Xanthomonas arboricola Diseases of Stone Fruit, Almond, and Walnut Trees: Progress Toward Understanding and Management

Jay Ram Lamichhane

French National Institute for Agricultural Research (INRA), UAR 1240 Eco-Innov Research Unit,
78850 Thiverval-Grignon, France

Stone fruit (*Prunus* spp.: apricot, cherry, peach, nectarine, plum, and sloe), almond (*Prunus* spp.) (37,104), and walnut (*Juglans* spp.) (53) crops are among the most economically important tree crops worldwide and are cultivated to a different extent on all continents (25) (Table 1). The number of countries growing these crops has increased in the last decade with a subsequent increase in acreage globally (25). Consumer health awareness in recent years has created a demand for food sources with higher therapeutic properties. More specifically, stone fruits and nuts are rich in antioxidants and omega-3 fatty acids, essential in preventing or reducing the risk of cancers and heart disease (12,95).

Throughout the range of cultivation, *Prunus* spp. and *Juglans* spp. are often subjected to pathogen attack. Among them, *Xanthomonas arboricola* has become markedly important over the last decade. The putative pathovars of *X. arboricola*, pv. *pruni* and pv. *juglandis*, cause bacterial canker and spot (90) and bacterial blight (91) on stone fruits and almond, and on walnut, respectively. Besides cultivated species, all the ornamental *Prunus* species and hybrids can be affected by this bacterium (94). Of these, Japanese plum, peach, and nectarines are the most affected (79).

In recent years, disease outbreaks caused by *X. arboricola* on *Prunus* and on *Juglans* have increased, as has international concern. In the last decade, disease outbreaks have been reported from Iran (36), Spain (71), Switzerland (74), Taiwan (87), and the United States (S. K. Mohan and V. Bijman, *unpublished*), and on ornamental *Prunus* spp. from Italy (54) and the Netherlands (97). Similarly, recent outbreaks on walnut were reported from France (32), Iran (30), Lithuania (15), and Turkey (68). The rate at which these outbreaks are occurring suggests the possibility of future epidemics. To address the consequences of such disease emergencies, it is important to understand the epidemiology of these diseases, about which little is known to date.

Both bacterial canker and spot on *Prunus* spp. (90) and bacterial blight on *Juglans* spp. (91) were first described in the United States at the beginning of the twentieth century. Since then, the diseases have spread throughout the globe (16). *X. arboricola* is listed as a quarantine organism in the EU phytosanitary legislation (EU Directive 2000/29/CE) and in the European and Mediterranean Plant Protection Organization (EPPO A2 list) lists (21). In contrast, *X. arboricola* infecting *Prunus* spp. is not considered of quarantine concern by any other regional plant protection organizations.

Overall, the spread of phytopathogenic bacteria occurs through multiple short- and long-distance dissemination pathways. Cultural practices (grafting, pruning, etc.) and vectors such as mites or insects are the major source of local dissemination, while wind-driven rain, aerosol, and the inter-regional, national, and continental trade of nursery materials are the major sources of long-distance movement of plant-pathogenic bacteria (40,49). Some phytopathogenic bacteria, such as *X. arboricola*, are able to infect fruit and nuts (23,59) and consequently might be introduced at long distances through imported fruit. Of these dissemination pathways, dissemination through international trade of infected nursery material is the most serious problem for the effective control of plant-pathogenic bacteria (40). Because of their relatively long life cycle, stone fruits and nuts provide a constant niche for the survival and multiplication of bacterial pathogens. Bacterial pathogens might survive in woody plant tissues that provide protection against adverse climatic conditions or man-made control treatments. Latent infections markedly increase the risk of dissemination through vegetative propagation (44,47). This method is the most practiced technique for propagation of woody plants and can easily lead to the spread of latent infections. For this reason, propagation of disease-free plants in nurseries is an important step in producing pathogen-free planting material.

A previous study on the effect of *X. arboricola* on *Prunus* spp. reported three major economic factors: (i) reduced quality and marketability of fruit, (ii) reduced orchard productivity, and (iii) increased costs of nursery production. This study estimated that crop losses in Australia during years favorable to the disease were 3.1 million Australian dollars annually on *Prunus* spp. (94). Similarly, economic losses in Italy during epidemic years were estimated at over 10,000 € per ha (94). During years of severe infection, 25 to 75% of peach fruit has been reported as unmarketable (22). Bacterial blight of walnut can cause reductions in yield up to 70% as the pathogen attacks all herbaceous and woody parts of the plant (50,59,60).

