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Recent Progress in Understanding and Controlling Bacterial Canker of Tomato in Eastern North America

Bacterial canker of tomato (*Lycopersicon esculentum* Mill.), caused by *Clavibacter michiganensis* subsp. *michiganensis* (Smith) Davis et al, has caused major economic losses in commercial tomato production worldwide. Losses from canker are caused primarily by wilting and collapse of plants, but fruit spotting, also known as bird's-eye spot, reduces the value of fresh-market tomatoes. The disease can occur on pepper and several other members of the Solanaceae, but tomato is the only crop on which it is economically significant.

Since its discovery in a Michigan greenhouse in 1909, canker has been reported from virtually all tomato-growing regions of the world (40). In North America, epidemics have occurred in the U.S. Midwest (1930s and 1980s), Ontario (1960s and 1980s), and North Carolina (1960s), causing yield losses of up to 80% for individual growers and 5–10% regionally (40). Erwin F. Smith (38) first named the pathogen *Bacterium michiganense*, then *Aplanobacter michiganense*. After additional attempts at renaming, including *Pseudomonas michiganensis*, *Phytomonas michiganensis*, *Erwinia michiganensis*, and *Mycobacterium michiganense*, the accepted nomenclature became and stayed

Corynebacterium michiganense for nearly 50 years. In the 1980s, the pathogen was reclassified in the genus *Clavibacter*, on the basis of new knowledge about its cell wall composition, and became *Clavibacter michiganensis* subsp. *michiganensis* (10).

Reliable control of canker remains an elusive goal. The highly sporadic nature of canker outbreaks helps explain the slow pace of progress in improving the efficacy of management practices. Like sightings of the Loch Ness monster, canker epidemics have provoked intense but fleeting interest. As soon as the epidemics subside, so does support for research. The history of canker research reflects a start-and-stop pattern, well described by Strider (40), who reviewed progress in canker research from 1910 to 1969.

In 1984, serious canker epidemics in the midwestern United States and Canada triggered a surge of research. The findings of this new research have significantly improved techniques for pathogen detection, seed sanitation, and resistance breeding. They also have raised the level of understanding of canker epidemiology and clarified the potential value of chemical control. Much research during this period was coordinated and summarized at annual tomato bacterial canker workshops held in eastern and midwestern North America during 1985–1990. Our article will highlight these recent advances, along with concurrent applied research on bacterial canker of tomato from other parts of the world.

Symptoms

The wide variety of symptoms caused by *C. m. michiganensis* can be differentiated on the basis of whether they

develop from systemic or localized infections. If infection occurs from inoculum carried with seed or through wounds directly into vascular tissue, symptoms of systemic infection, particularly wilting, usually appear first. But when infection occurs through broken trichomes or natural openings such as hydathodes after epiphytic spread of the pathogen, localized symptoms such as marginal necrosis and leaflet spotting may appear first. To further complicate matters, localized infections also can progress into the vascular bundles and lead to systemic symptoms under certain circumstances. The complex of symptoms appearing at a certain place and time is highly variable and is dictated by such circumstances as plant age, infection site, cultivar susceptibility, and environmental conditions. As a result, identification of canker on the basis of symptoms alone can be inaccurate.

Localized infection. Marginal necrosis of leaflets frequently is an early symptom of localized infection. Sometimes referred to as the "firing stage," this appears first as distinct brown, dried margins on lower leaflets (Fig. 1A), sometimes separated from the green areas by a narrow zone of yellow tissue. The necrotic margin gradually widens and may cause shriveling of leaflets, leaves, and entire stems. Spray inoculation of very young plants in the greenhouse can produce small, white, blisterlike spots on cotyledons and leaflets (Fig. 1B), but this symptom is seldom seen in the field. In some years in North Carolina and other locations, however, white to tan spots appear on stems of field-grown plants (Fig. 1C).

Small (less than 0.3 cm in diameter), tan-brown lesions with white halos, called bird's-eye spots, on fruit (Fig. 1D)

often are described as the most reliable symptom for field diagnosis. But fruit spots caused by the bacterial spot pathogen, *Xanthomonas campestris* pv. *vesicatoria*, can have a similar whitish appearance when first occurring on green fruits. The spots caused by canker also can turn brown with age, mimicking mature fruit spots caused by *X. c. vesicatoria*. Fruit spots are not consistent findings in canker epidemics, so white spots on green fruit are not a foolproof indicator of canker. On pink to red fruit, however, haloed white spots are likely caused by the canker pathogen. Fruit infection through the vascular system sometimes appears as yellowing or browning of the vascular strands in fruit (40) (Fig. 1E).

