Association of Pectolytic Strains of *Xanthomonas campestris* with Soft Rots of Fruits and Vegetables at Retail Markets

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We thank J. E. Butterfield and R. Oseredczuk for help in collecting plant specimens and preparing culture media, respectively.
Accepted for publication 18 July 1986.

ABSTRACT

Liao, C. H., and Wells, J. M. 1987. Association of pectolytic strains of *Xanthomonas campestris* with soft rots of fruits and vegetables at retail markets. Phytopathology 77:418-422.

Five strains of pectolytic, yellow-pigmented bacteria were isolated from rotted specimens of tomato, bell pepper, cucumber, and papaya collected at retail markets. The bacteria possessed cultural, morphological, and physiological properties conforming to those of *Xanthomonas campestris*. Each of the five strains obtained was capable of causing soft rots of detached plant parts of eight different crops (including potato tubers, carrot roots, celery petioles, cauliflower and broccoli curds, and fruits of cucumber, bell pepper, and tomato). The pathogenicity of each strain to plants (tobacco, cucumber, bell pepper, cabbage, and tomato) grown in the greenhouse could not be conclusively determined. These soft-rotting xanthomonads might represent an unusual cluster of *X. campestris* that exclusively attack plant materials after harvest and cause only soft rot symptoms. The tomato isolate excreted pectate lyase, pectin esterase, and polygalacturonase in medium containing polygalacturonic acid or pectin but not in a medium containing glucose. Two strains of *X. campestris* pv. *campestris* also produced extracellular enzymes in pectate media and were capable of causing mild rots of potato slices and other plant parts. This study provides the first experimental results indicating that some postharvest rots of plant crops may be attributed to pectolytic xanthomonads.

Pectolytic activity in phytopathogenic xanthomonads has been observed in a large number of strains examined by several workers (1,5,11,15,26,28,31). Although pectolytic activity is often implicated in the ability of a bacterium to rot plant tissues (23), such a correlation does not fully account for the pathogenicity of xanthomonads. Symptoms caused by xanthomonads in the field, unlike those induced by soft rot erwinias and pseudomonads, are usually blights, cankers, and necrotic lesions (22). The reason xanthomonads encoded with pectolytic capability fail to induce typical soft rots in the field is not yet known. It has been suggested (4,7), however, that xanthomonads may be occasionally associated with rots of fleshy vegetables after harvest.

After harvest, plants and their products gradually lose vigor and defense mechanisms against invading microorganisms. Detached plant parts ready for marketing are therefore vulnerable to the attack of an array of bacteria that normally do not cause diseases of plants growing in the field. The storage organs of some plants, such as tubers of potatoes, are affected by several genera of pectolytic bacteria generally considered as saprophytes in soil, including *Clostridium* (19), *Bacillus* (10), and *Flavobacterium* (18). Previous studies on bacteria causing postharvest rots of vegetables have been limited to two genera (*Erwinia* and *Pseudomonas*). Efforts have not been made to investigate if pectolytic bacteria of other genera may be involved.

With these considerations, we reasoned that a reexamination of pectolytic bacterial flora associated with decays of fruits and vegetables was needed. A survey was conducted during which more than 127 soft-rotting isolates belonging to the genera of *Erwinia*, *Pseudomonas*, *Bacillus*, *Cytophaga*, and *Xanthomonas* were collected. Properties of the first four of these genera have been reported in depth elsewhere (16,17). This paper details the cultural, physiological, and pathological properties of five strains of yellow-pigmented bacteria tentatively identified as *X. campestris*. For comparative purposes, four known strains of *X. campestris* representing pathovars *campestris*, *phaseoli*, and *vesicatoria* were included.

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MATERIALS AND METHODS

Rotted plant specimens. Rotted fruits of tomato, bell pepper, cucumber, and papaya were collected from local food stores in the summer (June-September) of 1984. The specimens were used for isolations on the same day that they were brought into the laboratory. Rots caused by bacteria could be visually differentiated from those caused by fungi. Bacterial rots frequently led to total disintegration of fruit tissues, whereas lesions infected by fungal rots very often retained firmness and coherence. Specimens were regularly examined under the light microscope before isolations were conducted to confirm the presence of bacteria.

