PATHOGEN PROFILE

Xanthomonas hortorum – beyond gardens: Current taxonomy, genomics, and virulence repertoires

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Abstract

Taxonomy: Bacteria; Phylum Proteobacteria; Class Gammaproteobacteria; Order Lysobacterales (earlier synonym of Xanthomonadales); Family Lysobacteraceae (earlier synonym of Xanthomonadaceae); Genus Xanthomonas; Species X. hortorum; Pathovars: pv. carotae, pv. vitians, pv. hederae, pv. pelargonii, pv. taraxaci, pv. cynarae, and pv. gardneri.

Host range: Xanthomonas hortorum affects agricultural crops, and horticultural and wild plants. Tomato, carrot, artichoke, lettuce, pelargonium, ivy, and dandelion were originally described as the main natural hosts of the seven separate pathovars. Artificial inoculation experiments also revealed other hosts. The natural and experimental host ranges are expected to be broader than initially assumed. Additionally, several strains, yet to be assigned to a pathovar within X. hortorum, cause diseases on several other plant species such as peony, sweet wormwood, lavender, and oak-leaf hydrangea.

Epidemiology and control: X. hortorum pathovars are mainly disseminated by infected seeds (e.g., X. hortorum pv. carotae and vitians) or cuttings (e.g., X. hortorum pv. pelargonii) and can be further dispersed by wind and rain, or mechanically transferred during planting and cultivation. Global trade of plants, seeds, and other propagating material constitutes a major pathway for their introduction and spread into new...
geographical areas. The propagules of some pathovars (e.g., \textit{X. hortorum} pv. \textit{pelargonii}) are spread by insect vectors, while those of others can survive in crop residues and soils, and overwinter until the following growing season (e.g., \textit{X. hortorum} pvs \textit{vitis} and \textit{carota}). Control measures against \textit{X. hortorum} pathovars are varied and include exclusion strategies (i.e., by using certification programmes and quarantine regulations) to multiple agricultural practices such as the application of phytosanitary products. Copper-based compounds against \textit{X. hortorum} are used, but the emergence of copper-tolerant strains represents a major threat for their effective management. With the current lack of efficient chemical or biological disease management strategies, host resistance appears promising, but is not without challenges. The intraspecies genetic variability within the same pathovar poses a challenge for breeding cultivars with durable resistance.

**Useful websites:** https://gd.eppo.int/taxon/XANTGA, https://gd.eppo.int/taxon/XANTCR, https://gd.eppo.int/taxon/XANTPE, https://www.euroxanth.eu, http://www.xanthomonas.org, http://www.xanthomonas.org/dokuwiki

**KEYWORDS**

bacterial blight, carrot, dandelion, leaf spots, lettuce, pelargonium, tomato, \textit{Xanthomonas hortorum}

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### 1 | INTRODUCTION

The seven pathovars of \textit{Xanthomonas hortorum} collectively affect 65 plant species in 15 botanical families, including agricultural crops (e.g., tomato, carrot, lettuce), horticultural plants (e.g., pelargonium), and wild plants (e.g., dandelion). This pathogen profile gives the first comprehensive summary of \textit{X. hortorum} biology, including a history of its taxonomy and an account of its broad host range, and of its distribution and epidemiology, emphasizing intrapathovar differences. The genomics work done on this species is also summarized, with a special focus on pathogen–host interactions. Most previous literature on this pathogen deals with \textit{X. hortorum} as a homogenous entity. This pathogen profile highlights, for each section, intrapathovar similarities and differences, thus providing a nuanced and detailed look into the complexity of \textit{X. hortorum}.

### 2 | TAXONOMY UPDATE

The taxonomic history of the different \textit{X. hortorum} pathovars is long and complex (Figure 1), like that of the genus \textit{Xanthomonas}. The earliest reports of diseases caused by \textit{X. hortorum} date back to the 1890s, with the reports describing bacterial leaf spot and blight disease of English ivy in 1894 in Germany (Lindau, 1894), and bacterial blight of geraniums and bacterial leaf spot of lettuce in Massachusetts, USA, in 1898 and 1907, respectively (Stone, 1907; Stone & Smith, 1898). The first proper taxonomic description of the species causing bacterial leaf spot of lettuce, referred to as \textit{Bacterium vitians} (Brown, 1918), was published in 1918 (Figure 1). In the following years, \textit{B. hederae} and \textit{B. pelargonii} were isolated from diseased English ivy (Arnaud, 1920) and diseased geraniums (Brown, 1923), respectively. \textit{B. vitians}, \textit{B. hederae}, and \textit{B. pelargonii} were then reclassified in the genus \textit{Phytomonas} (Bergey et al., 1923; Burkholder & Guterman, 1932). \textit{Phytoponas carota} (originally proposed as "\textit{Pseudomonas carota}"") was characterized as the bacterium responsible for bacterial blight of carrot (Kendrick, 1934).