Systemic infection. Wilting, the most conspicuous symptom, may be noticed first. Plants systemically infected as young seedlings may wither and collapse relatively rapidly (Fig. 1F), whereas older plants develop wilt symptoms slowly and gradually, if at all. Sometimes, leaflets wilt unilaterally (Fig. 1G), but the entire leaf eventually succumbs. The vascular tissue of infected stems shows a yellowish discoloration, later changing to brown, which is especially noticeable at the nodes in vertically split stems.

The disease gets its name from stem cankers developing under specific circumstances, usually after wilting is under way. As the pathogen spreads from xylem to nearby phloem and parenchyma cells, light yellow to brown streaks develop along diseased stems and on the undersides of petioles (Fig. 1H). These streaks gradually darken and sometimes split open, resulting in dark brown cankers that reveal extensive necrosis of pith and cortex (Fig. 1I).

Detection and Identification

Tomatoes produced in eastern and midwestern North America are grown primarily from transplants. It is possible that infested or infected seeds act as sources of primary inoculum for canker epidemics, producing asymptomatic infected seedlings. Infection can spread rapidly during transplant production by mowing, handling, and splashing water (5). Systemically infected transplants typically wilt and die 2–8 weeks after transplanting (5,8,21). Highly sensitive and reliable techniques for screening seed lots and transplants are clearly essential for control of the disease, but such techniques have been unavailable until recently. In 1984, a serious canker epidemic in the midwestern United States was traced to “certified disease-free” transplants grown in Georgia (25). The source of inoculum for this epidemic has never been established. However, the 1984 epidemic led the industry to question existing screening techniques, typically, the plating of 200 seeds per lot on nonselective media and visually

examining the transplants. Since then, screening techniques have been improved considerably and new tools have been developed to enhance diagnostic accuracy and convenience.

Semiselective media. The SCM medium of Fatmi and Schaad (16) was among the first semiselective media for isolating *C. m. michiganensis*. It was sufficiently sensitive to detect one infected seed in 10,000, and colony morphology of *C. m. michiganensis* was distinct from that of saprophytic bacteria. Various workers have improved the sensitivity of SCM agar by reducing or eliminating potassium tellurite from the recipe and/or substituting mannose for sucrose (39,44). The D2ANX medium (9), a modification of the D2 medium (30), also is utilized by researchers and seed-testing companies. Another agar medium, KBTS, permitted faster colony development (6 vs. 13 days) and a 10-fold greater sensitivity than did SCM (12). *C. m. michiganensis*, however, exhibits more than one colony type on both SCM and KBTS, and colony types vary somewhat among strains. These and other semiselective media used to recover the pathogen from seed, plant tissue, and soil are compared in Table 1.

The development of improved semiselective media represents a significant advance for the seed and tomato industries, but published comparisons of the available media are few (13,36). Because no one medium is foolproof, many state certification programs, seed-testing laboratories, and industry seed-screening programs currently use several media simultaneously. Determination of the most suitable media also will depend on the type of sample assayed (e.g., seed, plant tissue, soil) and the specialized needs of the investigation (e.g., routine screening, research, regulation).

Antibiotic-resistant mutants of *C. m. michiganensis* have become valuable research tools for field studies of canker. The use of mutants resistant to rifampicin (2,5,6,27) or streptomycin (32) has greatly facilitated selective recovery of the pathogen from seed, debris, soil, and plant tissue on media (e.g., NBY, CNS) amended with the appropriate antibiotics.

Seed assay. The existence of improved semiselective media has made possible large-scale screening of seed lots for *C. m. michiganensis* as well as for other seed-borne bacterial pathogens. In these procedures, samples of 10,000–30,000 seeds typically are ground dry or blended with a buffer solution, and a buffer suspension is diluted and plated on one or more semiselective media, with or without preliminary centrifugation (15,31). Seed lots testing positive for canker typically are rejected for sale or planting.

Transplant assay. Traditionally, transplants grown in the southern United

States for shipment to northern production areas have been certified free of disease on the basis of visual inspection (25). Many infected seedlings are not detected visually, however, because the latent period in young transplants lasts for several weeks (8). A new assay, the stem-print method in which the cut end of a stem is pressed against the surface of semiselective media, allows rapid, convenient screening of great numbers of transplants (23,24). Unfortunately, to ensure a reliable sample for certification, screening transplants for canker by the stem-print method is probably impractical and too costly (25).