Isolation media and methods. The crystal-violet polypectate (CVP) medium of Cuppels and Kelman (9) was used as an isolation medium, but the concentration of sodium polypectate (Sunkist Grower Co., Inc., Ontario, CA) was reduced to 9 g/500 ml of medium as suggested (27). The CVP medium was occasionally enriched with 0.1% yeast extract and later used to isolate a pectolytic strain of *Cytophaga* sp. (17) and two pectolytic, yellow-pigmented xanthomonads (PF 083 and CJ 093, Table 1). Primary isolations were performed according to the conventional streak-plate method. A loopful of rotted tissues was streaked onto an agar plate, and incubation was at 26 C for 2 days. Single colonies were individually picked and successively cloned for purity on the same medium at least three times. For long-term preservation, a low-salt medium containing beef extract (1%), proteose peptone (1%), and agar (0.9%) was stab-inoculated with bacteria and subsequently overlaid with a layer (2–3 cm) of sterile mineral oil.

Bacterial strains. In addition to five strains of pectolytic, yellow-pigmented bacteria (PYB) obtained in the study (Table 1), four known strains of *X. campestris* (pv. *campestris* 42 and 43, pv. *phaseoli*, and pv. *vesicatoria*) were included. These known strains were provided by E. Civerolo (USDA/ARS, Beltsville, MD). The orange-pigmented *Cytophaga* sp. (strain PF 062) and the yellow-pigmented *Pseudomonas* sp. (strain SJ 074) were isolated from rotted bell pepper (17) and zucchini squash (16), respectively. The orange-pigmented *Flavobacterium pectinovorum* (strain 19399) was obtained from the ATCC (Rockville, MD). The orange-

pigmented mutant of *E. carotovora* subsp. carotovora (SR319) was induced by chemical mutagenesis (Liao, *unpublished*).

Bacterial characterization. Bacteriological tests were performed according to the determinative schemes described by Dye (12,13) and by Bradbury (3). These included Gram-staining; flagella staining; cellular morphology; motility; oxidase reaction; presence of arginine dihydrolase; nitrate reduction; hydrolysis of esculin, urea, and starch; gelatin hydrolysis; digestion of milk proteins; production of indole, H_2S, and fluorescent pigments; hydrolysis of Tween 80; anaerobic growth; tolerance of NaCl and triphenyl tetrazolium chloride; and use of asparagine as carbon and nitrogen source.

Utilization of carbon sources. The minimal medium (pH 7.0) of Chatterjee et al (6) containing K_2HPO_4 (0.7%), KH_2PO_4 (0.2%), $MgSO_4$ $7H_2O$ (0.02%), $(NH_4)_2SO_4$ (0.1%), and agar (1.5%) was supplemented with yeast extract (0.01%) and used for the experiments. A total of 24 carbon sources (Table 2) were tested. The carbon sources were filter-sterilized and were added after the basal solutions were autoclaved. Each carbon source was added into the medium to a final concentration of 0.4%. Ethanol and propylene glycol were tested at a final concentration of 3% in the medium. Bacterial strains were streaked onto agar plates by sterile toothpicks, usually four bacterial strains per agar plate. Samples were incubated at 26 C and results were recorded 1 wk after inoculation.

Growth at 4 and 37 C. Because growth at elevated temperatures is useful for differentiating species of *Xanthomonas* (3,13) and growth of soft rot bacteria at low temperatures is an important factor in storage and transport of plant crops (20), the yellow-pigmented strains of bacteria were tested for growth at 4 and 37 C. A yeast extract-dextrose-calcium carbonate agar medium (12) and nutrient broth enriched with yeast extract (0.1%) were inoculated with bacteria and incubated at both temperatures for 7 days. Growth in broth medium was determined by an increase of optical density, and growth on agar medium was determined by the appearance of mucoid slime.

Color and slime formation. Two media previously suggested (12,22) for the examination of yellow pigmentation and mucoid slime production by the genus *Xanthomonas* were used. Preparation of yeast extract-dextrose-calcium carbonate agar medium and sucrose-peptone agar were made as described previously (12).

Assays of pectolytic ability and pectic enzymes. Ability of bacteria to liquefy polypectate was assayed primarily on CVP medium, and a positive reaction was indicated by the formation of a pit. Excretion of pectolytic enzymes was also tested in a medium (MM-9, pH 7.2) containing glycerol (0.5%), yeast extract (0.2%), $MgSO_4$ $7H_2O$ (1 mM), $CaCl_2$ $2H_2O$ (1 mM), polygalacturonic acid (0.4%), and agar (1.5%). After incubation at 26 C for 2 days, the inoculated MM-9 agar plates were flooded with a saturated solution of copper acetate. Excretion of pectic enzymes into agar media was indicated by the formation of a halo surrounding the bacterial growth (2). The presence of pectate lyase, pectin esterase, polygalacturonase, and pectin lyase in culture filtrates was determined by the methods described by Starr and Nasuno (31) except that the minimal medium of Chatterjee et al (6) was used.