Subsequently, the four species were transferred to the genus \textit{Xanthomonas} as \textit{X. hederae}, \textit{X. carota}, \textit{X. pelargonii}, and \textit{X. vitians} (Dowson, 1943; Starr & Burkholder, 1942). Concurrently, the bacterium responsible for the bacterial blight of Russian dandelion, first reported in the USSR (Sigrianski, 1936), was designated as \textit{X. taraxaci} (Niederhauser, 1943). Those five pathogens were considered to be individual \textit{Xanthomonas} species until the introduction of the infrasubspecific epithet "pathovar" (Young et al., 1978), followed by the publication of the first Approved Lists in 1980 (Skerman et al., 1980). The taxonomic status of \textit{X. hortorum} pvs \textit{vitis} and \textit{carota} was unclear, and three variants were distinguished: the former pathotype strain, which is nonpathogenic on lettuce, was labelled "type A", while "\textit{X. hortorum} pv. \textit{vitis}" or "\textit{X. hortorum} pv. \textit{carota}" could only be distinguished by their host range and were thus transferred as pathovars of the polytypic species \textit{Xanthomonas} (Young et al., 1978).

Based on DNA–DNA hybridization (DDH) (Palleroni & Bradbury, 1993; Vauterin et al., 1995), these five \textit{X. campesiris} pathovars were classified as pathovars of the new species \textit{X. hortorum} (Figure 1). The pathotype strain CFBP 5858 T (LMG 733 T = NCPPB 939 T) of \textit{X. hortorum} pv. \textit{hederae} was designated as the species' type strain. The taxonomical status of "\textit{X. hortorum} pv. \textit{vitis}" was unclear, and two variants were distinguished: the former pathotype strain, which is nonpathogenic on lettuce, was labelled "type A", while "\textit{X. hortorum} pv. \textit{vitis}" or "\textit{X. hortorum} pv. \textit{carota}" could only be distinguished by their host range and were thus transferred as pathovars of the polytypic species \textit{Xanthomonas} (Young et al., 1978).
A group of strains causing bacterial spot of tomato and pepper (Solanum lycopersicum and Capsicum annuum) was originally named "Pseudomonas gardneri" (Śutic, 1957). Some years later, it was suggested to be part of genus Xanthomonas (Dye, 1966), but it was not formally described as X. gardneri until the beginning of the 21st century (Jones et al., 2004). The taxonomical history of the Xanthomonas strains causing bacterial spot of tomato and pepper has been thoroughly reviewed (Osdaghi et al., 2021; Potnis et al., 2015).

Strains associated with bacterial bract spot of artichoke (Cynara scolymus) were first reported in the 1950s as members of the Xanthomonas genus (Ride, 1956), yet the official description as X. cynarae was only provided in 2000 (Trébaol et al., 2000). Although a few phylogenetic studies demonstrated the high
Genetic relatedness between \textit{X. hortorum}, \textit{X. cynarae}, and \textit{X. gardneri} (Parkinson et al., 2009; Young et al., 2008), they were only recently formally accepted as the same taxonomic entity (Morinière et al., 2020; Timilsina et al., 2019).

Genomic, phenotypic, and pathogenicity analyses were first used to prove the synonymy of \textit{X. cynarae} and \textit{X. gardneri} and reclassify them as pathovars of \textit{X. cynarae} (Timilsina et al., 2019). In that same study, \textit{X. hortorum} and \textit{X. cynarae} were acknowledged to be paraphyletic species but were kept separate, based on previous wet-lab DDH results. However, only the type strain of \textit{X. hortorum} was included in the 2019 study. A comprehensive analysis revisited the taxonomy of those strains, and included all type, pathotype, or representative strains of \textit{X. hortorum} and \textit{X. cynarae} (Morinière et al., 2020). Standard genome-to-genome comparison parameters, such as average nucleotide identity (ANI), in silico DDH (isDDH), and tetranucleotide frequencies (Tetra), between \textit{X. hortorum} and \textit{X. cynarae} fell into the transition zone of the species boundary (Morinière et al., 2020), a concept described previously (Richter & Rosselló-Móra, 2009; Rosselló-Móra & Amann, 2015). Phylogenetic reconstructions suggested a continuous evolution and diversification of pathovars and phenotypic data did not reveal stable diagnostic traits allowing distinction between \textit{X. cynarae} and \textit{X. hortorum} strains. \textit{X. cynarae} was then suggested to be a later heterotypic synonym of \textit{X. hortorum} and both species were combined into an extended \textit{X. hortorum} species including seven pathovars (Figure 2): \textit{X. hortorum} pvs \textit{hederae}, \textit{pelargonii}, \textit{vitians}, \textit{carotae}, \textit{taraxaci}, \textit{cynarae}, and \textit{gardneri} (Morinier et al., 2020).

