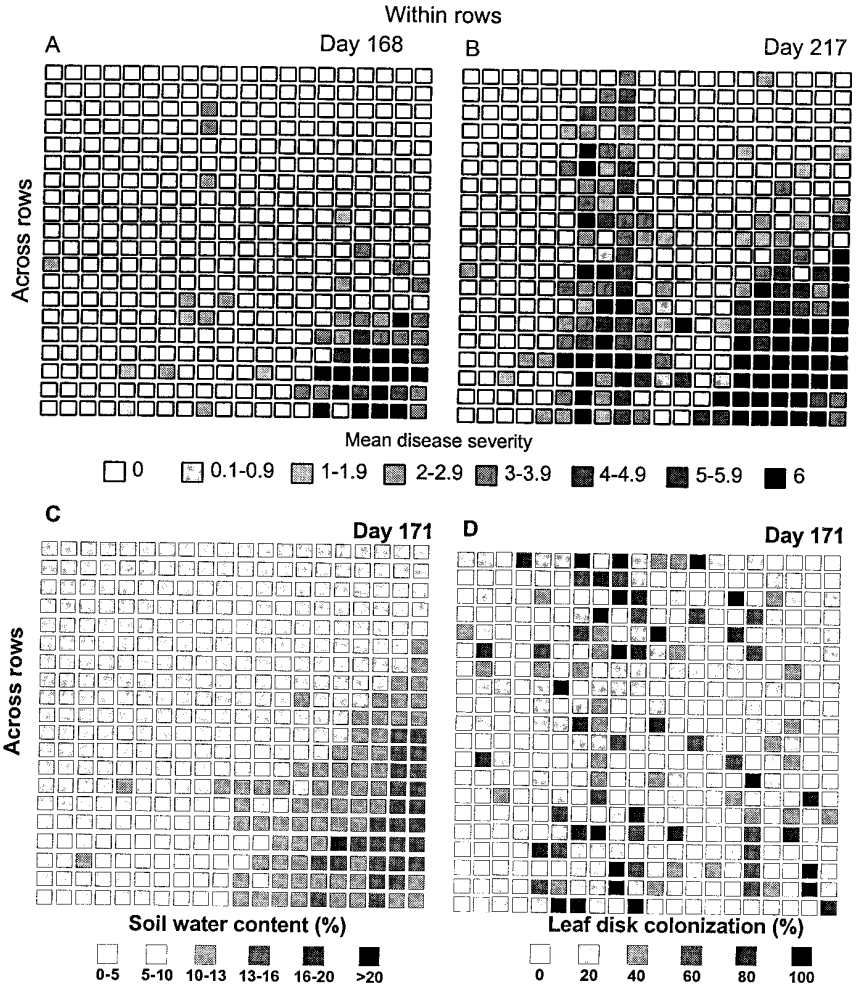

Fig. 12. Spatial pattern map of disease severity caused by *Phytophthora capsici* on bell pepper at (A) day 168 and (B) day 217 in a naturally infested field. Spatial pattern map of (C) gravimetric soil water content and (D) propagule levels of the pathogen in soil at day 171 in the same field.

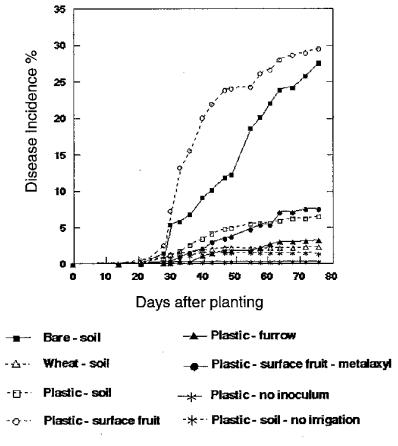

Fig. 13. Incidence of plant mortality caused by *Phytophthora capsici* on bell pepper in artificially infested plots affected by cultural and chemical control strategies.

structed at both ends of the field to accommodate drainage of large volumes of water from rainfall events or prolonged irrigation so excess water does not back up into the field. Furrows also need to be unobstructed between beds at both ends of the rows to allow water to drain from the field readily.