The objectives of this review are (i) to provide an overview of *X. arboricola* diseases of stone fruit, almond, and walnut trees, and (ii) to discuss current and future management strategies. The focus is not on the detection and identification of *X. arboricola* from stone fruit and nuts nor on *X. arboricola* disease of hazelnut, which have been described elsewhere (38,47,69,70,73).

Taxonomic Relationships

The *Xanthomonas arboricola* complex includes phytopathogenic bacteria responsible for emerging diseases worldwide (13,32,47). This species, currently divided into seven pathovars (39,102), causes diseases in a range of perennial plants such as hazelnut, poinsettia, poplar, *Prunus* spp., and *Juglans* spp. (39,72,79,102). *X. arboricola* infecting *Prunus* spp. and hazelnut

Corresponding author: J. R. Lamichhane,
E-mail: jayram.lamichhane@gmail.com,
Jay-Ram.Lamichhane@grignon.inra.fr,
Phone: +33(0)130815415, Fax: +33 (0)1 30 81 52 07

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(the putative pv. *pruni* and pv. *corylina*, respectively) are listed as quarantine organisms in the EU phytosanitary legislation (EU Directive 2000/29/CE) and in the European and Mediterranean Plant Protection Organization lists (EPPO A2 list) (21,22). The phylogenetic relationships, based on the *rpoD* housekeeping gene, among a worldwide collection of *X. arboricola* revealed that strains isolated from poplar are divergent from the main *X. arboricola* cluster formed by all other strains (33). At the same time, strains isolated from *Prunus* spp. (pv. *pruni*) constitute a homogeneous group from all other pathovars, which in turn are quite heterogeneous (33,77,102,111).

The initial taxonomy of the genus *Xanthomonas* was based on the original host of isolation, which led to a large number of species (14). A further work, based on the phenotypic characteristics, clustered the *Xanthomonas* isolates into eight phenotypic groups (100). Immediately after this work, Vauterin et al. (102) reclassified the *Xanthomonas* species on the basis of DNA-DNA hybridization. This reclassification grouped the *Xanthomonas* species into

different categories, and pathogens of trees have been renamed *X. arboricola*. All currently named *X. arboricola* pathovars came from a group of bacteria previously named *X. campestris*. The exception is the strawberry pathogen, pv. *fragariae*, which was not described at the time. The species name “*arboricola*,” from Latin “tree dwellers,” was first attributed by Vauterin et al. (102) and justified by including bacteria that live and cause diseases of tree species.

Although attempts to clarify the naming of pathovars have been made since 1978 (20,110), confusion still exists. According to the standards, for designating a novel pathovar, it is necessary to demonstrate by pathogenicity tests that the pathogen has a distinct host range or causes a distinct disease when compared with previously described pathogens. However, to date, no host range study of *X. arboricola* pathovars, renamed from *X. campestris*, was performed. Debate continues with regard to what constitutes different pathovars among plant-pathogenic bacteria (49,101). For example, in their comparative study with strains of *X. arboricola* pv. *populi*,

Table 1. Harvested areas (ha) of fruit and nut crops throughout the world (FAO 2012)

Continents	Stone fruits				Nuts	
	Apricot	Cherry	Peach and Nectarine	Plum and Sloe	Almond	Walnut
Asia	294,929	148,588	982,736	1,875,850	214,107	641,314
Europe	102,170	190,466	235,087	511,467	643,413	142,948
Africa	79,092	5,259	82,843	46,730	441,148	8,381
Northern America	5,014	36,613	59,036	33,906	315,590	98,980
South America	3,957	17,899	84,093	45,047	9,021	25,547
Oceania	6,734	2,819	19,861	3,362	28,500	8,074
World	491,896	401,644	1,463,656	2,516,362	1,651,779	925,244

Fig. 1. Symptoms of bacterial spot and canker caused by *Xanthomonas arboricola* pathovars on stone fruit. Leaf spots (A) followed by yellowing and browning (B) and characteristic lesions on peach fruit (C, D, and E). Necrotic lesions on apricot leaves (F) and fruit (G) and a characteristic twig canker (H). Photos courtesy of M. Cambra except part H, which belongs to the author.

