

Various Plant Diseases Caused by *Xanthomonas* Species

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ABSTRACT

Xanthomonas is a Gram-negative, aerobic, short rod-shaped bacterium belonging to the family Pseudomonadaceae. This genus includes several pathovars, which are mainly plant pathogens. Extracellular proteases, and Type II secretion systems chiefly help these bacteria in colonizing the host plant. It produces a characteristic yellow pigment, xanthomonadin, which often is used as a chemotaxonomic and diagnostic marker of this genus. Xanthan gum produced by *Xanthomonas* is commercially important. It is an important additive in the food industry. Recently, *Xanthomonas* was also observed to undergo programmed cell death (PCD), the morphological and biochemical features of which closely resemble eukaryotic PCD. The determination of the genus *Xanthomonas* and its species is relatively easy, however, the characterization of *X. campestris* pathovars poses problems. An unambiguous identification of the pathovars of *X. campestris* can be of great use in plant pathology. The *X. campestris* pathovars that are defined by the host or disease symptoms are difficult to identify by other phenotypic characteristics. *X. campestris* group is the largest of all and causes diseases in many plant species. It is, therefore, classified into pathovars differentiated by the host reaction. However, application of the newer techniques of classification has been useful. A relationship of nutritional properties, host specificity and DNA homology groups has been observed. Genetic diversity among the strains of different pathovars of *X. campestris* has also been studied for a number of pathovars. It is believed that the variability could be more pronounced in the regions where the host plant originated. Ribosomal RNA and DNA probes could be useful tools for the epidemiological studies and in following the genetic evolution of the strains.

How to cite this paper: Dr. Dilip Kumar Sharma "Various Plant Diseases Caused by *Xanthomonas* Species" Published in International Journal of Trend in Scientific Research and Development (ijtsrd), ISSN: 2456-6470, Volume-6 | Issue-6, October 2022, pp.867-875, URL: www.ijtsrd.com/papers/ijtsrd51977.pdf



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KEYWORDS: diseases, plants, *Xanthomonas*, species, bacteria, pathovars, identification

INTRODUCTION

Members of this genus are short Gram-negative rods of linear shape, which are generally 0.4–0.7 µm wide and 0.8–2 µm long. The bacteria exist singularly or in pairs, and they are motile due to a single flagellum (~1.7–3.0 µm long). These bacteria have a GC content of 63.3–69.7 mol.%. They are catalase positive, urease, oxidase negative (or weakly positive), nondenitrifying or nitrate reducers, and they can produce H₂S but not indole or acetoin. Their growth is inhibited by 6% NaCl; 30% glucose; 0.01% lead acetate, methyl green, or thionin; and by 0.1% (and usually by 0.02%) triphenyl tetrazolium chloride. Proteins are readily digested by these bacteria and some species are able to hydrolyze cellulose, pectin, starch, and Tween 80. They are chemoorganotrophic, able to use various carbohydrates and salts of organic acids as their sole

carbon source, and strictly aerobic (as they have respiratory metabolism with oxygen as the terminal electron acceptor)[1,2]

The main fatty acids found in cells of this genus are 9-methyl decanoic acid (C11:0 iso), 3-hydroxy-9-methyl decanoic acid (C11:0 iso 3OH), and 3-hydroxy-11-methyl dodecanoic acid (C13:0 iso 3OH). This composition of fatty acids serves as a useful criterion to differentiate *Xanthomonas* from other bacteria. The optimal growth temperature for *Xanthomonas* is 20–30°C depending on the species, with the minimum temperature for growth being >4°C and the maximum being 27.5–39°C. These bacteria ideally grow at pH 6.5–7.5, but anything less than pH 4.5 inhibits growth.

Xanthomonas metabolize glucose using the Entner–Doudoroff pathway in conjunction with the tricarboxylic acid (TCA) cycle pathway. The pentose phosphate pathway may also be used but this only accounts for a small portion (8%–16%) of the total glucose consumed. The glyoxylate cycle may also be used for substrate catabolism and energy production.