Serology. The commercial availability of an antiserum to *C. m. michiganensis* (Agdia, Inc., Elkhart, IN) has created new opportunities to use enzyme-linked immunosorbent assay (ELISA) techniques in detecting the pathogen. Stephens et al (39) found that the limit of detection of pure cultures of the pathogen was 10^4 cfu/ml, or 10^3 cells per microtiter plate, and that ELISA OD readings were proportional to bacterial concentration as measured by direct counts on semiselective media. Gitaitis et al (23) screened young seedlings for the pathogen by expressing sap from stems or by pressing the cut end of a stem directly into ELISA wells coated with the antiserum. The method detected *C. m. michiganensis* in symptomless plants and was specific for the pathogen. Limitations of this assay are that it gives no information about the viability of the pathogen and yields no culture for confirmatory testing.

Immunoisolation. Immunoisolation, a technique combining serology and growth on agar media, shows promise for improving both selectivity and sensitivity of assays for *C. m. michiganensis*, as well as for other bacterial plant pathogens (43). Plastic or glass beads or rods are coated with specific antibodies to trap bacterial cells in a sample extract, and the bound organisms are desorbed and plated on a suitable medium. Ruissen et al (35) reported a significant decrease in the ratio of non-target bacteria to *C. m. michiganensis* after such an immunoisolation procedure.

FAME analysis and Biolog plates. Fatty acid methyl ester (FAME) analysis uses fatty acid composition, as determined by gas chromatography, to differentiate among unknown isolates of bacteria and fungi. Gitaitis and Beaver (22) constructed an extensive library of FAME profiles of *C. m. michiganensis*. These researchers found that the ratio of percentage content of specific FAMES was distinct from the ratios of morphologically similar species of bacteria recovered from tomato plants and seeds and various field sites. All isolates identified by FAME analysis as *C. m. michiganensis* were confirmed by testing