Hajri et al. (33) observed that even more pathovars belonging to the *X. arboricola* complex may harbor a variety of assorted strains. These results suggest that populations of *X. arboricola* are common plant residents and their presence in association to plants does not necessarily imply pathogenic behavior. Indeed, Sawada et al. (83) reported the presence of phylogenetically diverse pectolytic *X. arboricola* strains associated with bacterial spot of grapevine. However, the authors did not propose a new pathovar due to the diversity and weak pathogenicity of the strains. Recently, *X. arboricola* has also been reported to cause disease on jujube (*Zizyphus zuzuba*) (61) and on mango (*Mangifera indica* L.) (76), other woody plants. Also here, the authors refrained from proposing a new pathovar. Indeed, during the pathogenicity tests, strains isolated from one species also caused disease on other species (62), indicating that they can infect a broad host-range. Similar reports on the lack of host specificity of another plant-pathogenic bacterium, *Pseudomonas syringae*, have been recently reviewed on a large number of woody (49) and annual (J. R. Lamichhane, A. Messean, and C. E. Morris, *unpublished*) plants. Taken together, it can be speculated that the current *X. arboricola* pathovars might have a wider host range than expected. Therefore, before assigning the term pathovar to a new causal agent on a new host species, the host range of existing pathovars should be investigated.

Disease Symptoms

Bacterial canker and spot of *Prunus* spp. Overall, both herbaceous (leaves, buds, young shoots, fruit and nut shells) and woody (twigs, branches, and main trunk) plant parts can be affected by the disease (23,58,81; Figs. 1 and 2). However, no symptoms occur on

the flowers. Symptoms of *X. arboricola* on stone fruit trees are reported to differ throughout the range of cultivation. In Italy, bacterial spot differs from those commonly described (6). The authors reported that symptoms occur only on leaves and fruit of peaches and nectarines, while canker symptoms occur on the branches and trunks of plum.

On peach leaves, symptoms first appear on the lower surface as pale green to yellow, circular or irregular areas with a light tan center. Over the time, symptoms enlarge and also appear on the upper leaf surface, where angular, deep-purple, brown or black spots are visible (Fig. 1A). The tissue surrounding these spots may turn yellow. Spots are generally concentrated at the leaf tip where bacteria accumulate in rain or dew droplets. Severely infected leaves turn yellow (Fig. 1B) and drop from the plant. On peach fruit, small brown spots appear on the surface and become sunken over time (Fig. 1C and D). Often, the margins of the spots are water-soaked, and light green haloes may develop, giving the fruit a mottled appearance. Pitting and cracking may occur in the vicinity of the spots as the fruit enlarges (Fig. 1C to E). These cracks are usually small and difficult to see but became extensive if young fruits are heavily infected. A gummy exudate may ooze from the wounds, especially after rain, and may be confused with damage caused by insects. On peach twigs, cankers occur in the spring at the apex of overwintering twigs. Symptoms begin with small, water-soaked, slightly darkened, superficial blisters that may extend up to 10 cm along the twig. During severe infections, the whole twig may be girdled and cause tip dieback. When the lower part of the tip also becomes dark, this is known as “black-tip” injury. Early twig infections often lead to cankers late in the summer. These

Fig. 2. Typical symptoms of *Xanthomonas arboricola* on almond. Necrotic spots surrounded by chlorotic haloes on leaves (A), sunken and corky lesions with oozing gum on fruit (B), lesions on a nut with dehydrated mesocarp (C), and dark brown spots on the nut endocarp (D). Photos courtesy of M. Cambra.

cankers are water-soaked, and dark-purple spots form around the lenticels.

Unlike the cankers on peach, those on plum are perennial and develop continuously on young twigs. The inner bark of the twigs is often penetrated by the pathogen, leading to the formation of large cankers that deform and kill the twigs. On plum fruit, symptoms are similar to those observed on peach fruit. However, sunken black lesions may develop on some cultivars. Symptoms on apricot leaves (Fig. 1F) and fruits (Fig. 1G) are also similar to those on peach, while those on twigs (Fig. 1H) resemble those observed on plum. Likewise, leaf symptoms on cherries are similar to those on peach, but fruit symptoms are uncommon. In some cases, however, early infections on cherries may cause distorted fruits.

On almond, leaf symptoms are similar to those observed on peach (Fig. 2A). In early spring, infected fruits show sunken corky lesions with oozing gum that streams or clumps (Fig. 2B). The sunken lesions become raised following dehydration of the mesocarp in summer (Fig. 2C). Sometimes circular dark spots appear on

the endocarp and may affect the nut (Fig. 2D). Infected fruits either fall prematurely or remain attached to the trees and mummify over time. Mummified fruits harbor viable bacteria and serve as potential inoculum sources (81).