Irrigation management. Both rainfall and irrigation have large effects on the time of onset and final incidence of Phytophthora blight epidemics (4,8,10,23,60). Disease incidence can become very high after either heavy rainfall or frequent drip irrigation (60). Propagule densities of *P. capsici* in soils are highest early in epidemic development in plots that are irrigated frequently and are highly correlated with high soil water content and disease incidence early in the season (61). In fact, disease occurrence in fields is spatially correlated with areas of fields where high soil moisture occurs early in the season (Fig. 12A and C) (23,37). Propagules of the pathogen may be distributed widely in soil in a given field (Fig. 12D), but disease develops initially where conditions of soil moisture are conducive (37).

Irrigation frequency, duration, and the mode of irrigation can all affect the incidence of Phytophthora blight epidemics (4,10,11,60). Disease incidence and severity are more severe and onset occurs earlier with more frequent than with less frequent irrigation episodes (11,12,60). A less frequent irrigation schedule of 21 days versus 7 days resulted in less Phytophthora blight without a reduction in yield (11). In areas where furrow irrigation is used, alternate-row irrigations can reduce the incidence of Phytophthora root rot in pepper to a greater extent than a combination of irrigation of every row and application of fungicides (4,17). This strategy reduces the amount of free water that runs down furrows, thus reducing inoculum spread and subsequent disease.

Depth of placement of drip irrigation emitters in soil can also have a large impact on Phytophthora blight epidemics (10). Drip irrigation close to the stem or crown of the plant results in high disease, whereas subsurface drip irrigation results in lower levels of disease (10). Drip irrigation lines positioned 15 cm below ground level in the plant row result in the most efficient control of Phytophthora blight in the field without reducing yields (10). Early-season propagule densities of the pathogen in soil are higher near the drip irrigation line than in drier soils opposite the drip line (61). Irrigation stimulates zoospore discharge from sporangia and dispersal in soil and also stimulates root growth, thus making root contact with inoculum more probable. In arid agriculture regions, subsurface irrigation encourages root growth deep in the soil profile and minimizes inoculum dispersal near the crown and major roots of the plant at the surface (10). Thus, the plant can escape disease by irrigation management.

Soil moisture in polyethylene mulch culture of peppers can be maintained at ψ_m of 20 to 40 J/kg in coarse-textured soils utilizing tensiometers placed at 15- and 30-cm depths within the bed. Irrigation can thus be timed based on actual reading of ψ_m (22). Phytophthora blight can be effectively managed by avoiding excessive levels of high soil moisture and excessive cyclical changes in soil moisture in the beds.

Maintenance of an irrigation water source free from the pathogen is also a very important management strategy for Phytophthora blight. If irrigation ponds contain inoculum of the pathogen and are used as a source of water for drip or overhead irrigation, results can be disastrous (Fig. 16). Use of filtered irrigation water from subsurface wells can reduce the problem of contamination of water supplies by the pathogen. In addition, testing water samples for the presence of the pathogen and if necessary subsequent treatment of water with chlorine or fungicides can reduce propagule levels of the pathogen. Water from fields with a history of disease should not be drained into irrigation water supplies.

Problem: *P. capsici* splashes from soil in the row or on polyethylene mulch from between rows to foliage and causes infections.

Management strategy: Reduce splash dispersal of inoculum from soil with straw mulch between rows or on bare soil with stubble from a cover crop.