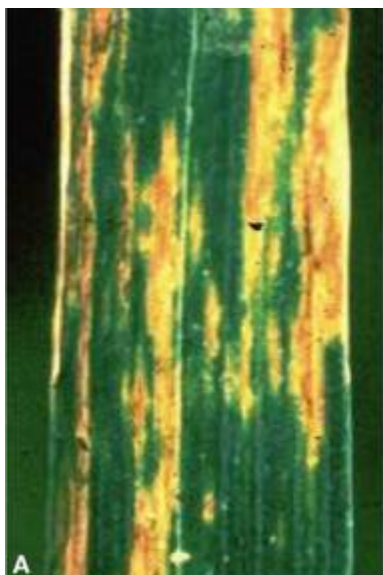
Most *Xanthomonas* species can grow in chemically defined medium containing minerals, ammonium, nitrogen, a suitable carbon source (i.e., glucose), and amino acids (usually glutamate or methionine). They also show satisfactory growth on nutrient agar (peptic digest of animal tissue, sodium chloride, beef extract, yeast extract, and agar at 5, 5, 1.5, 1.5, and 15 g/L, respectively) with or without yeast extract supplementation, GYCA medium (glucose, yeast extract, CaCO₃, and agar at 10, 5, 30, and 20 g/L, respectively), GPPYA medium (glucose, proteose peptone, yeast extract, and agar at 10, 5, 5, and 20 g/L, respectively), and YM agar (glucose, peptone, yeast extract, and agar at 20, 5, 3, and 17 g/L, respectively). Other culture media containing starch may be used for the general growth of *Xanthomonas*. These are usually fortified with antimicrobials, such as cephalixin, kasugamycin, chlorothalonil, gentamycin, brilliant cresyl blue, methyl green, and methyl violet to make them selective for *Xanthomonas*; Features that distinguish *Xanthomonas* from other related bacteria [3,4] (i.e., *Pseudomonas* and *Enterobacteriaceae* species) include their ability to hydrolyze starch and their independence from using asparagine as a source of carbon and nitrogen. Culture media for xanthan production have been widely studied and these may have different characteristics to those intended for bacterial growth.

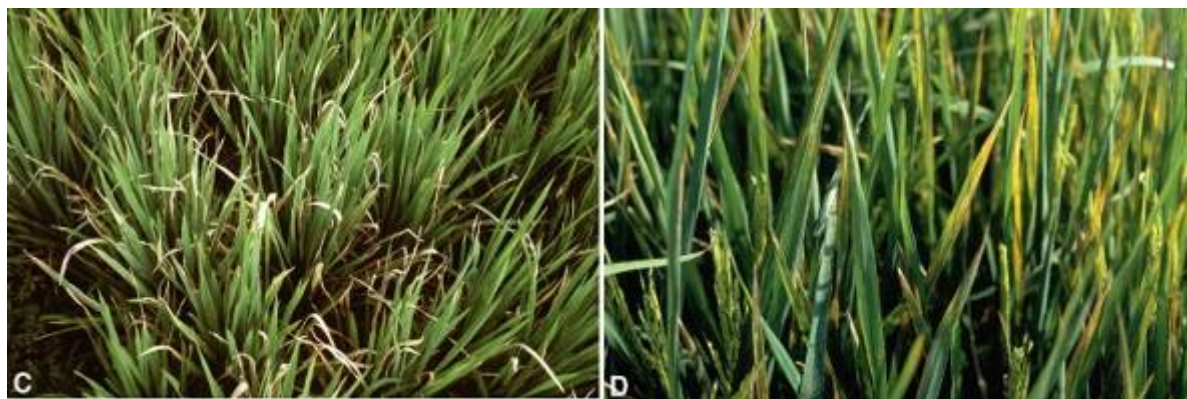
Xanthomonas strains capable of causing spoilage of salad vegetables and fruits can grow on pectate agar media commonly used for isolation of soft-rotting *Pseudomonas* and *Erwinia*. *Xanthomonas* strains,

however, can be readily differentiated from pseudomonads based on their ability to produce yellow-pigmented xanthomonadin and mucoid xanthan gum. Like other xanthomonads, soft-rotting *Xanthomonas* are unable to grow in the minimum medium without the addition of organic supplements. The xanthomonads are sensitive to those antimicrobials incorporated in *Pseudomonas* selective agars, for example triphenyl tetrazolium chloride and others. For isolation of plant-pathogenic *Xanthomonas*, a number of antimicrobials such as cycloheximide methyl green and vancomycin are frequently used. A number of selective agar media for isolation of a specific species or pathovars of *Xanthomonas* are available. It has not been determined if these selective agars are suitable for isolation of soft-rotting strains of xanthomonads.[5,6]