3 | HOST RANGE

Making a distinction between natural and experimental hosts of plant-pathogenic bacteria is important to better understand the extent of their host range (Bull & Koike, 2015). The natural host range of a pathogen consists of naturally infected plants (i.e., in nonexperimental settings), and is the criterion for pathovar identification and classification (Dye et al., 1980). The experimental host range includes plants that show symptoms after artificial inoculation. Its scope depends on the choice of plant species and of inoculation procedures. The experimental host range provides invaluable information on the pathogen’s potential to adapt to new host plants (Jacques et al., 2016).

Each \textit{X. hortorum} pathovar has its own natural host range and the experimental host ranges of multiple pathovars have been studied. Additionally, many unassigned strains within \textit{X. hortorum} have also been isolated from multiple different plants (e.g., wheat, peony, and hydrangea). Most of the reported natural hosts of \textit{X. hortorum} belong to the Geraniaceae, Araliaceae, and Asteraceae families, while most of the reported experimental hosts of the pathogen belong to Asteraceae (Table 1). \textit{X. hortorum} affects more than 65 plant species in 15 botanical families, as summarized in Table 1.

![Whole-genome phylogeny of representative Xanthomonas hortorum strains. The tree was constructed using PhyloPhlAn v. 0.40 (Segata et al., 2013) as previously described in Morinière et al. (2020)](image)
| X. hortorum pv. | Isolated from* | Family | Plant genus | Plant species | Host range typeb | Diseasec | References |
|----------------|----------------|--------|-------------|---------------|-----------------|----------|------------|
| carotae        | Apiaceae       | Daucus | carota      | N             | BLB             | Kendrick (1934); Myung et al. (2014); du Toit et al. (2014) |
| cynarae        | Asteraceae     | Cynara | scolymus    | N             | BBS             | Trébaol et al. (2000) |
|                | Solanaceae     | Capsicum | annuum    | E             | NA              | Timilsina et al. (2019) |
| gardneri       | Asteraceae     | Cynara | scolymus    | E             | NA              | Timilsina et al. (2019) |
|                | Euphorbiaceae  | Euphorbia | heterophylla | N             | BS              | Araújo et al. (2015) |
|                | Solanaceae     | Solanum | lycopersicum | N             | BS              | Jones et al. (2004); Quezado-Duval et al. (2004); Timilsina et al. (2019) |
|                |                | Capsicum | annuum    | N             | BS              | Jones et al. (2004); Timilsina et al. (2019) |
|                |                | Solanum | americanum | E             | BS              | Araújo et al. (2015) |
|                |                | Nicandra | physaloides | E             | BS              | Araújo et al. (2015) |
|                | Brassicaceae   | Arabidopsis | thaliana | E             | NA              | Cândido et al. (2008) |
| hederae        | Araliaceae     | Hedera | helix       | N             | BLS             | Arnaud (1920); Trantas et al. (2016) |
|                |                |          | canariensis | N             | BLS             | Suzuki et al. (2002) |
|                |                |          | nepalensis (var. sinensis) | N             | BLS             | Zhang et al. (2015) |
|                |                |          | rhombea     | E             | NA              | Suzuki et al. (2002) |
|                |                |          | colchica    | E             | NA              | Leyns et al. (1984) |
|                | Schefflera     |          | atinophylla | N             | BLS             | Chase (1984); Norman et al. (1999); Tolba (2017) |
|                |                |          | arboricola  | N             | BLS             | Chase (1984); Norman et al. (1999) |
|                | Fatsia         | japonica | N           | BLS             | Chase (1984) |
|                | Polyscias       | spp.     | N           | BLS             | Norman et al. (1999) |
|                | Plerandra       | elegantissima | E           | NA              | Chase (1984) |
| pelargonii     | Geraniaceae    | Pelargonium | capitatum | N             | BB              | Knauss and Tammen (1964) |
|                |                |          | peltatum    | N             | BB              | Starr et al. (1955) |
|                |                |          | quercifolium | N             | BB              | Knauss and Tammen (1964) |
|                |                |          | radens      | N             | BB              | Knauss and Tammen (1964) |
|                |                |          | scandens    | N             | BB              | Knauss and Tammen (1964) |
|                |                |          | zonale      | N             | BB              | Leyns et al. (1984) |
|                |                |          | × domesticum | N             | BB              | Stapp (1958) |
|                |                |          | × fragrans  | N             | BB              | Knauss and Tammen (1964) |
|                | Geranium       | maculatum | N           | BB              | Stapp (1958) |
|                |                | pratense  | N           | BB              | Starr et al. (1955) |
|                |                | sanguineum | N           | BB              | Starr et al. (1955) |
|                |                | sylvaticum | N           | BB              | Stapp (1958) |
| Euphorbiaceae  | Euphorbia      | pulcherrima | E           | NA              | Rockey et al. (2015) |