Modifications in cultural practices, including growth of pepper in a no-till cover crop, can have a large impact on the development of Phytophthora blight epidemics in bell pepper (Fig. 17). Dispersal of soil inoculum can be suppressed and final incidence of disease can be greatly reduced when pepper is grown in stubble from a fall-sown, no-till rye or wheat cover crop (65) (Fig. 13). In controlled field experiments, final disease incidence was highest and pathogen spread occurred within and across rows when pepper was planted into bare soil and all dispersal mechanisms were operative (Fig. 13). Inoculum moved rapidly down black polyethylene mulch with rainfall events, and disease onset was earliest in these plots. The fungicide metalaxyl applied in the irrigation system did not suppress within-row spread of surface inoculum from a sporulating fruit on plastic but did limit across-row spread; final disease incidence in metalaxyl-treated plots was less than 10%. Pathogen dispersal mechanisms were modified most dramatically by the no-till cropping system

Fig. 14. (A) High incidence of Phytophthora blight using polyethylene mulch without raised bed culture. (B) Crown raised bed construction prior to laying polyethylene mulch. (C) Bell pepper production on well-constructed raised beds with polyethylene mulch culture. (D) Water accumulation at the ends of rows between beds where drainage ditches were not established to allow excess water to leave fields following rain events.

Fig. 15. (A) Pepper transplanted into soil on a small ridge in bare ground culture. (B) A water wheel transplanter that holds water and punctures polyethylene mulch and soil prior to manually transplanting peppers. (C) Recently transplanted peppers with a water wheel transplanter. Note the depression around the base of each transplant. (D) Supplemental soil added around the base of a pepper transplant to fill in the depression following transplanting with a water wheel transplanter in polyethylene mulch culture.

(Fig. 13). We know little about the biological effects of green manures, living mulches, or intercropping with summer cover crops on epidemic development in this pathosystem. Further experiments are needed to examine the effects of different kinds of cover crops, including nitrogen fixing legumes, on disease suppression and yield of bell pepper.

Problem: Inoculum of the pathogen persists in soil.

Management strategy: Use long crop rotation schedules, soil solarization, or organic amendments to reduce pathogen propagule levels in soil.

Crop rotation. Peppers should not be produced in a field that has had a crop of peppers, cucumbers, muskmelons, pumpkins, winter squash, summer squash, watermelons, eggplants, or tomatoes for at least 3 years because propagules of *P. capsici* persist in field soils following the repeated growth of susceptible crops. Oospores of the pathogen are capable of survival in the absence of a host crop, but viability declines to a large extent after 27 weeks (7). Oospores remained viable and capable of causing disease in a greenhouse bioassay after 16 weeks (7). Sporangia and zoospores have limited survival ability in soil and are not detectable after 4 weeks (7). Propagule densities of the pathogen are greatly reduced in the absence of a susceptible crop; thus crop rotation is an excellent and straightforward strategy to reduce disease incidence in subsequently grown susceptible crops.

Soil solarization and organic amendments. Experiments have been conducted to evaluate the use of soil solarization or soil amendments with organic materials on the incidence of Phytophthora blight in bell pepper (15,33,55,75). Soil solarization involves the heating of soil under clear polyethylene mulch during the hottest months of the summer and has been demonstrated to reduce levels of many soilborne pathogens (15,75). Soil solarization alone reduced disease incidence from 39.8 and 42.9% to 24.1 and 19.7% in 2 years of field tests in Turkey (75). In fact, disease incidence following solarization was not significantly different from disease incidence following soil treatment with methyl bromide in this study (75). Unfortunately, soil solarization often only kills pathogen propagules at shallow depths in soil. Propagule densities of *P. capsici* at 10-cm depths after solarization were similar to those in methyl bromide–treated soil, but no reductions in propagule densities occurred at soil depths of 25 cm after solarization treatments (15). Soil solarization has been used effectively to control Phytophthora blight in plastic houses in Italy (55).

Fewer studies have been conducted to examine the effect of soil amendments on Phytophthora blight. Soil amendments with chitosan or crab shell waste were suppressive to Phytophthora blight in some years in Florida, but results were variable (33). Further field work with organic soil amendments including animal manures and composted plant materials is needed to test their efficacy in suppression of Phytophthora blight before recommendations can be made.

Problem: Most pepper varieties currently grown are susceptible to *P. capsici.*

Management strategy: Deploy pepper varieties with resistance to the pathogen in the field on a wider scale.