Assays of cellulases and chitinases. Soft-rot bacteria were often characterized by their ability to depolymerize not only pectic substance but other macromolecules such as starch, cellulose, protein, and chitin. Methods for detection of starch and protein hydrolysis have been described elsewhere (12,27). Procedures for assays of cellulase and chitinase are not readily available and are presented here.

The medium (CM-3) containing yeast extract (0.1%), carboxymethyl cellulose (3%), agar (1.5%), and minimal salts (6) was inoculated with bacteria and incubated at 26 C for 3 days. Incubated agar plates were flooded with Congo red (0.1%), left standing for 15 min, and bleached with 1 M NaCl or acidified with 1 N HCl. Cellulase activity was revealed by the appearance of a halo surrounding bacterial growth or frequently by the formation of a pit (shallow depression) similar to that observed on CVP medium. The CM-3 medium containing colloidal chitin (1%) was used to detect chitinase activity. Colloidal chitin was prepared according to the methods of Stanier (29). Chitin flakes (Sigma Chemical Co., St. Louis, MO) were dissolved in 50% cold H_2SO_4 and subsequently precipitated with two volumes of water. Colloidal chitin precipitate was washed three times with water. Excretion of chitinase into agar media was detected by the formation of a clear zone surrounding the bacterial growth.

Assay of macerating ability. Detached plant parts of eight different crops of unknown cultivars were used to study the soft-rotting ability of cultured bacteria (Table 3). Plant materials were surface sterilized in a 1% solution of sodium hypochlorite for 10 min. Slices of potato tubers, celery petioles, carrot roots, cucumber fruits, and curds of cauliflower and broccoli were placed on water

TABLE 1. Isolation of pectolytic organisms from rotted specimens

Sources of isolate	Crop origin	Month isolated (1984)	Specimens examined (no.)	Pectolytic strains isolated	
				Total[a]	Yellow-pigmented[b] (strain)
Tomato	NJ	July	12	8	1 (TJ 071)
Bell pepper	FL	Aug	45	40	1 (PF 083)
Papaya	HI	June	2	1	1 (PP 061)
Cucumber	NJ	Sept	11	7	2 (CJ 092, CJ 093)

[a] Belonging to *Erwinia, Pseudomonas, Cytophaga, Bacillus,* or *Xanthomonas.*

[b] Strains PF 083 and CJ 092 were isolated on crystal-violet polypectate medium enriched with yeast extract (0.1%); the remaining strains were isolated on unenriched crystal-violet polypectate medium. Strains were designated collectively as PYB.

TABLE 2. Utilization of 24 carbon sources by five strains of pectolytic, yellow bacteria (PYB) associated with rotted specimens and by four known strains of *Xanthomonas campestris*[a]

C sources	PYB (Strain)					*X.c.*			
	(TJ071)	(PF083)	(PP061)	(CJ092)	(CJ093)	*campestris* #42	*campestris* #43	*phaseoli*	*vesicatoria*
Glucose + 4 others[b]	+	+	+	+	+	+	+	+	+
Adonitol + 8 others[c]	−	−	−	−	−	−	−	−	−
Polygalacturonic acid	+	+	+	+	+	+	+	−	−
Pectin	+	+	+	+	+	−	−	−	−
Polypectate	+	+	+	+	+	+	+	+	+
Mannose + 2 others[d]	+	+	+	+	+	+	+	+	+
Tartrate	−	+	−	−	−	−	−	−	−
Lactose	+	+	+	−	−	−	−	−	−
Glycerol	+	+	+	+	+	−	−	−	−
Maltose	+	+	+	+	+	±	−	−	−

[a] +, growth; −, no growth, ±, limited growth.

[b] Sucrose, mellibiose, xylose, trehalose.

[c] Mannitol, α-methylglucoside, propylene glycol, propionate, alanine, 2-ketogluconate, erythritol, rhamnose.