Bacterial blight of walnut. As with *Prunus* spp., bacterial blight on *Juglans* spp. affects all parts of the plant (Fig. 3). On walnut, however, even flowers (catkins) are subjected to the infection. In general, dark brown to black spots develop on new leaves, stems, and the apical portion of fruit shells (59,63; Fig. 3). Late-season infections on maturing nuts can discolor the shell and nutmeats, making them off-grade or unsalable. In severe infection, many nuts may fall prematurely, while others reach full size. In these remaining nuts, the kernel often becomes blackened, dried, and wrinkled (26). *X. arboricola* is also a primary causal agent of a disease complex called brown apical necrosis. Other associated pathogens include fungi, especially species of *Alternaria* and *Fusarium* (8). In addition to the usual cankers on walnut, *X. arboricola* also causes a newly reported vertical oozing canker

Fig. 3. Typical symptoms of bacterial blight on walnut. Necrotic lesions surrounded by chlorotic haloes on upper leaf surfaces (A); necrotic lesions on a lower leaf surface (B), stem (C) and nut (D); and apical necrosis on nuts (E and F). Photos courtesy of Daiva Burokiene (A, B, and D), Antonia Ninot (C), and Katherine Evans (E and F).

(32,59). Vertical cankers appear on the main trunk, which often lead to trunk deformities. During summer, infected trees form black oozing exudates that stain the bark (32).

Epidemiology and Predisposing Factors

Ground-cover and weeds, within and outside of orchards, are one of the most important reservoirs of plant-pathogenic bacteria, such as *Pseudomonas syringae* (19,52), *Xanthomonas campestris* (99), and *Xylella fastidiosa* (86). However, no studies have been published on the role of weeds and orchard ground-covers as reservoirs of *X. arboricola*. Future studies should address such issues with potential implications for the establishment of *X. arboricola* and its management.

Infected dormant buds, leaf scars, and cankers previously formed on woody plant parts are sources of primary inoculum on *Prunus* spp. and *Juglans* spp. (6,60,79,113; Fig. 4). These plant parts are commonly typical overwintering sites of the pathogen (60,79,113). On *Prunus* spp., Zaccardelli et al. (113) reisolated a field inoculated, rifampicin-resistant mutant from overwintered leaves. However, they were not able to reisolate the wild-type strain from naturally infected fallen leaves showing leaf spots. This raises questions on the survival capacity of *X. arboricola* on fallen

leaves. Further studies are needed to determine if fallen leaves might be another source of primary inoculum in the following season.

Once *X. arboricola* from overwintering sites infects newly formed leaves in the spring, it multiplies epiphytically on *Prunus* and *Juglans* trees. The bacteria can switch from a saprophytic to a parasitic lifestyle and penetrate through natural openings like stomata. They can also enter plants through wounds caused by both natural (leaf drop, hail, frost) and man-made acts (pruning, harvesting) (9,47,88). For this reason, infections are more frequent and severe during vegetative growths in the spring, especially when accompanied by frequent rainfalls.

Epiphytic *X. arboricola* pv. *pruni* populations may be produced by asymptomatic presence of bacteria (57) or by exudate forming leaf lesions that persist on leaves (88) and serve as inoculum on peach fruit. The same is true for plums (7) and walnuts (60). In addition, *X. arboricola* is capable of penetration through leaf scars, following leaf shedding in autumn, which then can become an overwintering site (84,113).

Both leaf wetness and water congestion can markedly influence the establishment of infection (115). Experimental studies showed that a continuous film of water extending from the leaf surface

Fig. 4. Disease cycle of *Xanthomonas arboricola* on *Prunus* spp. and walnut. Infected dormant buds, leaf scars, and cankers are sites where the pathogen overwinters. These plant parts are sources of primary inoculum of the pathogen. In mid to late spring, *X. arboricola* begins to multiply and spread to newly formed leaves where it has an epiphytic phase. The pathogen switches from a saprophytic to pathogenic lifestyle once climatic conditions are conducive. Leaf infections generally occur from mid to late spring, and leaf lesions provide the inoculum for late season fruit and nut infections. The pathogen can infect woody tissues when these are wounded, and the infection could occur until late autumn. Catkins and newly formed buds could also be latently infected already in winter. Infected leaves, buds, and catkins are sources of secondary inoculum of the pathogen that infects newly formed fruits and nuts.

through stomata into the substomatal chamber is necessary for penetration of *X. arboricola* into leaves and development of symptoms (55,56). Another experimental greenhouse study showed the development of only slight necrosis when water-congested leaves were allowed to dry immediately after inoculation or to remain wet up to 18 hours (115). However, necrosis levels increased once leaf surface remained wet 24 to 48 hours. This explains that the duration of leaf wetness influences the severity of disease.

It is also important to note that the number of lesions induced by *X. arboricola* on peach was directly proportional to the inoculum concentration (18). A previous study reported that the time of symptom appearance does not influence disease progress, but that progress of the infection influences symptom development (6). The authors proposed two factors to explain this finding: (i) the weather was warmer and drier and so less favorable for disease development, and (ii) shoot growth had ceased and emergent leaves were mature. Zehr and Shepard (115) also found that necrosis after experimental inoculation is most severe on the youngest leaves.