Numerous attempts have been made to find sources of resistance to *P. capsici* in bell peppers; yet few resistant cultivars are deployed commercially (2,34,49,58). One of the first commercial cultivars with resistance to Phytophthora blight was Adra from Abbott & Cobb Seed Co., Feasterville, PA (11). The resistant cultivar Emerald Isle was released from Harris Moran Seed Co., Modesto, CA. Unfortunately, Adra and Emerald Isle did not possess sufficient horticultural characteristics to be accepted by the majority of bell pepper growers in the United States. Recently, the resistant cultivar Paladin was released by Novartis Seeds Inc., Rogers Brand, Boise, ID. Paladin possesses excellent resistance to the crown rot phase of Phytophthora blight and has excellent horticultural characteristics that enable it to be marketed commercially (Fig. 18). However, Paladin does not possess resistance to the foliar phase of Phytophthora blight, which is common in high rainfall areas. Therefore, regularly scheduled applications of a copper fungicide must be applied from midseason until the end of the season to assist in control of this phase of the disease on Paladin. Additional new sources of germ plasm and breeding efforts are needed to identify and map resistance genes in bell pepper to *P. capsici* and develop durable levels of resistance in pepper.

Problem: Resistance to the fungicide metalaxyl has been found in populations of *P. capsici* in fields.

Management strategy: Use fungicide mixtures, alternative fungicides, or biological alternatives to reduce populations of resistant isolates in the field.

Chemical measures can be integrated into Phytophthora blight management programs to provide control of the pathogen in areas of the field where high soil moisture may accumulate, since cultural practices are generally not completely implemented or effective in a given field. The first line of defense against this disease needs to focus on strategies that reduce soil moisture conditions conducive for disease. Use of fungicides alone for control of Phytophthora blight without the implementation of ecologically based practices can result in a high incidence of disease in *P. capsici*–infested fields.

Captafol (trade name Difolatan) was one of the most effective fungicides for the control of the foliar phase of Phytophthora blight and received emergency registration (Section 18 specific exemption of the Federal Insecticide Fungicide and Rodenticide Act) in New Jersey in 1980 and 1981 (31,51,68). However, Captafol was withdrawn from the U.S. marketplace in 1982 and never received federal registration for use on peppers to control Phytophthora blight.

In the early 1980s, the systemic fungicide metalaxyl (trade name Ridomil, Novartis Crop Protection) was demonstrated to provide excellent control of the crown rot phase of Phytophthora blight (30,42, 43,51,68). Metalaxyl received a federal registration for the control of Phytophthora blight of peppers in the United States in the 1990s. Two applications of metalaxyl are required at 30-day intervals following the

Fig. 16. Phytophthora blight on bell pepper grown on black polyethylene plastic. The pathogen was distributed through the field via a contaminated irrigation pond and drip irrigation.

Fig. 17. Pepper grown in stubble from a fall-grown no-till wheat cover crop. The wheat straw was mowed and distributed in the furrows to slow splash dispersal of the pathogen, thus greatly reducing disease.

Fig. 18. Bell pepper cultivar Paladin, which is resistant to *Phytophthora capsici,* on the left and a susceptible local variety of a cherry pepper on the right.

initial application at planting in order to maintain control of Phytophthora blight and avoid phytotoxicity of the older leaves. Foliar applications of a copper-containing fungicide are then made every 7 to 10 days from 2 to 3 weeks following the last metalaxyl application until the end of the season (22).