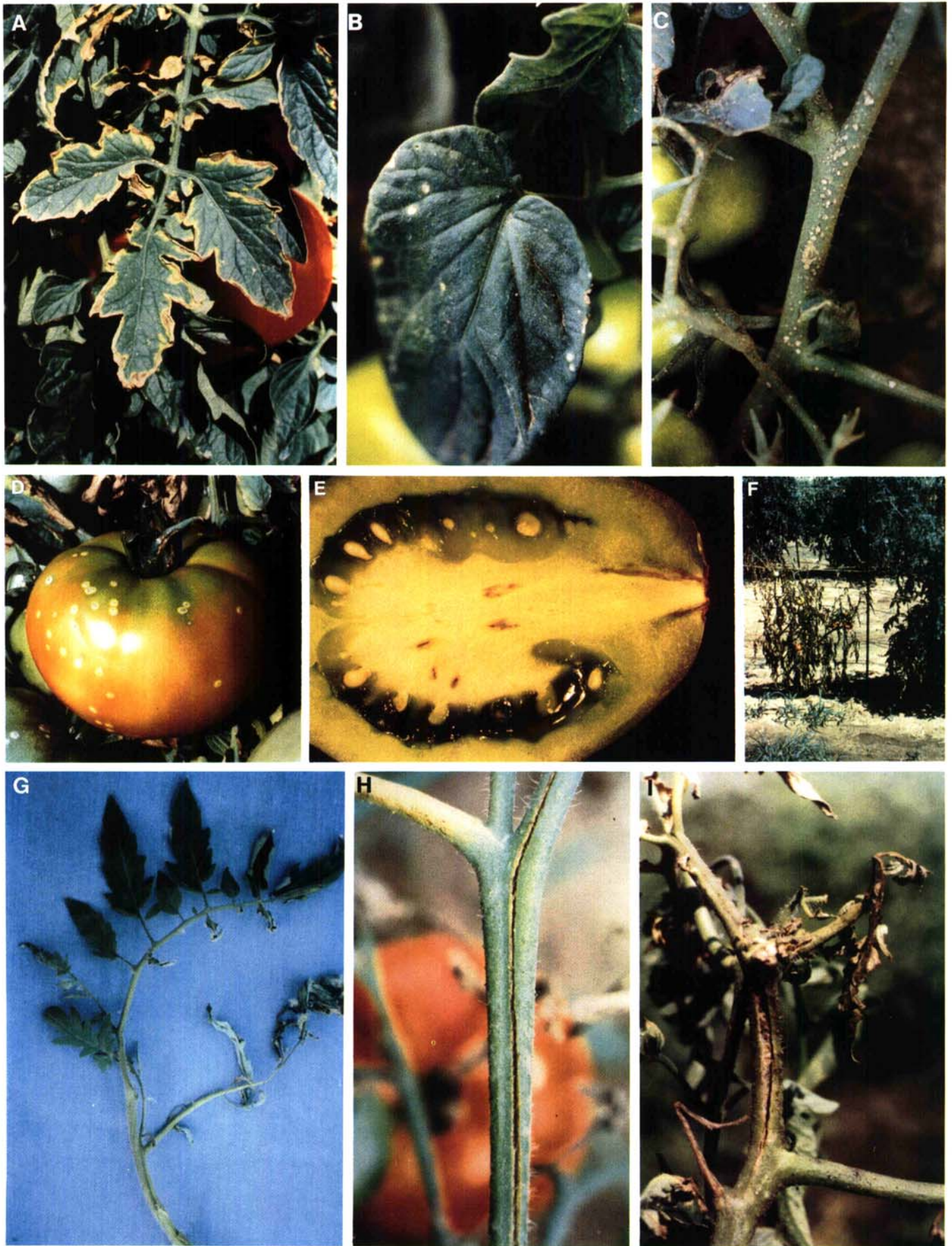


Fig. 1. Symptoms of bacterial canker of tomato: (A) Marginal necrosis of leaflets; small, raised white blisters (B) on cotyledons and leaflets in a greenhouse and (C) on stems in the field; (D) bird's-eye spots on fruit; (E) browning of vascular traces in fruit caused by systemic infection; (F) wilting and collapse of systemically infected transplants; (G) wilting of leaflets on one side of the rachis; and (H) early and (I) later stages of canker development.

for hypersensitivelike reaction and pathogenicity. Compared with semi-selective media and ELISA, however, FAME analysis was a less sensitive and more laborious method of detecting latent infections in tomato seedlings (23).

Microtiter plates whose wells are coated with appropriate reagents to perform 95 standard microbiological tests for bacterial identification simultaneously (Biolog, Inc., Hayward, CA) have been used to confirm identity of isolates of *C. m. michiganensis* (29). When plates designed for identification of gram-negative bacteria were used, only about 50% of strains of *C. m. michiganensis* assayed were identified correctly by the Biolog system (J. B. Jones, *personal communication*). The recent introduction of plates designed specifically for gram-positive bacteria, including *C. m. michiganensis*, should improve the accuracy of this assay for the canker pathogen.

Biolog plates and FAME analysis have compressed from weeks to hours the time needed for isolate characterization. Although the expense, labor, and skill requirements of the FAME assay may sometimes preclude its use in screening seed lots or transplants, its superior speed has led to its routine use by the Georgia Department of Agriculture in isolate identification.

Pathogenicity tests. Pathogenicity bioassays are indispensable for confirming the identity of most phytopathogenic coryneform bacteria. Use of tomato plants to assay for the canker pathogen is constrained by the relatively long interval (3 days to several weeks) between inoculation and symptom expression (21).

A hypersensitivelike reaction, formation of discrete local lesions, has been noted on leaves of tobacco (*Nicotiana tabacum* L.) after inoculation with *C. m. michiganensis*, but the response is erratic among strains and depends upon temperature. Recently, foliage of four-o'clock (*Mirabilis jalapa* L.) was shown to develop distinct symptoms of a hypersensitivelike reaction within 48 hours of inoculation (21). The reaction was temperature-insensitive and consistent for all 35 strains of the pathogen tested. Four-o'clock is now used as a standard pathogenicity test for the canker bacterium in seed lot assays by the Georgia Department of Agriculture and by many other seed-testing organizations.

DNA and plasmid analysis. After performing restriction endonuclease digestion and electrophoresis of total genomic DNA of 13 strains of *C. m. michiganensis* from Ontario, Finnen et al (18) found a DNA fragment approximately 5.9 kb in size that was common to all strains. When a similarly sized (5-kb) fragment of chromosomal DNA, obtained in a similar manner from a clone of a California isolate, was used as a probe, it distinguished pathogenic strains of *C. m. michiganensis* from an avirulent strain, other *C. michiganensis* subspecies, and all other bacterial species tested (41). The extreme specificity of the 5-kb chromosomal fragment for *C. m. michiganensis* and its presence in all strains tested in two geographic locations suggest that it has exciting potential as a diagnostic test for the pathogen.