(Continues)
**Table 1** (Continued)

| X. hortorum pv. | Isolated from<sup>a</sup> | Family | Plant genus | Plant species | Host range type<sup>b</sup> | Disease<sup>c</sup> | References |
|----------------|---------------------------|--------|-------------|----------------|--------------------------|-----------------|------------|
| taraxaci       | Taraxacum                 | kok-saghyz | N            | BLS            | Brown (1918); Morinière et al. (2020) |
| vitians        | Asteraceae                | Lactuca | sativa      | N              | BLS                      | Brown (1918); Morinière et al. (2020) |
|                |                           | serriola| N            | BLS            | Toussaint et al. (2012); Morinière et al. (2020) |
|                |                           | biennis | E            | NA             | Toussaint et al. (2012) |
|                |                           | officinale | E            | NA             | Toussaint et al. (2012); Morinière et al. (2020) |
|                |                           | Sonchus | oleraceus    | E              | NA                       | Toussaint et al. (2012) |
|                |                           | asper   | E            | NA             | Toussaint et al. (2012) |
|                |                           | Artemisia | biennis   | E              | NA                       | Toussaint et al. (2012) |
|                |                           | Matricaria | discoidea | E              | NA                       | Toussaint et al. (2012) |
|                |                           | Arctium  | minus       | E              | NA                       | Toussaint et al. (2012) |
|                |                           | Gnaphalium | uliginosum | E              | NA                       | Toussaint et al. (2012) |
|                |                           | Ambrosia | artemisiifolia | E            | NA                       | Toussaint et al. (2012) |
|                |                           | Galinsoga | quadradiata | E              | NA                       | Toussaint et al. (2012) |
|                |                           | Senecio | vulgaris    | E              | NA                       | Toussaint et al. (2012) |
|                | Solanaceae                | Nicotiana | tabacum    | E              | NA                       | Sahin et al. (2003); Al-Saleh et al. (2011); Morinière et al. (2020) |
|                |                           | Solanum | lycopersicum | E/N?           | BLS                      | Sahin et al. (2003); Al-Saleh et al. (2011); Morinière et al. (2020) |
|                |                           | Capsicum | annuum     | E              | NA                       | Sahin et al. (2003); Al-Saleh et al. (2011) |
|                | “nigromaculans”            | Arctium  | lappa       | N              | BLS                      | Parkinson et al. (2009); Dehghan-Niri and Rahimian (2016) |
|                | Unassigned                | Asteraceae | annua      | N              | BLS                      | Ssekiwoko et al. (2009) |
|                |                           | Cichorium | intybus    | N              | BLS                      | Zacaroni et al. (2012) |
|                |                           | Calendula | officinalis | NA             | NA                       | Parkinson et al. (2009) |
|                |                           | Lamiaceae | Lavandula  | N              | BLS                      | Koike et al. (1995) |
|                |                           |         | dentata    | N              | BLS                      | Koike et al. (1995); Roberts and Parkinson (2014) |
|                |                           |         | angustifolia | N              | BLS                      | Koike et al. (1995); Roberts and Parkinson (2014) |
|                |                           |         | × intermedia | N              | BLS                      | Rotondo et al. (2020) |
|                |                           |         | × ginginsii | E              | NA                       | Rotondo et al. (2020) |
|                | Oleaceae                  | Olea     | europaea    | NA             | NA                       | Young et al. (2010) |
|                |                           | Prunus   | vulgaris    | N              | BLS                      | Nejad et al. (2012) |
|                | Hydrangeaceae             | Hydrangea | quercifolia | N              | BLS                      | Cottyn et al. (2021); Uddin et al. (1996) |
|                |                           |         | arborescens | N              | BLS                      | Cottyn et al. (2021) |
|                | Paeoniaceae               | Paeonia  | spp.        | N              | BB                       | Oliver et al. (2012); Klass et al. (2019) |
|                | Poaceae                   | Triticum | sp.         | E              | NA                       | Egorova et al. (2014) |
|                | Poaceae                   | Hordeum  | vulgare     | E              | NA                       | Egorova et al. (2014) |
|                | Poaceae                   | Secale   | cereale     | E              | NA                       | Egorova et al. (2014) |
|                | Poaceae                   | Avena     | sativa      | E              | NA                       | Egorova et al. (2014) |
|                | Lauraceae                 | Persea   | americana   | NA             | NA                       | Parkinson et al. (2009) |
|                |                           | Persea   | americana   | NA             | NA                       | Parkinson et al. (2009) |

<sup>a</sup>To ensure consistent botanical taxonomy, plant species nomenclature was checked on the World Flora Online database (WFO, 2021).