Resistance to metalaxyl has been reported in many oomycete pathogens (47). Until recently, metalaxyl-resistant isolates of *P. capsici* had only been reported in the laboratory after mutagenesis (5,9). Recently, the manufacturer replaced metalaxyl with mefenoxam (trade name Ridomil Gold). Mefenoxam is the active component contained in the fungicide metalaxyl and is applied at similar frequencies and methods as metalaxyl, but at lower rates of manufactured product. Mefenoxam was used widely in peppers for the first time in 1997. Disease occurred in fields that were treated with multiple applications of mefenoxam in 1997 in North Carolina and New Jersey (53). Infected plants from 12 fields in North Carolina and one in New Jersey were sampled, and *P. capsici* was isolated from tissue. A total of 161 isolates were screened for sensitivity to mefenoxam in petri dish assays. Thirty-three percent of the isolates were sensitive, 10% of the isolates were intermediate in sensitivity, and 57% of the isolates were resistant to mefenoxam (53). Resistance frequencies ranged from 25 to 100% within sampled populations from individual fields (53). The greatest number of resistant isolates was recovered from fields where Ridomil Gold was used alone rather than in combination with other fungicides. Both mating types were found among resistant isolates, suggesting that these isolates may persist as oospores in soil. Mefenoxam-resistant isolates of *P. capsici* have also been reported recently from fields in Italy, Georgia, and Michigan (36,44,54). Alternative fungicides with activity against oomycete pathogens have not been adequately evaluated in the field for Phytophthora blight, and none are presently labeled. However, a number of compounds with action against oomycete pathogens are currently being evaluated as alternatives.

Work is underway by a number of researchers to test alternative fungicides and biologicals for management of Phytophthora blight on bell pepper. Spread of *P. capsici* was greatly reduced and disease incidence was low in peppers grown in rock wool hydroponic systems that were treated with the nonionic surfactant Aqua-Gro 2000L (Aquatrols, Cherry Hills, NJ) (70). The surfactant reduced the dispersal of zoospores in the hydroponic solution from a point source of inoculum and killed zoospores. An extensive review of the mode of action of biosurfactants has been published (71). In another study, tomato and pepper plants grown in a greenhouse hydroponic system were treated with formulations of phosphite (Nutri-Phite), which is the salt of phosphorous acid (21). The incidence of Phytophthora blight was significantly reduced by treatment with phosphite; yet the pathogen was isolated from plants in which symptoms did not occur (21). These alternative chemical methods of disease control may have applications for Phytophthora blight in field situations where inoculum is dispersed into fields from infested irrigation water, but further field trials are needed to confirm or refute this hypothesis.

Outlook

Phytophthora blight of bell pepper has increased in occurrence and severity in recent years in many areas of the United States. In some regions, this situation may be exacerbated by intensive production of susceptible crops in the same fields with minimal rotation to nonhost crops. In other areas, development of fungicide-resistant isolates may be the source of the problem. Effective management of the disease will require ecologically based approaches such as those described in this paper. In addition, innovative research to develop and implement improved methods for detection of the pathogen in soil are needed so that fungicides can be applied to soil only where necessary and more judiciously rather than on a widespread scale. The development of fungicide resistance in *P. capsici* populations poses new problems for the use of Ridomil Gold, which is currently one of the few labeled compounds available for chemical control of the root and crown rot phase of this disease on pepper. Resistance management plans will be needed to reduce future occurrences of resistance to mefenoxam in populations of *P. capsici* in the field. Improved monitoring methods for detection of pathogen resistance to this fungicide are also needed in this and other *Phytophthora* species. Durable host resistance may represent one of the most effective means of disease management, yet few resistant cultivars are currently available with horticultural traits that are acceptable to growers. Management of soil water via manipulation of cultural practices that reduce dispersal of *P. capsici* will continue to be the key to an ecologically based system for management of Phytophthora blight in bell pepper.

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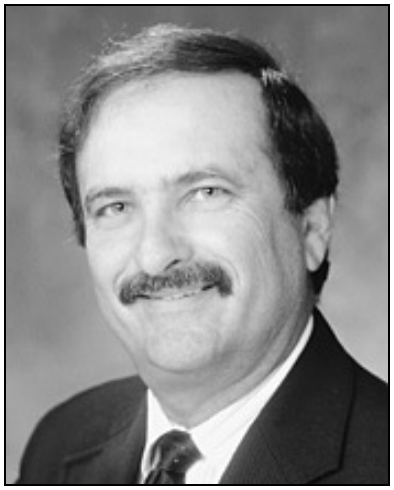

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