Plasmid content of *C. m. michiganensis* is quite variable among strains. The number of plasmids per cell ranged from zero to three (3,18), presence or

absence of common plasmids was uncorrelated with pathogenicity (3,41), and some plasmids were lost after storage of isolates (3). These findings suggest that the potential for using plasmid assays as a routine diagnostic tool is limited. On the other hand, plasmid profiles have shown potential value as a means of differentiating isolates and of pinpointing the source of inoculum recovered from diseased plants in the field (3).

Seed Sanitation

Since the 1930s, research on seed treatments for canker control has involved evaluation of the effectiveness of fermentation, hot water, hydrochloric acid, acetic acid, sodium hypochlorite, and various antibiotics. Yet the results of many such trials are difficult to interpret because they used artificially infested seed and quantified neither incidence nor concentration of *C. m. michiganensis* in seed samples before and after treatment. Recent studies utilizing systemically infested seed and the new semiselective media provide more reliable comparisons. Fermentation, used routinely to extract tomato seeds from pulp, sharply reduced populations of *C. m. michiganensis* but frequently failed to eradicate them (14). In a grow-out test, Dhanvantari (14) determined that 96 hours of fermentation at 20 C was required to eradicate the pathogen and that a 1-hour treatment with 0.6 M HCl or a 15-minute treatment with 0.05% *o*-hydroxydiphenyl resulted in a much lower incidence of canker in seedlings than did a 15-minute soak in 0.6% NaOCl. Soaking of one artificially infested seed lot in 0.6 M HCl for 1 hour reduced incidence of canker symptoms

Table 1. Semiselective agar media for isolation of *Clavibacter michiganensis* subsp. *michiganensis*

Medium	Colony pigmentation and morphology	Incubation period (days)	Assay uses	Comments	References
SCM	Small, dark gray mucoid; fluidal with dark gray center; or olive white, or red	9-12	Seeds ^a	Atypical colonies can be circular, flat, raised, or convex with entire margins; such colonies are butyrous, dark gray to black, and pathogenic ^b	15,16
mSCM	Clear, mucoid, yellow flecks in center	7-9	Seeds	Modified version of SCM; fewer contaminants, colonies easier to recognize	44
CNS-LiCl-PBS	Yellow, glistening, convex	6	Seeds, plants	CNS minus LiCl and polymyxin B sulfate	5,6,14,28
KBTS	Yellow with deep green to black centers; two types: large fluidal and small mucoid	6	Seeds	Some interference by <i>Pseudomonas</i> spp.	12
D2ANX	Yellow	6-10	Seeds, plants	Interference by one isolate of <i>P. solanacearum</i> ^c	9
D2	Pale yellow, 1-2 mm convex, glistening	3-4	Plants	Poor sensitivity and selectivity ^d	30
SMCMM	Yellow	3-4	Leaves, soil		36
BHI			Seeds		31

^aPoor selectivity in soil assay (B. N. Dhanvantari, *unpublished*).

^bR. D. Gitaitis (*unpublished*).

^cM. D. Ricker (*unpublished*).

^dB. N. Dhanvantari (*unpublished*).

in the resulting seedlings from 38% to 0.1%. Fatmi and Schaad (17) also found that at room temperature, neither NaOCl nor Ca(OCl)₂ eradicated the pathogen from all seeds. Fatmi and Schaad (17) recommended a 20-minute treatment of *C. m. michiganensis*-infested seed lots with either water at 52 C or 0.25% acidified cupric acetate. Although not 100% efficacious, Ca(OCl)₂ is used widely by the tomato-seed industry because it is easy and safe for workers to handle, yields consistent results, and maintains seed quality (J. Hubbard, *personal communication*). While these treatments are very effective in reducing seed contamination, none should be considered fail-safe for canker eradication.

Ecology and Epidemiology

Field production of transplants.

Tomato growers in eastern North America traditionally have obtained transplants from Georgia and Florida, where they are direct-seeded in late winter and early spring. The seedlings are clipped repeatedly with rotary mowers to ensure size uniformity. Recent studies have documented clearly the risks associated with this practice. Chang et al (5) showed that mowing of transplant beds with a few infested plants initially present increased the incidence of systemically infected plants 100-fold and that handling of transplants during harvest and shipment raised infection incidence an additional three- to fivefold. Plants of a susceptible cultivar that were infected during clipping or handling lost as much as 46% of their potential yield, and each 10% rise in infection incidence resulted in a yield decline of 5–7% (7). Results of another study showed that the terminal end of clipped stems became infected within 2 days and that the canker bacteria multiplied and spread rapidly, colonizing the stem 10 cm below the terminal end within 1 week (23). Results of field experiments showed that a transmission rate from seed to seedling of 0.01% could initiate a serious epidemic in tomato production fields (5,23). At current seeding rates, one infested seed in 10,000 could result in 100 ± 25 infection foci per hectare in direct-seeded beds, after which clipping of the tops could result in thousands of plants with latent systemic infections (23). Clearly, extremely sensitive seed-certification tests for *C. m. michiganensis* are needed, because the potential for canker outbreaks created by cultural practices during field production of transplants is explosive. A recent review (25) outlines steps taken by the Georgia transplant industry to reduce the risk of disease transmission.