<sup>b</sup>N, natural host; E, experimental host; NA, not applicable.

<sup>c</sup>Disease type is only mentioned in the event of a natural host. BLS, bacterial leaf spot; BBS, bacterial bract spot; BLB, bacterial leaf blight; BS, bacterial spot; BB, bacterial blight; NA, not applicable.

X. hortorum pv. hederae is primarily known as a pathogen of English ivy (*Hedera helix*) (Arnaud, 1920; Trantas et al., 2016), but has also been isolated from diseased plants belonging to other *Hedera* species (Table 1). Some X. hortorum pv. hederae strains are pathogenic on several other plants of the Araliaceae family (e.g., Schefflera spp.) in natural ecosystems (Table 1). The experimental host range of
X. hortorum pv. hederae includes false aralia (Plerandra elegantissima), Japanese ivy (Hedera rhombea) (Suzuki et al., 2002), and Persian ivy (Hedera colchica) (Leyns et al., 1984), but X. hortorum strains have not been reported on those plants in natural conditions. Another X. hortorum pathovar, pv. pelargonii, naturally occurs on a wide range of plant species from the genera Geranium and Pelargonium in the Geraniaceae family (Table 1). Some strains of X. hortorum pv. pelargonii cause mild symptoms on poinsettia (Euphorbia pulcherrima) in experimental conditions (Rockey et al., 2015).

X. hortorum pv. vitians is a pathogen of cultivated lettuce (Lactuca sativa) and probably infects its closest wild relative, the prickly lettuce (Lactuca serriola) (Morinière et al., 2020; Toussaint et al., 2012). This pathovar can be pathogenic on diverse weeds from the Asteraceae family (Table 1) (Toussaint et al., 2012). In greenhouse infection tests, several strains were weakly pathogenic on tomato and two pepper cultivars (C. annuum ‘Marengo’, a sweet pepper, and C. annuum ‘Cayenne Long Slim’, a cayenne pepper) (Al-Saleh et al., 2011; Morinière et al., 2020; Sahin et al., 2003).

To our knowledge the only known hosts of X. hortorum pvs carotae and taraxaci are their respective initial hosts of isolation. X. hortorum pv. carotae is pathogenic on wild carrot (Daucus carota) and its cultivated subspecies (D. carota subsp. sativus) (Kendrick, 1934; Myung et al., 2014; Temple et al., 2013), while Russian dandelion (Taraxacum kok-saghyz) is the only reported host of X. hortorum pv. taraxaci (Niederhauser, 1943) (Table 1).

The only recorded natural host of X. hortorum pv. cynarae is artichoke (Cynara scolymus) (Trébaol et al., 2000) and the pathogen also caused leaf spot symptoms in infiltrated C. annuum pepper leaves (Timilsina et al., 2019) (Table 1). X. hortorum pv. gardneri is one of the four xanthomonads responsible for bacterial spot of tomato and pepper, alongside X. euvesicatoria pv. euvesicatoria, X. euvesicatoria pv. perforans, and X. vesicatoria (Jones et al., 2004; Osdaghi et al., 2021; Potnis et al., 2015). X. hortorum pv. gardneri strains were isolated from spot symptoms on tomato and pepper (Jones et al., 2004), as well as the weed plant Euphorbia heterophylla (Araújo et al., 2015). Some X. hortorum pv. gardneri strains are pathogenic on tomato or pepper, while other strains are pathogenic on both (Potnis et al., 2015). Moreover, greenhouse inoculations with X. hortorum pv. gardneri resulted in limited necrosis on artichoke leaves (Timilsina et al., 2019), in chlorotic spots on Arabidopsis thaliana (Cándido et al., 2008), and in leaf lesions on American black nightshade (Solanum americanum) and apple of Peru (Nicandra physaloides) (Araújo et al., 2015).