Leaf lesions provide secondary inoculum that readily infects both early and late-season fruit and nuts (Fig. 4). Concerning late-season fruit infection, in peach, fruit were affected later in the season than leaves with lower incidence and severity (6). This could be related to the lower density of stomata on the fruit surface compared to leaves. In addition, fruit are not subject to water congestion because their stomata chambers are less influenced by the hydrostatic pressure of the xylem. A delay in disease appearance on fruit compared to that on leaves was previously reported (82,88), as well as a lack of correlation between leaf and fruit infection (105).

Diseases caused by *X. arboricola* show a typical start/stop pattern, the severity of which depends mostly on spring weather conditions. According to Stefani (94), the unpredictable pattern of bacterial epidemics experienced in different regions of the world may be related to: (i) differential pathogenicity features of bacterial strains, (ii) variations in susceptibility of plant species and cultivars, and (iii) cropping conditions, such as irrigation, fertilization, and pruning time and frequency.

The occurrence of primary and secondary infections on *Prunus* spp. and *Juglans* spp. depends mainly on environmental conditions. Frequent periods of moisture from late bloom to a few weeks after petal fall are highly conducive to primary infections on fruit and leaves of peaches and nectarines (6). Warm seasons with temperatures of 19 to 28°C, frequent rains, winds, and heavy dews during the growing season can favor the development of secondary infections (24,115). By contrast, few infections occur when the climate is warm and dry (79) as when it is cool, given that *X. arboricola* is a mesophilic bacteria and requires temperatures over 20°C for its reproduction (115).

Disease incidence is highly correlated with cultural practices and stress caused by unfavorable soil and climatic conditions (28,46,55,84,115). Bacterial canker and spot of *Prunus* spp. are more common and most severe in areas where stone fruits are grown on light, sandy soils and the environment is humid and warm during the growing season. Stress factors such as spring frost, drought, and winter pruning predispose plants to bacterial blight (47). Moreover, nutrient deficiency and excessive mineral fertilization predispose plants to *X. arboricola* (106). The occurrence of spring frost can create micro-lesions on plant tissues through which *X. arboricola* may enter and establish infection (46).

Pathogen Diversity

An in-depth knowledge of pathogen diversity is critical in developing reliable detection methods. Very low levels of diversity were reported among *X. arboricola* strains isolated from *Prunus* spp., and high levels from walnut. However, it should be highlighted that these strains have been isolated exclusively from diseased plant tissues without considering *X. arboricola* populations from the healthy plants. Because this pathogen is an epiphyte, a surprising population diversity might be present on annual weeds and orchard

ground-covers and on perennial plants. Further investigations are needed to unveil this hypothesis given its implication in disease epidemiology and management.

Based on multiple-locus variable-number analysis, strains isolated from diseased cherry laurel in the Netherlands were clustered in two groups (10). Likewise, based on fluorescent amplified fragment length polymorphism and housekeeping genes, Boudon et al. (13) analyzed strains isolated from infected stone fruits in western Europe and the United States and reported a low diversity among the strains. The authors also found the same bacterial genotype in five countries on three continents. A recent study, based on the housekeeping genes from a worldwide collection of strains, further validated a lack of relationship among strains due to geographic origin (33). This almost clonal global population can be associated with the limited genetic diversity of its host (13,112). In contrast, a high genetic diversity was reported among strains of *X. arboricola* isolated from walnut, where relationship among strains due to geographic origin was possible (51,85). This could be because Persian walnut is propagated by locally grown seeds adapted to different environments, allowing the selection of different *X. arboricola* populations (85). A distinct genetic lineage of *X. arboricola* strains pathogenic to walnut was recently reported, highlighting an even wider diversity among these strains than what was known (32).

Molecular Basis of *Xanthomonas arboricola* Pathogenesis on Woody Plants

The advent of the genomic era has provided insights into several controversial issues concerning plant-microbe interaction. There has been little progress to date with *X. arboricola*, which can be mainly attributed to the lack of whole genome sequences. However, given the economic importance of *X. arboricola* diseases on woody plants, there are several ongoing studies on the molecular basis of this pathogen's interactions with its hosts. Although different studies underlined the role of host selection in the population structure of individual *X. arboricola* strains (32,73), other important aspects need to be addressed. Of special importance are environmental selection, gene flow, and genetic drift, which can influence the overall population structure of the pathogen. A recent study based on the type III effector genes of all seven pathovars of *X. arboricola* revealed that type III effector repertoires vary in size among the intraspecific pathovars (73). In particular, the *Prunus* spp., hazelnut, and *Juglans* spp. strains were reported to have the largest type III effector repertoires compared to other *X. arboricola* pathovars. The type III secretion system is known to be fundamental to parasitic fitness and pathogenicity (4). Our lack of host range knowledge within *X. arboricola*, however, inhibits understanding of whether a larger number of effector repertoires among its pathovars of stone fruits and nuts could be correlated with their capacity to attack a broader host range. Two other scenarios can be proposed. First, the higher number of effector repertoires could be due to a redundancy of the type III secretion proteins (i.e., homologous effectors), similar to other pathosystems (27,45). And second, since all of these pathovars carrying a larger number of effector repertoires attack woody plants, it can be speculated that among these effectors are some that are involved in degrading woody tissues or compounds that constitute the secondary lignin typical of woody plants (5). If these pathovars can degrade lignin, this information might be essential in breeding for resistance to *X. arboricola*.