[d] Cellobiose, galactose.

agar (0.6%) and inoculated with approximately 0.1 ml of a bacterial suspension containing approximately 2×10^8 colony forming units per milliliter in sterile water. To inoculate intact fruit of tomato and bell pepper, the epidermis was wounded with a 25 G syringe needle. A cotton swab was used to smear a bacterial suspension on the wound site. Inoculated fruit was incubated at room temperature (20 C) for 4 days. Degree of tissue maceration was rated on a scale of 0–5. Tests were repeated at least four times with three to six replications per experiment. Fruits or slices of detached plant parts inoculated with sterile water were used as controls.

Test pathogenicity. Plants of tobacco (*Nicotiana tabacum xanthi*), cucumber (*Cucumis sativus*), bell pepper (*Capsicum annuum*), cabbage (*Brassica oleracea* var. *capitata*), and tomato (*Lycopersicon esculentum*) were grown in the greenhouse. The stem and petiole of each plant (2 mo old) were pricked with a 25 G syringe needle. A bacterial suspension containing 2×10^8 colony forming units per milliliter in sterile water was smeared onto the wound site with a cotton swab. Leaves of tobacco plants were infiltrated with a bacterial suspension according to the method previously described (27), to test hypersensitive reactions. Inoculated plants were placed in the greenhouse and covered with a plastic bag during the first 18–24 hr after inoculation, to ensure high humidity. Plants were examined daily for symptoms for 3 wk after inoculation.

RESULTS

Isolation. Five strains of PYB were isolated from rotted tomato, pepper, papaya, or cucumber fruits (Table 1). Although PYB were not recovered as frequently as other pectolytic bacteria, repeated isolations of PYB from various fruits originating from different places at different months of the year suggested that association of this group of organisms with soft rots was not uncommon. Colonies formed by PYB on CVP medium containing bromothymol blue as a pH indicator were distinguishable from those formed by pectolytic erwinias and pseudomonads. The former exhibited mucoid growth and greenish yellow coloration, whereas the latter had a nonmucoid and creamy or pinkish white appearance. In each case, pits formed around colonies. Because homogeneous colonies of only one type (either yellowish green or creamy white) were found on primary isolation plates, there was no indication of multiple infection by different pectolytic bacteria.

Characterization. The PYB were Gram-negative and motile with a single polar flagellum, which was faintly visible under a phase-contrast microscope after staining with silver nitrate (27). In addition to mucoid growth, PYB could be readily differentiated from other yellow (or orange) pigmented soft-rot bacteria on the basis of nine bacteriological tests (Table 4). The PYB and four known strains of *X. campestris* were subjected to 10 physiological tests to determine the relationship of PYB to *X. campestris*. Results of these tests were compared with those reported for other *Xanthomonas* spp. (Table 5) (3). The PYB possess properties that are characteristic of *X. campestris* and could be readily differentiated from other type species of *Xanthomonas* (*X. fragariae*, *X. albilineans*, *X. axonopodis*, and *X. ampelina*) by their ability to digest milk proteins, their relatively faster growth rate and higher tolerance to NaCl. The PYB seem to constitute a uniform group; none of the physiological tests could be used to distinguish one strain from another. The PYB were similar to two strains of *X. c.* pv. *campestris* but differed slightly from *X. c.* pv. *vesicatoria* and *X. c.* pv. *phaseoli* in their ability to grow at 4 C and in their ability to hydrolyze starch.

Utilization of carbon sources. All nine strains of xanthomonads included in the study grew in media containing glucose, sucrose, α-D(+)-melibiose, D(+)xylose, and D(+)trehalose but were unable to grow in media containing D-mannitol, α-methylglucoside, propylene glycol, propionic acid, β-alanine, 2-ketogluconate,

TABLE 3. Comparison of macerating ability of five strains of pectolytic, yellow bacteria (PYB) associated with rotted specimens and four known strains of *Xanthomonas campestris*

	Average maceration indices[a]								
	PYB (Strain)					*X.c.*			
Plants	(TJ071)	(PF083)	(PP061)	(CJ092)	(CJ093)	*campestris* (#42)	*campestris* (#43)	*phaseoli*	*vesicatoria*
Potato	5.0	5.0	5.0	5.0	5.0	3.6	1.5	0	0
Bell pepper	5.0	5.0	5.0	5.0	5.0	2.7	0.3	0	0
Cucumber	3.8	4.1	4.5	4.8	4.2	0	0	0	0
Cauliflower	5.0	5.0	5.0	5.0	5.0	0	0	0	0
Broccoli	5.0	5.0	5.0	5.0	5.0	0	0	0	0
Tomato	5.0	4.8	4.9	3.8	4.1	1.8	0.4	0	0
Carrot	3.6	4.1	2.8	3.1	3.6	3.1	0.8	0	0
Celery	2.1	1.8	3.1	2.7	1.9	1.3	1.7	0	0

[a] Maceration was judged on a 0–5 scale representing 0, 20, 40, 60, 80, and 100% maceration, respectively.