Overwintering. Overwintering of *C. m. michiganensis* in infested tomato debris could initiate epidemics in subsequent growing seasons. Recent field studies tracked populations of rifampicin-resis-

tant mutants of the pathogen in debris. Populations declined gradually but persisted at least 200 days in Illinois (6) and at least 850 days in Iowa (27; M. L. Gleason, *unpublished*). Tomato debris decomposed and populations of *C. m. michiganensis* declined faster when debris was buried in soil than when held at the soil surface. In Iowa, overwintered infested debris caused a canker epidemic and resulted in a significant yield loss of 27% in processing tomatoes (27). This was the first direct evidence that overwintered debris can cause economic losses in a subsequent crop. In Georgia, the pathogen does not survive the summer in debris in the transplant fields but can overwinter in the more recalcitrant debris from fall tomato fruit production (20). The recent overwintering studies reinforce the value of two widely recommended cultural practices for canker control: rotation away from tomatoes for more than 2 years and deep plowing after harvest to accelerate the decomposition of debris.

Dissemination and infection in production fields. In addition to seeds, transplants, and infested debris, alternative host species and volunteer tomato seedlings provide means for *C. m. michiganensis* survival (40). The mechanisms of dissemination in production fields are believed to include splashing water, pesticide spraying, pruning, tying, and harvesting. These mechanisms suggest that *C. m. michiganensis*, like many other phytopathogenic bacteria, persists as an epiphyte on leaf surfaces. Recent studies confirm that the pathogen can maintain large epiphytic populations on leaves of tomato (6,27,42) and smaller populations on various other solanaceous and non-solanaceous species (6,42). Epiphytic populations on tomato were largest on young leaves (42), on relatively canker-susceptible cultivars (6), and in the presence of free water (26,42).

The significance of epiphytic populations of *C. m. michiganensis* in the canker disease cycle seems to depend upon many circumstances. In field studies with processing tomatoes, secondary spread of the pathogen from foci (systemically infected transplants) to nearby plants resulted in marginal necrosis and in bird's-eye fruit spots (6,34) as well as in vascular discoloration of stems (34), but yields were unaffected (34). On the other hand, planting into overwintered, infested debris resulted in large epiphytic populations, followed by wilting of leaves and a significant reduction in yield (27). These findings suggest that at least for processing tomatoes, the impact of dissemination on disease development depends upon the source of inoculum and upon the degree to which it is dispersed in the field.

On fresh-market tomatoes, common cultural practices such as pruning, tying, and staking create wounds that can allow

epiphytic populations of *C. m. michiganensis* to invade plants. A recent experiment documented that manual pruning of plants harboring epiphytic populations of *C. m. michiganensis* accelerated colonization of the vascular system and reduced yields significantly (2). This study showed that pruning poses a serious risk to the grower when the pathogen is present as an epiphyte. Vascular colonization, although slower than on pruned plants, also was extensive even in the absence of obvious wounding. This raised the question of how epiphytic populations gained entry in the absence of wounding. One explanation was provided by Carlton et al (1), who noted that several weeks after guttation droplets on tomato leaflets were inoculated with the pathogen, marginal necrosis appeared, followed by leaflet withering and vascular colonization of the rachis (Fig. 2). Exudation and withdrawal of guttation droplets through hydathodes thus provided a mechanism of entry for epiphytic populations into tomato plants. This mode of entry has also been demonstrated for *X. c. pv. campestris*, the causal agent of black rot of cabbage.

Incubation period and disease severity.

One of the most puzzling aspects of canker epidemiology is the great variability in duration of the period between infection and symptom expression. The incubation period for systemic symptoms in various studies ranges from 7 to 84 days (8). Earlier studies pointed to low temperature, plant age, and low-nutrient status as factors that could delay symptom expression. Chang et al (8), in the first quantitative study of factors affecting incubation period, reported that incubation period was longer and symptom development less severe with older plants, temperatures cooler or warmer than 25 C, moderately resistant cultivars, and lower inoculum concentrations. Conditions favoring the most rapid development of symptoms also induced the most severe symptoms.