The understanding of the molecular basis among individual pathogens and their specific hosts needs to be accelerated through advances in genomic sequencing. Whole genome sequences of a strain from hazelnut (35) and another from peach (75) were recently completed. The release of these genomes represents a significant contribution toward research on the pathogenesis of *X. arboricola* on woody plants. Future studies based on comparative genomic analyses are needed to identify underlying molecular mechanisms that promote the evolution and adaptation of the pathogen to diverse environments and host plants. A recent study identified a new genetic lineage within *X. arboricola* that causes a

more severe disease on walnut than those previously reported (32). The underlying forces that led to the emergence of a new *X. arboricola* disease should be the subject of future investigations. It is especially important to understand the acquisition of virulence-associated genes by horizontal gene transfer, the occurrence of accessory and mobile genetic elements, and spontaneous mutations among *X. arboricola* pathovars (33).

Breeding for Resistance

Host resistance is an important component of integrated pest management. However, little work has been done describing resistance against *X. arboricola*. The paradox of fruit and nut trees resistance to *X. arboricola* diseases is that either sources of resistance are not known or resistant cultivars lack specific desirable fruit and marketing characteristics. Breeding programs should therefore focus on the introgression of resistance to commercial cultivars from other sources, such as wild species or others with less acceptable marketing characteristics. Also, the possibility of exploiting genetic engineering for the development of resistant cultivars needs to be considered. An example is resistance breeding in the United States, where a breeding program has released cultivars of peach resistant to *X. arboricola* (65,66; Table 2). Despite the availability of highly resistant peach cultivars (43,89,105), however, considerable variation among these cultivars has been reported in disease incidence from year to year since weather conditions are of the greatest importance for the onset and development of epidemics. According to Yang et al. (108), in years with climatic conditions favorable for infection, all of these genotypes showed at least some symptoms. This suggests the need of a more durable multi-gene resistance to the pathogen.

Marker-assisted breeding has been used recently to develop stone fruit varieties with resistance or increased tolerance to *X. arboricola*. Socquet-Jugard and others (92) identified a microsatellite marker (UDAp-452) on apricot co-segregated with resistance to *X. arboricola* and two flanking microsatellites (BPPCT037 and BPPCT038A). The authors demonstrated that when dividing the population according to the alleles of UDAp-452, the subgroup with the unfavorable allele had a higher disease incidence than the group with the favorable allele. Use of the favorable allele led to a reduction in disease incidence of 35.6%. Likewise, different peach genotypes obtained from a cross between susceptible and resistant plants have been used to construct linkage maps and to map quantitative trait loci (QTLs) (108). More specifically, 14 QTLs with an additive effect on *X. arboricola* resistance were detected, including four major QTLs on linkage groups (LG) 1, 4, 5, and 6. It was observed that two major QTLs, Xap.Pp.OC-4.1 and Xap.Pp.OC-4.2, on LG4 were associated with *X. arboricola* resistance in leaves. Similarly, the QTL Xap.Pp.OC-5.1 on LG5 was associated with bacterial resistance in both leaves and fruits, while Xap.Pp.OC-1.2 on LG1 and Xap.Pp.OC-6.1 on LG6 were only associated with pathogen resistance in fruit. Collectively, these results suggest a separate regulation of leaf and fruit resistance to *X. arboricola* in peach as well as participation of genes involved in general plant response to biotic stress (92,108).

Table 2. Peach, plum and walnut accessions/cultivars resistant to *Xanthomonas arboricola*

Species	Country	Accessions or cultivars	References
Peach	USA	Clayton, Cador, Senitel	66,80
Plum	USA	Robusto, Segundo, Rubysweet, Bruce	98
Walnut	China	Jinboxiang 3	96
		Yunxin Gaoyuan	107
		Yunxin 90303	117
		Luguo 4	116
	Slovenia	Krnc, Z-60, Z-62	93
	Turkey	19 Genotypes	3

Although the above studies represent a first step toward marker-assisted breeding of new stone fruit varieties with an increased tolerance to *X. arboricola*, to date no tightly linked markers or isolation of genes associated with pathogen resistance have been reported. Both peach and apricot are likely to suffer from low-density linkage maps and not enough diversity between parents to allow for more markers to be analyzed (108).