TABLE 4. Comparison of properties of soft-rotting xanthomonads (five strains of pectolytic, yellow bacteria [PYB]) and other soft-rotting yellow-pigmented bacteria

Properties	PYB	*Cytophaga* sp. (PF 062)	*Flavobacterium*[a] sp.	*Pseudomonas*[b] sp. (SJ 074)	*Erwinia*[c] *carotovora* (M-9)	*Flavobacterium pectinovorum* (ATCC 19399)
Morphology	Rod	Long rod, filament	Round rod	Rod	Round rod	Long rod, filament
Pigmentation	Yellow	Orange	Yellow/orange	Yellow	Orange	Orange
Flagella (no.)	1	0	0	≥1	≥5	0
Motility	Motile	Gliding	No	Motile	Motile	Gliding
Spreading growth	No	Yes	No	No	No	No
Fluorescence	No	No	No	Yes	No	No
Anaerobic growth	No	No	No	No	Yes	No
Mucoid growth	Yes	No	No	No	No	No
Cellulase	Yes	Yes	NT	No	Yes	Yes
Amylase	Yes	Yes	NT	No	No	Yes
Chitinase	No	Yes	NT	No	No	Yes

[a] Data from Lund (18). NT = not tested.
[b] Isolated from rotted zucchini squash.
[c] Induced from mutation in the laboratory, parent strain *E. carotovora* subsp. *carotovora* (SR319).

TABLE 5. Physiological tests used to identify five strains of pectolytic, yellow bacteria (PYB) associated with rotted specimens[a]

		Xanthomonas campestris			*Xanthomonas*[b]			
	PYB	*campestris*	*phaseoli*	*vesicatoria*	*fragariae*	*albilineans*	*axonopolis*	*ampelina*
Mucoid growth	+	+	+	+	+	−	−	−
Hydrolysis								
Gelatin	+	+	+	+	+	±	−	−
Esculin	+	+	+	+	−	+	+	−
Starch	+	+	−	−	+	−	+	−
Milk proteins	+	+	+	+	−	−	−	−
Urease activity	−	−	−	−	−	−	−	+
Growth (37 C)	+	+	−	+	−	+	+	−
Growth (4 C)	+	+	−	−	ND	ND	ND	ND
Maximum Nacl tolerance (%)	2.5	2.5	2.5	2.5	1.0	0.5	1.0	1.0
Growth rate at 26 C	Fast	Moderate	Moderate	Moderate	Slow	Slow	Slow	Slow

[a]+, positive reaction; −, negative reaction; ±, variable; ND, not determined.
[b]Data from Bradbury (3).

erythritol, or L-rhamnose (Table 2). Minor differences in utilization of certain carbon sources were observed among PYB and four known strains of *X. campestris*. The PYB utilized glycerol and pectin, whereas none of the known *X. campestris* strains was able to do so. The pepper isolate (PF 083) was the only strain that utilized D-tartrate. The cucumber isolates (strains CJ 092 and CJ 093), unlike other strains of PYB, were unable to utilize lactose.

Pectolytic activity and excretion of pectic enzymes. The ability of PYB to liquefy pectate gels was noticed initially on CVP medium during primary isolations. Pectolytic activity was also detected in two strains of *X. c.* pv. *campestris* but not in the one strain each of *X. c.* pv. *vesicatoria* and *X. c.* pv. *phaseoli* that we examined. To confirm further the excretion of pectic enzymes, bacteria were grown in MM-9 agar medium containing 0.4% polygalacturonic acid. Bacterial strains that were pectolytic in CVP medium also excreted pectic enzymes (presumably pectate lyase) into MM-9 medium. The tomato isolate (strain TJ 071) grew in minimal medium containing glucose, polygalacturonic acid, or pectin. Pectate lyase was detected in culture media containing either polygalacturonic acid or pectin but not in media containing glucose. Production of pectate lyase by TJ 071 was inducible. Either pectin esterase or polygalacturonase activity was occasionally detected but was weak. There was no detectable activity of pectin lyase.