Several *Xanthomonas* species and pathovars attack each of the cultivated cereals and wild grasses, and some of them cause severe losses to their respective hosts. The most common bacterial diseases of these crops are bacterial stripe, bacterial blight, stripe, or streak of several cereals

(*X. campestris* pv. *translucens*), bacterial leaf blight of rice (*X. oryzae* pv. *oryzae*) bacterial leaf streak of rice and leaf scald of sugarcane (*X. albilineans*). The symptoms appear on leaf blades and sheaths as small, linear, water-soaked areas that soon elongate and coalesce into irregular, narrow, yellowish, or brownish stripes. Droplets of white exudate are common on the stripes. Severe infections cause leaves to turn yellow and die from the tip downward, they also retard spike elongation and cause blighting. Small lesions form on the kernels as well. The diseases develop mainly in rainy, damp weather. Bacteria overwinter on the seed and in crop residue and are spread by rain, direct contact, and insects. The main control measures are use of disease-free or treated seed and crop rotation.[7,8]





Symptoms due to *Xanthomonas*

Discussion

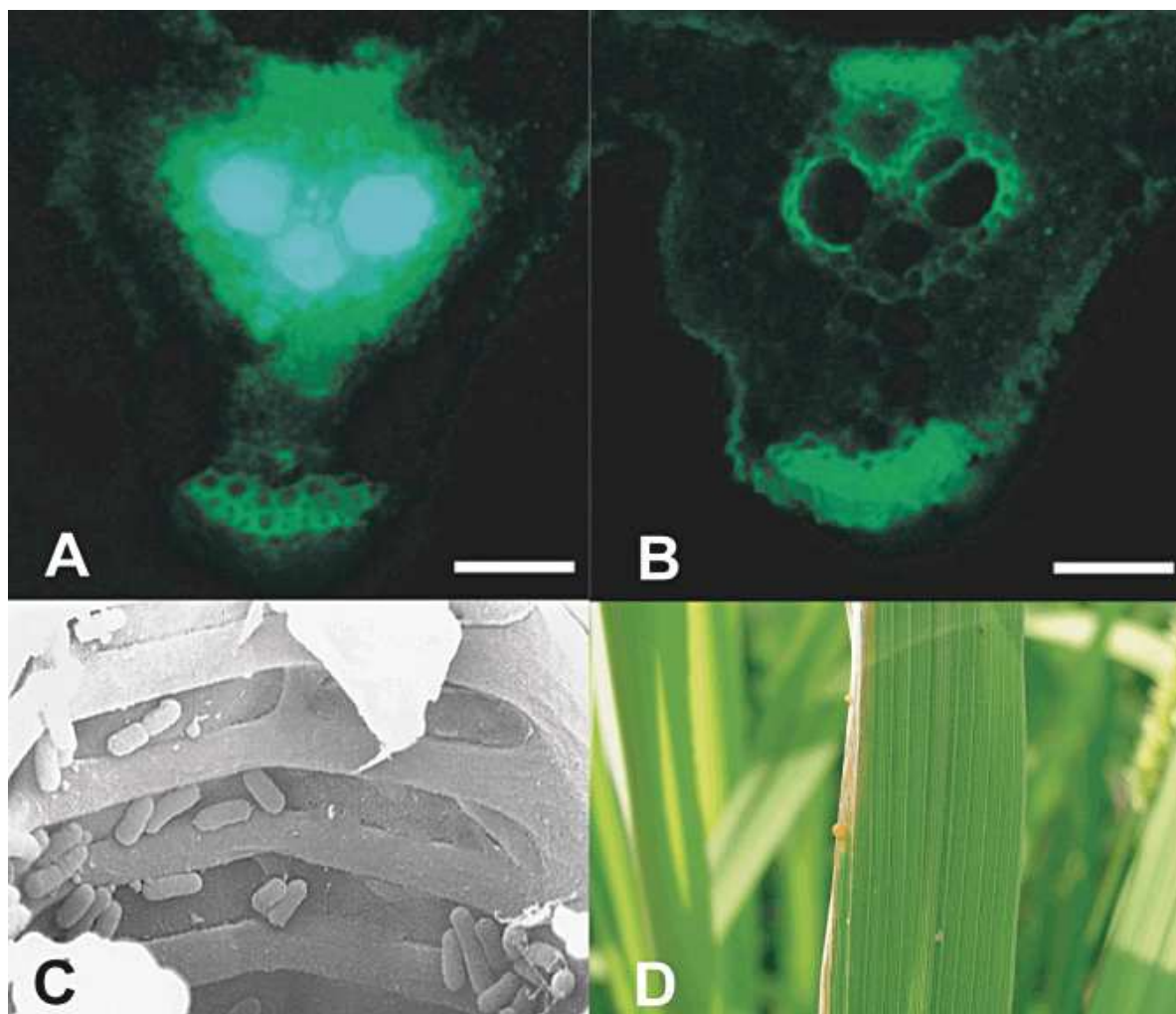
Bacterial leaf spot-The disease is caused by *Xanthomonas eleusinae* Rangaswami, Prasad, Eswaran. Linear spots are seen on both upper and lower surfaces of the leaf blade spreading along the veins. The spots measure 2–4 mm long, but often extend up to 25 mm or more. In the beginning, spots are light yellowish brown, but soon become dark brown. At the advanced stage, the leaf splits along the streak giving a shredded appearance. All the leaves, including the tender shoots, in a plant are affected. The bacterium mainly affects the leaves, but at times characteristic streaks may be found on the peduncle.