Host Resistance

Progress in developing genetic resistance to canker has been modest. Moderate resistance has been found in wild relatives of tomato, including *L. pimpinellifolium* (L.) Mill., *L. hirsutum* Humb. & Bonpl., and *L. peruvianum* (L.) Mill. Several tomato cultivars with resistance or tolerance have been introduced, but few commercial cultivars used in eastern or midwestern North America possess significant tolerance to canker. Comparison of results among screening trials is complicated by wide variation in inoculation procedures and strain aggressiveness. In field screening of cultivars having a wide range of resistance, Chang et al (4) found that both the time required for appearance of first symptoms and the severity of symptom development were normally distributed.

Thus, resistance ratings of cultivars could be assigned on the uniform basis of standard deviations below or above the mean. Gardner et al (19) evaluated and crossed numerous lines in an ongoing program whose goal is to combine resistance to both canker and early blight. These investigators currently are screening F₅ offspring of these crosses (R. Gardner, *personal communication*). Poysa (33) recently reported that six F₈ breeding lines exhibited significantly higher yield and fruit size than the moderately resistant parents, Hawaii 7998 and Irat L-3, and a susceptible parent, Purdue 812, following wound inoculation through either the roots or a petiole.

Another approach to developing resistance has been induction of mutations. DeVries-Paterson and Stephens (11) found that both somaclonal variation and gamma irradiation induced canker-resistant mutations in tomato and other *Lycopersicon* species but that somaclonal variation was more efficient.

Chemical Control

In most of eastern North America, effectiveness of copper-containing bactericides for canker control has not been well documented. The exception is western North Carolina, where frequent rainfall and prolonged wet periods make the foliar blight phase of canker unusually severe. In this environment, sprays of commercially available copper products every 5–7 days, alone or mixed with various contact fungicides, reduced foliar blight and/or fruit spotting significantly (37).

Summary and Outlook

Assays of seed lots for *C. m. michiganensis* and other seedborne bacterial pathogens by seed companies and government agencies are becoming routine. Recent advances have introduced faster, more efficient, and more reliable methods of isolation, chemical and microbiological characterization of isolates, and pathogenicity bioassays. Instead of assaying 200-seed samples per lot, replicated 10,000- to 30,000-seed samples are now standard (16,25). These changes should increase confidence in seed certification procedures for tomato growers and the seed industry. The new diagnostic tools also have opened up countless new avenues for canker research.

Despite major improvements in seed certification and sanitation, the risk of canker epidemics remains. The impact of the industry's transition to labor-intensive hybrid seed, shifting the center of tomato seed production from North America to Southeast Asia over the last 15 years, on contamination of seed lots is unknown. As recent studies of field production of transplants have shown, a single infected or infested seed in 10,000 can initiate an epidemic under favorable conditions. Clearly, even more sensitive seed assay techniques (e.g., immunoisolation, DNA probes, and polymerase chain reaction techniques) are needed. A pressing need also exists for environmentally safe seed treatments that can eradicate the pathogen under the seed coat without reducing seed germination or storage life.

In part because of the perceived threat

of canker in field-produced transplants, the tomato industry in eastern and midwestern North America is rapidly shifting to nonclipped, greenhouse-grown transplants. Nevertheless, the sources of inoculum for several recent outbreaks of canker in production fields have been traced to infected greenhouse transplants. *C. m. michiganensis* may spread rapidly in greenhouses, but the epidemiology of canker in this environment has received little study. Some highly modernized greenhouses use automated clippers to control height of tomato transplants (W. Nesmith, *personal communication*), a practice likely to increase the risk of canker epidemics enormously. Research to elucidate the mechanisms of spread of the pathogen in the greenhouse environment is a top priority of the tomato industry.

Recent progress in understanding the behavior of the pathogen in production fields has again underscored the value of cultural techniques—use of certified transplants, fall plowing to bury crop residue, rotation away from solanaceous crops for a minimum of 2 years, control of weeds and tomato volunteers, and avoidance of pruning—to reduce the risk of canker outbreaks. Many important epidemiological questions remain unanswered, however. For example, the role of alternative hosts and volunteer tomato seedlings in overwintering of canker has not been investigated. Another question is how water availability and other environmental stresses affect rate and severity of disease development.