Macerating ability. Experiments were conducted to investigate whether pectolytic activity detected in five strains of PYB and two strains of *X. c.* pv. *campestris* could be correlated with their ability to macerate fresh plant materials. The average degree of maceration of eight types of plants, caused by nine strains of bacteria examined, is summarized in Table 3. The PYB caused total maceration (rating of 5) of inoculated slices of potato tubers, cauliflower or broccoli curds, and bell pepper fruit. Celery petiole, carrot roots, and fruits of tomato and cucumber were relatively resistant to the attack of PYB, and there was less vigorous maceration observed in inoculated tissues. Two pectolytic strains of *X. c.* pv. *campestris* included in the study induced relatively mild rot in five (potato, bell pepper, tomato, carrot and celery) of the eight crops. In contrast, *X. c.* pv. *vesicatoria* and *X. c.* pv. *phaseoli*, which had no pectolytic activity in pectate media, were unable to induce rots in any of eight plants tested.

Pathogenicity to living plants. Attempts were made to determine if the PYB were able to cause diseases of tomato, cucumber, bell pepper, cabbage, and tobacco plants grown in the greenhouse. No obvious symptoms developed in stems or leaves of plants inoculated with PYB. The hypersensitive (necrotic) reaction did not occur in inoculated tobacco plants. It was not determined, however, whether the PYB survived and colonized the inoculated plants.

DISCUSSION

Five strains of soft-rotting yellow-pigmented bacteria directly isolated from decayed produce were identified as *Xanthomonas* according to morphological, cultural, nutritional, and physiological tests. The soft-rotting xanthomonads obtained in the study could be readily differentiated from other yellow (or orange) pectolytic bacteria (Table 4) and were identified as *X. campestris* on the basis of 10 physiological tests (Table 5). A separate study has been directed to examine the pigments produced by different groups of yellow bacteria (Table 4). Preliminary results show that soft-rotting xanthomonads produce a pigment with a maximum absorption at 435 mμ, which can be detected in *X. c.* pv. *campestris* but not in other groups of yellow bacteria (Liao, *unpublished*).

Although the soft-rotting xanthomonads differed from three pathovars of *X. campestris* (pv. *campestris*, pv. *phaseoli*, pv. *vesicatoria*) (Tables 2, 3, and 5), the relationship to other recognized pathovars is presently uncertain and needs to be investigated further. It remains a possibility that soft-rotting xanthomonads represent a distinct pathogenic cluster that attacks mainly detached plant parts without causing obvious symptoms in actively growing plants. Recently, certain xanthomonads with unknown pathogenicity have been detected in asymptomatic plants (24) or shown as epiphytes on asymptomatic hosts (14). An unusual strain of *X. campestris* causing necrosis of apple explants in tissue culture has been isolated from apparently healthy buds of apple (21). Further investigations are needed to determine if a link exists between soft-rotting xanthomonads in decayed specimens and the xanthomonads on (or in) asymptomatic plants.

In 1954, Burkholder (4) reported isolation of one xanthomonad and two pseudomonds (*P. marginalis* and *P. viridiflava*) from rotted lettuce. The xanthomonad caused rot of lettuce but not of potato slices (4). Our results strongly support Burkholder's findings (4). However, the xanthomonad obtained in this study have been shown to cause rots of detached parts of eight different plants, indicating that our isolates are probably different from Burkholder's isolate (4). At present the economic losses caused by soft-rotting xanthomonads have not been determined and may be relatively minor compared with that caused by pectolytic erwinias and pseudomonads.

This study presents observations of at least three anomolies that challenge the conventional understanding of the genus *Xanthomonas*: 1) Certain members of *Xanthomonas campestris* can cause typical soft-rot symptoms other than blights, cankers, or necrosis that are generally associated with the group; 2) The host-specificity (or the host-specialization) reported for phytopathogenic xanthomonads, although controversial (30), seems to be absent in the soft-rotting xanthomonads, which behave more like opportunistic pathogens; and 3) two pectolytic strains of *X. c.* pv. *campestris* were able to infect and subsequently macerate in the laboratory the tissues of five plants that are not natural hosts of the organism.

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