Bacterial blight-**Bacterial blight is caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*).** The symptoms of bacterial blight can be seen during the seedling stage in the form of grayish-green rolled leaves which turn yellow as the disease progresses. As the disease progresses further, the yellow color changes to straw-colored wilt leaves and ultimately the death of whole seedlings. Bacterial blight mostly occurs in tropical and temperate regions of the world, especially in irrigated and rainfed areas when strong winds are coupled with heavy rains. Blight is the most destructive rice disease in Asia and resulted in a historic epidemic in India during the late 1970s[9,10]

Bacterial leaf blight (BLB), caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), is found in both tropical and temperate regions. BLB also occurs in Australia, Africa, Latin America, the Caribbean and the USA. Yield losses of 10%–50% from BLB have been reported. Outbreaks of BLB are most common during the monsoon season in South-East Asia and India. Rice was introduced for cultivation into the USA (North Carolina) more than 200 years ago and has been cultivated in other parts of the USA for over 100 years. Although many rice diseases have either been introduced or developed on rice during the history of its cultivation in the USA, *Xoo* has not established in the USA. The climates of rice-producing areas in the USA and USA rice cultivation practices are not conducive to the long-term survival or spread of *Xoo*. For these reasons, *Xoo* is of low risk to US agriculture.

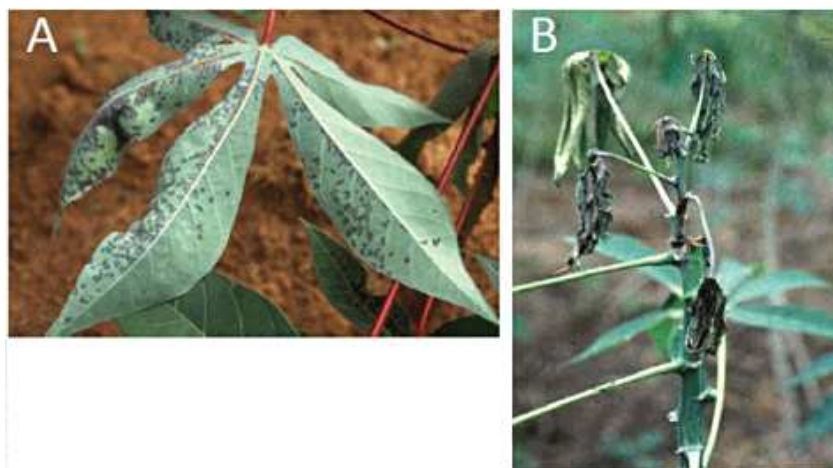
BLB is efficiently controlled by the use of resistant rice cultivars. However, because *Xoo* has the capacity to express effectors that suppress some host defence responses, often this resistance is eventually overcome. Resistance genes of the non-RD pattern recognition receptor class typically confer long-lasting resistance because they recognize conserved microbial signatures, which, when mutated, cripple the virulence of the pathogen. Control of the disease with copper compounds, antibiotics and other chemicals has not proven to be effective. [11,12]