Several unclassified X. hortorum strains cause disease on other plant species such as peony (Paeonia spp.) (Klass et al., 2019; Oliver et al., 2012) and sweet wormwood (Artemisia annua) (Sekiwoko et al., 2009) (Table 1). Strains causing an unknown disease of lavender (Lavandula dentata, L. angustifolia, and L. x intermedia) were first identified as X. campestris (Kolke et al., 1995), but reclassified as X. hortorum based on sequence data (Roberts & Parkinson, 2014; Rotondo et al., 2020). Strains reported as closely related to X. hortorum are sometimes unavailable in public or private strain collections, as is the case for angular leaf spot disease of oak-leaf hydrangea (Hydrangea quercifolia) observed in Georgia, USA (Uddin et al., 1996). Recently, similar strains were reported from leaf spot symptoms on hydrangea in Flemish (Belgium) nurseries (Cottyn et al., 2021). Greater burdock (Arctium lappa) is also likely to be a natural host of some unassigned X. hortorum strains (Dehghan-Niri & Rahimian, 2016).

Other studies suggesting that some strains belong to X. hortorum have not addressed Koch’s postulates. As such, it is unclear whether those strains belong to the species. For example, many X. hortorum strains were isolated from seed lots of several Poaceae plants in Russia (e.g., wheat, Triticum sp.; barley, Hordeum vulgare; rye, Secale cereale; and oat, Avena sativa) (Table 1). Infiltration of bacterial suspension through leaves induced vascular or local necrotic lesions in the corresponding Poaceae species (Egorova, 2015; Egorova et al., 2014). Two multilocus sequence analysis (MLSA) studies reported that strains belonging to X. hortorum have been isolated from diseased olive (Olea europaea) (Young et al., 2010), avocado (Persea americana), and pot marigold (Calendula officinalis) (Parkinson et al., 2009) (Table 1).

4 | DISEASE SYMPTOMS

The pathovars of X. hortorum can cause bacterial spot and/or bacterial blight on numerous plant species. X. hortorum pvs hederae, taraxaci, and vitians cause bacterial leaf spot on ivy (Figure 3a), dandelion (Figure 3e), and lettuce (Figure 3g), respectively. X. hortorum pvs carotae and pelargonii cause bacterial blight on carrot (Figure 3b) and geranium (Figure 3f), respectively. The symptoms of X. hortorum pv. gardneri can be observed on tomato (Figure 3c) and/or pepper (Figure 3d), depending on the strains, while X. hortorum pv. cynarae causes bacterial spot on artichoke bracts (Figure 3h). The disease symptoms caused by all these pathogens share common characteristics but also have some subtle differences.

Diseases caused by X. hortorum pathovars are characterized by round, water-soaked lesions on the abaxial surface of leaves (capitulum artichoke bracts, in the case of X. hortorum pv. cynarae) and are usually the first symptoms observed (Norman et al., 1999; Potnis et al., 2015; Pruvost et al., 2010; Ridé, 1956; Rockey et al., 2015; Schornack et al., 2008; Trébaol et al., 2000). These small water-soaked leaf spots rapidly expand to form angular necrotic lesions.

The presence of a chlorotic halo around spots or lesions is pathovar- or plant/cultivar-dependent. For example, a chlorotic halo is present around lesions caused by X. hortorum pvs pelargonii, hederae, and taraxaci, but its presence varies in angular leaf spot caused by X. hortorum pvs carotae, vitians, and gardneri (Daughtrey & Wick, 1995; Gilbertson, 2002; Myung et al., 2014; Nameth et al., 1999; Pruvost et al., 2010). In advanced infection stages, lesions and spots usually turn dark in colour (brown to black) on plant parts affected by X. hortorum pvs pelargonii, hederae, carotae, gardneri, and vitians. They can also coalesce (e.g., in the presence of X. hortorum pvs hederae, gardneri, and vitians), giving a papery appearance to leaves affected by X. hortorum pv. vitians (Bull &
In final infection stages, leaves usually harden and dry and, in the case of leaves affected by X. hortorum, a red-purple margin might appear on their upper surface (Suzuki et al., 2002).

Some very particular leaf symptoms are associated with certain X. hortorum pathovars. For example, X. hortorum pv. pelargonii can cause leaf margin wilting and V-shaped necrotic areas, depending on the plant species and cultivar (Daughtrey & Wick, 1995). The affected areas eventually drop off, and black stem rot occurs in case of a systemic infection. When the infection expands to the roots, it results in overall wilt and gradual plant death, but no decay or soft rot is observed (Daughtrey & Benson, 2005; Manulis et al., 1994).

Furthermore, leaves are not the only plant parts affected by X. hortorum. X. hortorum pv. gardneri affects tomato fruits, on which it causes characteristic star-shaped lesions with a raised, scabby appearance (Potnis et al., 2015). On unripe tomato fruits, symptoms look like water-soaked or slightly raised pale-green spots, sometimes surrounded by greenish-white halos. On tomato sepals, symptoms consist of brown lesions, which can turn necrotic; stem lesions are narrow, elongated, and raised (Potnis et al., 2015). X. hortorum pv. hederae occasionally affects stems and petioles (Suzuki et al., 2002), and X. hortorum pv. carotae causes disease on petioles, peduncles, stems, flowers, and leaflets (Gilbertson, 2002). Lesions caused by X. hortorum pvs carotae and vitians can be V-shaped (Gilbertson, 2002; Sahin, 1997; Scott & Dung, 2020; du Toit et al., 2014).