Understanding gene functions and molecular mechanisms underlying disease resistance is important for breeding programs. For example, release of the peach genome v1.0. in 2010 (http://www.rosaceae.org/gb/gbrowse/prunus_persica/) led to a candidate gene search between the two flanking markers BPPCT037 and BPPCT038A. Between the two flanking markers, three putative genes encoding leucine-rich repeat (LRR) receptor-like serine/threonine kinases were found using the peach genome annotations. Moreover, two genes encoding putative disease-resistance proteins and one encoding a putative F-box/LRR-repeat protein were found in this region. The availability of the peach genome sequence v1 and the growing availability of single nucleotide polymorphism markers (2,103) may encourage studies to develop high-density linkage maps and discover QTLs associated with important agronomic traits.

Susceptibility tests of different *Juglans* genotypes to *X. arboricola* in field trials showed no symptoms on *J. nigra* and widespread symptoms on *J. regia* (9). *J. regia* is the most important commercial variety of walnut and is often severely damaged by *X. arboricola* (9,26). Frutos (26) summarized an in-depth report on new accessions of *J. regia* and their behavior to the pathogen. However, this report only summarized some important accessions of *J. regia* from around the world with satisfactory levels of resistance to *X. arboricola* (Table 2). Aside from the resistance observed on *J. nigra*, field inoculation tests demonstrated an increasing order of susceptibility of *J. cinerea*, *J. sieboldiana*, *J. mandshurica*, and *J. bindsii* to the pathogen *X. arboricola* (9).

Disease Management

The management of a given disease should be based on the combination of several control measures. This requires an in-depth knowledge of the biology of a host and its pathogen as well as epidemiology of the disease. The use of healthy planting material excludes introduction of the pathogen in its latent form. To this aim, effective early detection methods are essential (see below). Once the pathogen is established in an area, control measures should be applied to reduce pathogen inoculum. Effective cultural practices such as treatment with copper-based compounds, elimination of the infected plant parts, and optimization of fertilization and irrigation practices are among the most important interventions to reduce the pathogen inoculum. In addition, elimination of weeds and orchard grasses is needed when they constitute a potential pathogen reservoir. Genetic diversity of the crop can be improved by planting mixed varieties or cultivars instead of a single variety or cultivar. Intercropping is another practice that might significantly reduce pathogen inoculum pressure and the consequent yield losses.

Concerning the use of healthy planting materials to control *X. arboricola* diseases, in Europe, phytosanitary measures, based on nursery inspections and implementation of the EPPO-approved certification scheme, should still be greatly improved to ensure the production of healthy planting materials. In the United States, nursery inspections and certification are a part of integrated pest management under the responsibility of the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS), because *X. arboricola*, as many plant-pathogenic bacteria, is commonly present as an epiphyte or endophytically as a latent infection where symptoms are not always expressed (31,49). Indeed, early detection of the pathogen in nursery materials is the only way to avoid its movement through global trade. International trade of plants and plant products is a major cause of rapid long-distance dissemination of bacterial pathogens. This underscores the need of molecular-based rapid diagnostic tests to determine the

presence of this pathogen in plant tissues, especially nursery materials. Development of these detection methods, however, should take into account pathogen diversity and not focus on a specific strain or pathovar. This is necessary to ensure the diagnostic confidence of a given method for pathogen detection. These methods must also be sensitive enough to detect very low numbers of bacteria. There are several recently developed early detection methods for *X. arboricola* (see 47 for detail), but further efforts are needed to improve the sensitivity of these methods.

The scarcity of resistant germplasm and the strong influence of weather conditions on disease development often represent a serious constraint in the management of *X. arboricola* diseases. Further, only a few effective yet economical bactericides are available, making control of bacterial diseases extremely difficult (1). Often, copper-based compounds are used in European countries to control *X. arboricola*. This has led to the development of several copper-resistant strains of the pathogen, such as those isolated from walnut orchards where intensive copper-based treatments were applied (29).