Xanthomonas oryzae pv. *oryzae* is a rod-shaped, Gram-negative bacterium. It produces a yellow soluble pigment, called xanthomonadin, and extracellular polysaccharide (EPS). EPS is important in the protection of bacteria from desiccation and for the attenuation of wind- and rain-borne dispersal. *Xoo* is disseminated by irrigation water systems, splashing or wind-blown rain, as well as by contaminated rice stubble from the previous crop season, which is the most important source of primary inoculum. *Xoo* infects the rice leaf typically through hydathodes at the leaf tip, broken trichomes, leaf margins and wounds in the leaves or roots, multiplies in the intercellular spaces and enters into xylem vessels. Within a few days of infection, bacterial cells and EPS fill the xylem vessels and ooze out from the hydathodes, and form beads of exudate on the leaf surface, a characteristic sign of the disease and a source of secondary inoculum.



The genus *Xanthomonas* currently consists of 20 species including *axonopodis* X. Six distinct genomic groups have been defined within *axonopodis* X., with many pathovars causing economically important diseases on different host plants of agronomic significance.

Cassava (*Manihot esculenta*) is the staple food of nearly 600 million people in the world's tropical regions. *Xanthomonas axonopodis* pv. *manihotis* (*Xam*) is the causal agent of CBB, a major disease, endemic in tropical and subtropical areas. This foliar and vascular disease severely affects cassava production worldwide. Losses of between 12% and 100% affect both yield and planting material. Over recent years, a significant recurrence of the disease has been reported in different regions in Africa and Asia. *Xam* induces a wide combination of symptoms, including angular leaf lesions, blight, wilt, stem exudates and stem canker. Host resistance is still the most effective way to control this disease.[13,14] However, no breeding strategy is being developed for the control of CBB disease. Only two cassava CBB resistance genes have been identified so far (C. Lopez, personal communication, Universidad Nacional, Bogota, Colombia). Plant defence responses to *Xam* have been well characterized. Genomic tools for cassava, such as a large expressed sequence tag (EST) database and a cassava microarray, have been developed and used for *Xam*-plant expression studies.



Bacterial blight of cotton is a disease affecting the cotton plant resulting from infection by *Xanthomonas axonopodis pathovar malvacearum* (Xcm) a Gram negative, motile rod-shaped, non-spore-forming bacterium with a single polar flagellum. The bacteria can affect the cotton plant during all growth stages, infecting stems, leaves, bracts and bolls. It causes seedling blight, leaf spot, blackarm (on stem and petioles), black vein and boll rot. On cotyledons small, green, water-soaked rounded (or irregular) spots form which turn brown. Cotyledons can be distorted if the infection is intense. Black and elongated lesions can girdle the hypocotyls and kill seedlings. On the leaves, scattered small dark-green, water-soaked, areolate spots, form measuring 1–2 mm on the lower surface, which appear translucent against transmitted light. The spots increase in diameter to 5 mm, become angular (due to leaf venation), brown and later turn dark brown to blackish, becoming visible on the upper surface. On susceptible cultivars numerous spots can occur, causing chlorosis, necrosis and distortion, and eventually defoliation.^[1] the black arm symptom is characterized by dark brown to black lesions which may coalesce and the extended necrosis then girdles the stem with blockage of the vascular system at infected sites which hinder the movement of water and nutrients through the plant system. Drooping of leaves is associated with this hindrance of water and nutrient movement. Cracking of the stem and gummosis is also observed in infected plants.[15,16] The resultant breaking of the stem which hang typically as a dry black twig is referred to as the ‘black arm’. The pathogen also reportedly causes blackening of the veins and veinlets, giving a typical ‘blighting’ appearance.