5 | GEOGRAPHIC DISTRIBUTION AND IMPORTANCE

X. hortorum includes a pathovar causing the most devastating bacterial disease of geranium (pv. pelargonii) (Manulis et al., 1994; Munnecke, 1954), an internationally regulated seedborne pathovar affecting carrot (pv. carotae) (Scott & Dung, 2020), and a pathovar reported in most lettuce-growing areas (pv. vitians) (Sahin, 1997). Furthermore, X. hortorum pv. gardneri, in addition to three other Xanthomonas spp., is a major pathogen on tomato and/or pepper (Jones et al., 2004; Osdaghi et al., 2021; Potnis et al., 2015). Diseases caused by X. hortorum pathovars have been reported in more than 40 countries across all continents except Antarctica (Figure 4), either as one-time reports or as frequent reoccurrences. One-time reports do not necessarily mean that the diseases are not recurring or currently present. Examples of frequent reoccurrences include X. hortorum pv. carotae in Canada and the USA (EPPO, 2021), X. hortorum pv. vitians in Canada and France (Morinière et al., 2020; Toussaint, 1999; Toussaint et al., 2012), and X. hortorum pv. gardneri in the USA and Brazil (Araújo et al., 2012, 2015, 2017; Potnis et al., 2015; Quezado-Duval et al., 2004), the second and sixth largest tomato producers in 2019, respectively, by gross production value (FAOSTAT, 2021).

Data on the economic impact of X. hortorum is not available for all its pathovars, as there are no reports documenting the cost of the damage caused by X. hortorum pvs cynarae, taraxaci, and hederae. When available, economic impact reports are not recent but are nonetheless informative about the scope of the importance of

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**FIGURE 3** Xanthomonas hortorum pathovars on various hosts. (a) English ivy leaf infected by X. hortorum pv. hederae. Courtesy of Forestry Images and the Penn State Department of Plant Pathology & Environmental Microbiology Archives. (b) X. hortorum pv. carotae symptoms on a carrot leaf. Photograph courtesy of E-phyta and Benoît Mériaux. (c) X. hortorum pv. gardneri symptoms on pepper (cv. Early Carl Wonder) leaves, 14 days postinoculation (dpi) with X. hortorum pv. gardneri Xg965. Photograph provided by Neha Potnis. (d) Field infection of tomato plant by X. hortorum pv. gardneri. Photograph provided by Eduardo Bernal. (e) Diseased dandelion leaf 12 dpi after inoculation with X. hortorum pv. taraxaci LM 16389 (= CFBP 8644). Photograph provided by Lucas Morinière. (f) X. hortorum pv. pelargonii on geranium (Pelargonium spp.). Photograph courtesy of Forestry Images and Nancy Gregory (University of Delaware). (g) Close-up of field infection of a lettuce leaf by X. hortorum pv. vitians. Photograph provided by Lucas Morinière. (h) Infection of artichoke head by X. hortorum pv. cynarae. Photograph courtesy of Johan Van Vaerenbergh

Koike, 2005). In final infection stages, leaves usually harden and dry and, in the case of leaves affected by X. hortorum pv. hederae, a red-purple margin might appear on their upper surface (Suzuki et al., 2002).
X. hortorum. For example, bacterial blight of geranium caused by X. hortorum pv. pelargonii is the most devastating bacterial pathogen of geranium and can lead to total geranium loss when environmental conditions are most favourable to this pathogen (Balaž et al., 2016; Manulis et al., 1994; Munnecke, 1954; Nameth et al., 1999). Most carrot seed growers in the Pacific Northwest region of the USA, an important region for US carrot seed production, consider X. hortorum pv. carotae detrimental to seed quality (Dr Jeremiah Dung, The Oregon State University, March 2021, personal communication). In Montreal, Canada, losses due to X. hortorum pv. vitians have led to complete destruction of lettuce fields (Toussaint, 1999). In Florida, USA, the pathovar caused an estimated loss of $4 million from the early to mid-1990s (Robinson et al., 2006), and also caused substantial economic losses in California and Ohio, USA (Carisse et al., 2000; Sahin, 1997). Losses due to X. hortorum pv. gardneri were estimated to cost the Midwestern US tomato-processing industry $7–8 million (Ma, 2015; Ma et al., 2011).