Once *X. arboricola* is present in a production area, its inoculum level must be reduced to limit crop damage. Periodic monitoring and quantification of epiphytic populations using effective techniques (48) is needed to avoid the under- or overestimation of the epiphytic population density. Once the population density exceeds the economic threshold, preventive treatments based on copper-based compounds should be applied to reduce inoculum levels. When symptoms of infection appear, pruning and elimination of infected plant parts, sealing of wounds, and applications of copper-based bactericides are recommended for control (47). The application of these compounds should follow events causing wounds on plants including autumn leaf fall, which provides several ports of entry for the pathogen (109). In addition, lesions caused by spring frost and hail are ideal infection ports for bacterial pathogens (49), and for this reason such events must be followed by prompt copper-based treatments.

Although copper-based formulations satisfactorily control epiphytic bacterial populations (88), they are ineffective once the pathogen enters the plant. These are contact pesticides and cannot reach pathogen populations inside dormant buds or cankers. Another constraint to the use of these products on *Prunus* spp. is damage to leaves and fruit (44). Undesired effects of copper on walnut tree performance and its fruit phytosanitary status have also been recorded (78). Because of these negative effects, alternatives to copper compounds are being sought. Alternatives have included the application of chemicals such as acibenzolar-S-methyl, an inducer of systemic acquired resistance (SAR) and prohexadione calcium, a growth regulator to control bacterial diseases (see 49 for detail). Moreover, several antimicrobial peptides, terpenes, and chitosans have been proposed as alternatives to conventional antibiotics (17) and might find promising applications in *X. arboricola* disease control. The effectiveness of these products in containing *X. arboricola* infection, however, still need to be tested under field conditions.

Little is known about the effectiveness of biological control agents to manage *X. arboricola* diseases of woody plants. However, there are some reports on the use of antagonistic bacteria to control *X. arboricola* disease on *Prunus* spp. (11,42) and walnut (67). Finally, although bacteriophages have been used successfully to manage several *Xanthomonas* diseases of annual plants (41), little progress has been made to control *X. arboricola* on woody plants. The only example in the literature on the use of selected bacteriophages to control *X. arboricola* disease is on peach (114). The authors reported that bacteriophages obtained from affected peach orchards are effective against *X. arboricola* disease on peach. This encourages the future study in finding alternatives to chemical compounds.

Closing Remarks and Perspectives

Crop loss assessments have been made for major annual crops (64), but little information is available for perennial crops (34).

Especially, estimation of crop losses due to *X. arboricola* will help to accurately define the importance of the diseases caused by this pathogen globally.

A better understanding of *X. arboricola* epidemiology is needed to improve cultural practices. Especially, the survival of the pathogen in the soil and irrigation water needs more attention given the existing knowledge gap. Research should be intensified to find alternatives to traditional chemical compounds for disease management; biological control and plant resistance especially need more focus.

Genetic studies of *X. arboricola* interactions with woody host plants need to be intensified. The availability of whole genome sequences should be exploited for comparative genomic analyses and also to pinpoint molecular mechanisms involved in the evolution and adaptation of the pathogen to diverse environments and host plants. Critical knowledge of the effector complement necessary for woody tissue invasion, canker formation, and systemic movement needs to be gained through comparative genomic analyses and subsequent genetic studies. These may lead to improved host resistance and could be the best means for control of *X. arboricola* diseases difficult to manage with conventional chemicals.

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Jay Ram Lamichhane

Dr. Lamichhane is a postdoctoral research associate at French National Institute for Agricultural Research (INRA), Grignon, France. He obtained a B.Sc. and his M.Sc. honors in agricultural sciences in 2005 and 2007, respectively, at the University of Tuscia, Viterbo, Italy. He then received a Ph.D. degree in 2011 in plant protection at the same university where he also worked as a PostDoc fellow for more than two years. Dr. Lamichhane's research focuses on the epidemiology and control of diseases caused by plant-pathogenic *Pseudomonas syringae* and *Xanthomonas arboricola* both on annual and on woody crops. However, he also has experience with beneficial (endophytic, epiphytic, and plant-growth-promoting rhizobacteria) and other phytopathogenic bacteria (*Agrobacterium tumefaciens*, *Clavibacter michiganensis*, *Pectobacterium carotovorum*, and *Xanthomonas* spp.), fungi (*Cytospora*, *Fusarium*), and oomycetes (*Phytophthora*). At the beginning of 2013, Dr. Lamichhane moved to France as a visiting PostDoc fellow. At the time, he worked on the host range determination of plant-pathogenic *Pseudomonas syringae* species complex at INRA, Plant Pathology Research Unit in Avignon. Since April 2014, he has been actively involved both in research and in coordination of European Research Area Network (ERA-Net). More specifically, he is involved within the EU funded ERA-Net project on coordinated integrated pest management and European Network for the Durable Exploitation of Crop Protection Strategies (ENDURE). Within these European networks, he focuses mainly on topics related to crop protection through an effective implementation of integrated pest management strategies.

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