Xanthomonas campestris pv. *vesicatoria* is a bacterium that causes bacterial leaf spot (BLS) on peppers and tomatoes. It is a gram-negative and rod-shaped. *Xanthomonas campestris* pv. *vesicatoria* survives on tomato and pepper plants, seeds, and debris from infected plants as it cannot live in the soil for more than a few weeks. The bacterium can also be found in association with wheat roots and some weed species which are both considered sources of inoculum as well as diseased tomato and pepper plants. In cold climates, *Xanthomonas campestris* pv. *vesicatoria* infection is mostly caused by contaminated seed material, both on and inside of seeds. If it survives on seeds, it will infect the cotyledons of the growing plant as it emerges from the seed coat. Internally infected seeds will produce diseased plants from the point of germination. Systemic symptoms such as wilting, yellowing, and dwarfing are not typical of plants infected at the point of germination. However, foliage loss can happen when localized symptoms on leaves become severe. If the bacterium survives on debris, it may infect healthy plants through stomata as well as wounds on leaves and fruit. It is spread by direct contact of plants with debris, human movement of the bacteria from debris to plants, and can easily travel from debris to healthy plants through saturated soils via water movement. Once infected, plants begin to develop lesions on the leaves as well as fruit, becoming inoculum sources for further infection.[17,18]



Results

Contaminated seeds, weeds, infected plant debris are the main route of transmission. Infection starts with epiphytic stage – i.e. bacteria grow on the aerial tissues of plant host (leaf, fruit, etc) followed by endophytic stage when bacteria enter and colonise host tissues through wounds or natural openings. When population of bacteria increases it re-emerges to the surface and is transmitted mainly by wind, rain or through seeds or agricultural machinery, while animal and insect vectors seems to play minor role.

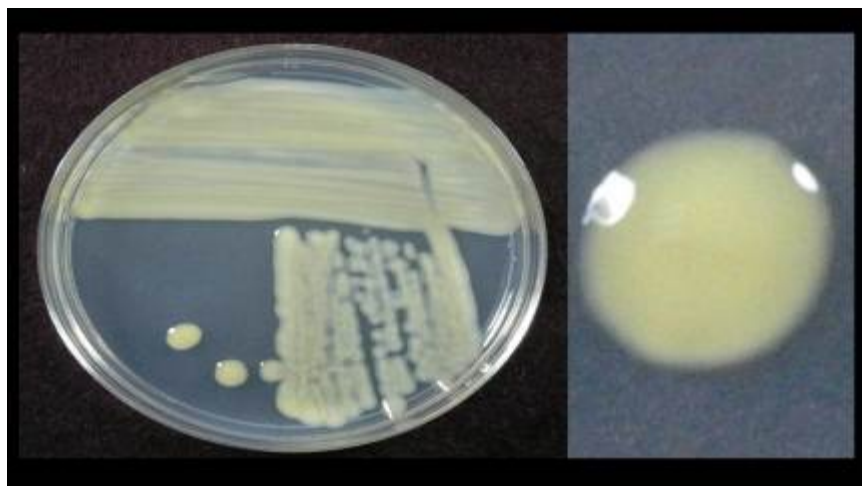
Xanthomonas uses surface polysaccharides, adhesion proteins and type IV pili to attach to the surface and can form biofilms to sustain abiotic stresses (UV, drought, etc). *Xanthomonas* produce xanthomonadins - yellow pigments that protect from radiation caused from natural light. Resistance to UV is mostly conferred by genes related to oxidative stress and DNA repair. Response to light is important in pathogenicity of these bacteria and regulates surface attachment and production of biofilm.