Progress in developing canker-resistant tomato cultivars is being made,

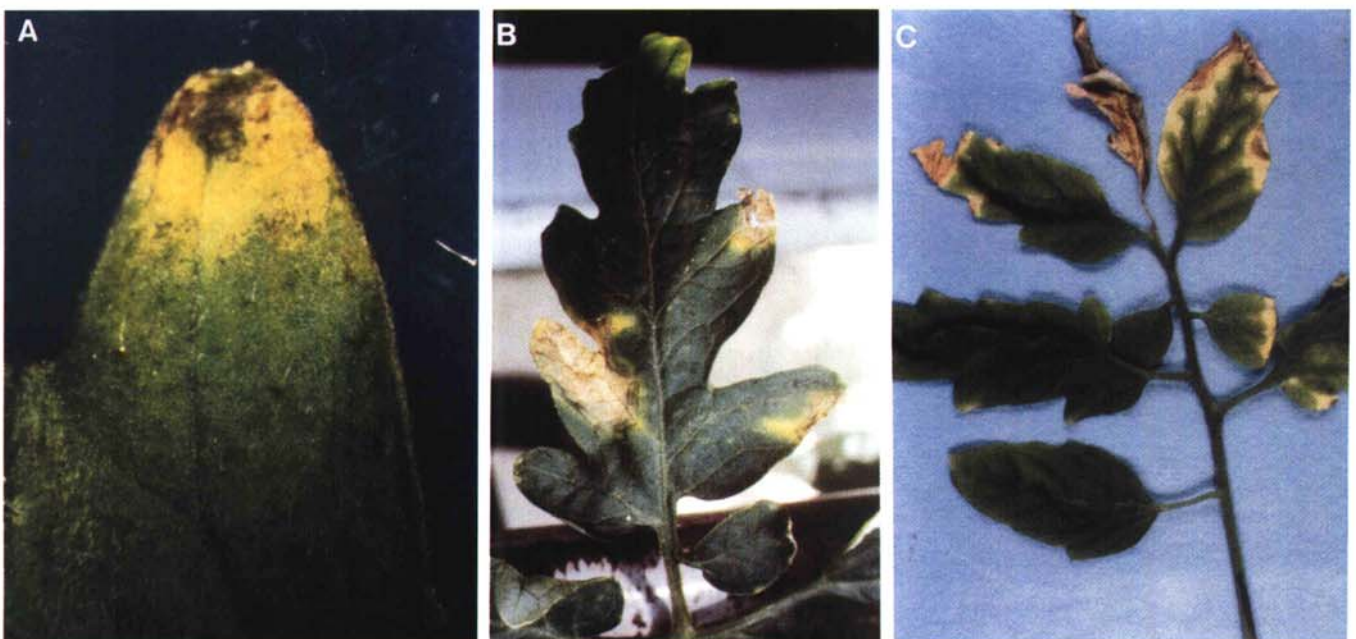


Fig. 2. Sequence of symptom development on tomato leaves after inoculation with *Clavibacter michiganensis* subsp. *michiganensis* in guttation droplets on a terminal leaflet: (A) Yellowing in the vicinity of the inoculation point, (B) necrosis along leaflet margins and main veins, and (C) collapse of the inoculated leaflet and neighboring leaflets.

through both traditional breeding and biotechnology approaches, but a great deal remains to be accomplished. Nevertheless, it seems probable that commercially viable cultivars with much-improved resistance to canker will become available in the near future. Finally, no wish list for canker control would be complete without including the development of a systemic, environmentally safe bactericide to oppose the pathogen in the field and the greenhouse.

Although continued research is needed in genetic resistance, seed sanitation, transplant certification, pathogen detection and identification, and cultural techniques, the tomato industry has reaped significant benefits from recent progress and has gained a wider margin of protection against future canker outbreaks.

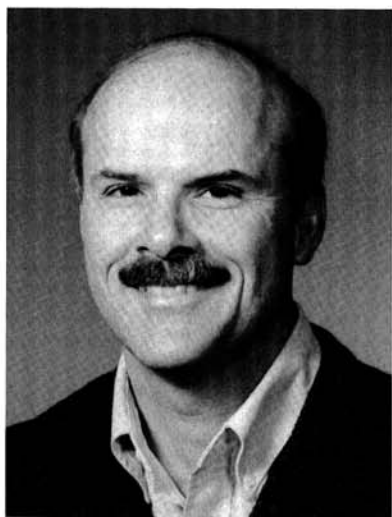
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