Xanthomonas possess almost all known secretion systems (types I to VI) that play different roles in the life and disease cycle, with type III secretion system (T3SS) being the key factor of pathogenicity. Typically, *Xanthomonas* T3SS injects a cocktail of 20-30 effector proteins that interfere with plant immune system and various host cellular processes. Many of the effectors are presumably redundant as individual deletions of effector genes does not impair virulence, however mutations in T3SS apparatus has strong effect. Secretion of the effectors is coordinated with expression of other virulence factors via shared regulatory networks. The effector repertoire has been proposed to be a determinant of host specificity. *Xanthomonas* actively kill other bacterial using type IV secretion system and defend itself from amoeba using type VI secretion system. [19]

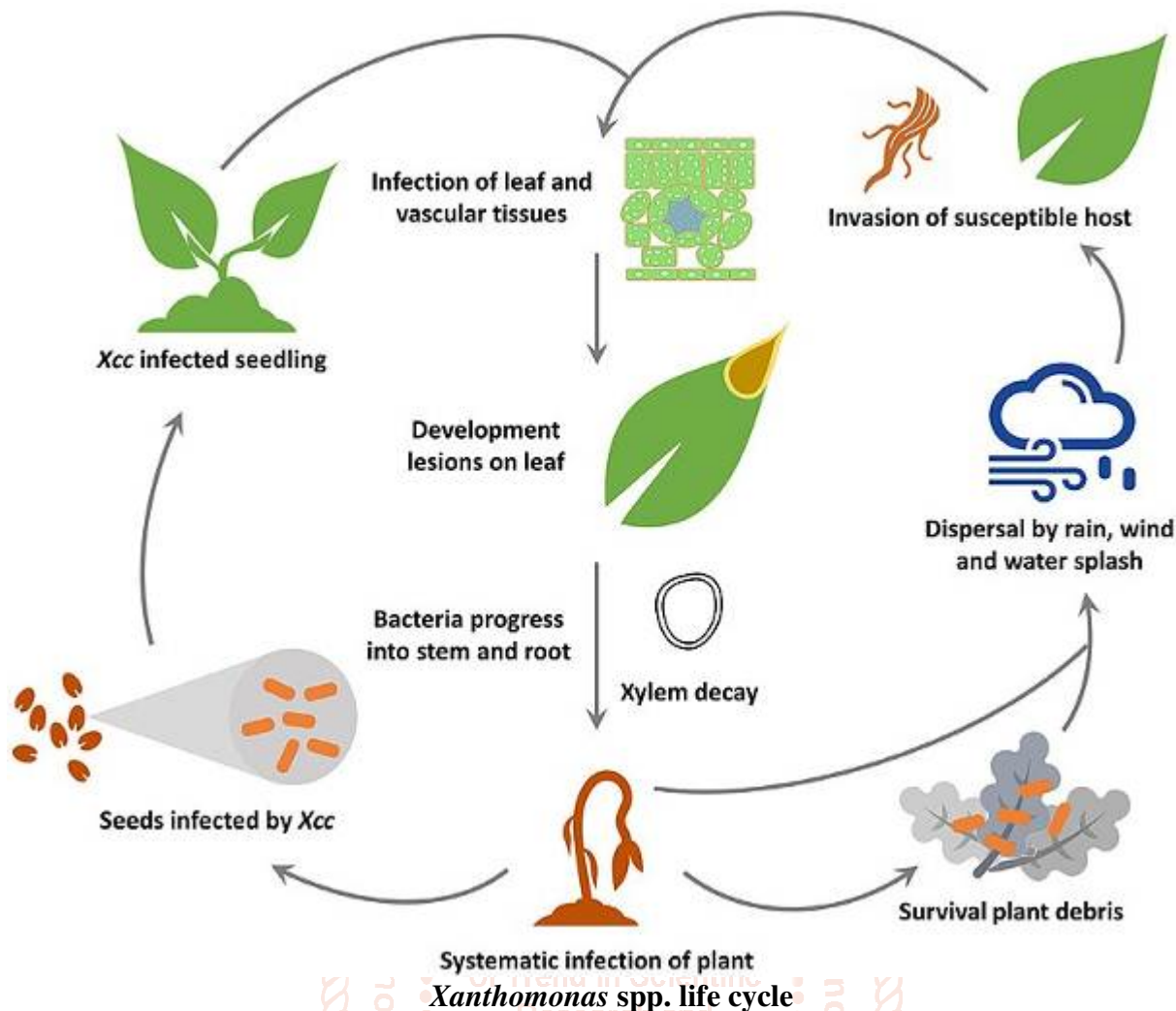
To prevent infections, limiting the introduction of the bacteria is key. Some resistant cultivars of certain plant species are available as this may be the most economical means for controlling this disease. For chemical control, preventative applications are best to reduce the potential for bacterial development. Copper-containing products offer some protection along with field-grade antibiotics such as oxytetracycline, which is labeled for use on some food crops in the United States. Curative applications of chemical pesticides may slow or reduce the spread of the bacterium, but will not cure already diseased plants. It is important to consult chemical pesticide labels when attempting to control bacterial diseases, as different *Xanthomonas* species can have different responses to these applications. Over-reliance on chemical control methods can also result in the selection of resistant isolates, so these applications should be considered a last resort.

Potential use of bacteriophages is also considered, however major limiting factors are their sensitivity to environmental conditions and in particular to UV radiation. Plant beneficial microorganisms or attenuated strains of *Xanthomonas* are being tested as a biocontrol reasoning that they could compete by occupying the same niche and even eradicate pathogenic strain. Generation of plant species resistant to *Xanthomonas* is another potential strategy.

Xanthomonas species produce an edible polysaccharide called xanthan gum that has a wide range of industrial uses, including foods, petroleum products, and cosmetics. Xanthan also plays role in the disease cycle of *Xanthomonas*. In particular, xanthan gum is one of the main components of biofilm matrix. Biofilms help these bacteria sustain abiotic stresses on the leaf surface. Genes for Xanthan gum biosynthesis comprise the gum operon (*gumB-gymM*) coding for 12 enzymes. Xanthan production by *Xanthomonas spp.* that thrive in vascular plant systems might block the water flow of the plant and as a result cause wilting.



Xanthomonas translucens on SPA media. Notice the yellow pigment



Conclusions

Phytopathogenic bacteria are economically important because they affect crop yields and threaten the livelihoods of farmers worldwide. The genus *Xanthomonas* is particularly significant because it is associated with some plant diseases that cause tremendous loss in yields of globally essential crops. Current management practices are ineffective, unsustainable and harmful to natural ecosystems. Bacteriophage (phage) biocontrol for plant disease management has been of particular interest from the early nineteenth century to date. *Xanthomonas* phage research for plant disease management continues to demonstrate promising results under laboratory and field conditions.[20,21] AgriPhage has developed phage products for the control of *Xanthomonas campestris* pv. *vesicatoria* and *Xanthomonas citri* subsp. *citri*. These are causative agents for tomato, pepper spot and speck disease as well as citrus canker disease. Phage-mediated biocontrol is becoming a viable option because phages occur naturally and are safe for disease control and management. Thorough knowledge of biological characteristics of *Xanthomonas* phages is vital for developing effective biocontrol products. Several *Xanthomonas* phages are evaluated for their potential as biocontrol agents against *Xanthomonas* species. So far, most of these

belong to order *Caudovirales* and are lytic to a broad range of host strains. They are isolated from diverse ecosystems and distributed across the globe depending on the presence of the pathogen they infect. Their structural integrity and functionality in *in vitro* conditions is maintained under optimal growth and storage conditions. Pathogenesis of *Xanthomonas* phages in bacteria induce molecular alterations that may have regulatory functions important during their life cycle. Although few studies have focused on this aspect of biology, more research is needed to understand their life cycle.

From their first discovery in filtrates to applications as phage/pathogen suspensions, or in combination with other antimicrobials or with UV-protectants or as cocktail/monophage treatments, phages have proved to be promising alternatives to agrochemicals and antibiotics. They can reduce disease severity or inhibit bacteria growth in diverse field settings. So far, two *Xanthomonas* phage-based biocontrol products are commercially available for plant disease control. As the transition into commercial products continues, more studies are needed to tap into the many unexploited potentials of *Xanthomonas* phages for a range of *Xanthomonas* related plant diseases.[22]

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