X. hortorum pv. gardneri is one of the four xanthomonads causing bacterial spot of tomato and pepper, and multiple reports have studied population structure shifts of those four species, especially in the USA and Brazil (Araújo et al., 2015, 2017; Egel et al., 2018; Pereira et al., 2011). In the USA, most early reported incidences of bacterial spot disease on tomato and pepper were caused by X. euvesicatoria pv. euvesicatoria but a population shift to X. hortorum pv. gardneri has been reported in published work (Egel et al., 2018; Ma, 2015; Ma et al., 2011) and personal communications (Dr Francesca Rotondo and Dr Sally A. Miller, The Ohio State University, March 2021, personal communication). However, recent surveys for tomato and pepper bacterial spot in Brazil have shown a limited presence of X. hortorum pv. gardneri (Araújo et al., 2017).

### 6 | EPIDEMIOLOGY

In general, X. hortorum pathovars thrive in warm, wet, and humid environments in fields and greenhouses (Dye, 1967; Gardner & Kendrick, 1921; Kendrick, 1934; Manulis et al., 1994; Strider, 1985; du Toit et al., 2005; Toussaint, 1999). During inoculation trials, X. hortorum pv. gardneri had a higher virulence at 20°C when compared to other bacterial spot pathogens of tomato and pepper (Araújo et al., 2011), and was more prevalent than other bacterial spot xanthomonads at higher altitudes (Araújo et al., 2017). Furthermore, X. hortorum pv. vitians has an optimal infection temperature of around 23°C (Robinson et al., 2006).

The pathovars colonize the plants through natural openings (e.g., hydathodes, stomata) or wounds (Bernal & Francis, 2021; Dougherty et al., 1974; Ridé, 1956; Schwartz et al., 2017). After gaining entry, they infect the plant vascular system (Barak et al., 2002; Munnecke, 1954). Mesophyll colonization is also possible for X. hortorum pvs pelargonii (Barel et al., 2015) and vitians (authors’ unpublished data). Infections of X. hortorum pvs pelargonii and vitians can sometimes be symptomless (Barak et al., 2002; McPherson & Preece, 1978).
The two primary sources of inoculum of *X. hortorum* pathovars are seeds and cuttings, although they can be disseminated through other means as well (e.g., insects, rain, and irrigation water) and can survive on weeds, crop debris, or in soils. Seed is a main source of inoculum for bacterial spot and blight caused by *X. hortorum* pv. *carotae*, *gardneri*, and *vitiens* (Barak et al., 2001, 2002; Kendrick, 1934; Kuan, 1985; Mtui et al., 2010; Sahin & Miller, 1997; du Toit et al., 2005, 2014). Contaminated seed, stecklings, or seedlings may initiate an epidemics in grower fields (McDonald & Linde, 2002; du Toit et al., 2005), which could result in a nonnormal pathogen distribution, as observed for *X. hortorum* pv. *carotae* populations (Scott & Dung, 2020). This can pose a challenge to the development of detection methods and durable resistant cultivars.

*X. hortorum* pv. *hederae* and *pelargonii* are mainly transmitted by infected cuttings (Chittaranjan & De Boer, 1997; Norman et al., 1999) because flowers such as geraniums are commonly vegetatively propagated by cuttings. Historically, propagating facilities were inadvertently responsible for distributing infected symptomless plant material (Nameeth et al., 1999).

Crop residues can allow *X. hortorum* pv. *carotae* and *vitiens* to overwinter for several months or until the following growing season (Christianson et al., 2015; Sahin et al., 2003). *X. hortorum* pv. *carotae* can persist in infected carrot foliage on soil for up to a year (Gilbertson, 2002). *X. hortorum* pv. *vitiens* can survive in crop debris for up to 1 month, in both summer and winter months (Barak et al., 2001; Fayette et al., 2018). *X. hortorum* pv. *vitiens* and *gardneri* can survive epiphytically or infect weeds, respectively (Araújo et al., 2015; Barak et al., 2001; Fayette et al., 2018). Soil or crop debris also act as an important inoculum source for *X. hortorum* pv. *carotae*, where it can survive for up to 3 months (Kendrick, 1934), and for pv. *pelargonii*, which can survive in soils for up to a year (Gilbertson, 2002). Survival in weeds, plant residues, and soils can serve as a secondary inoculum source in the presence of favourable hosts and environmental conditions (Gitaitis & Walcott, 2007). If bacterial populations are high, they can re-emerge from inside the plant tissue and serve as a secondary inoculum on the plant itself or on nearby hosts.

*X. hortorum* pv. *gardneri*, *carotae*, and *vitiens* are also disseminated by wind or rain, or mechanically transferred during planting and cultivation (Potnis et al., 2015; du Toit et al., 2005). *X. hortorum* pv. *carotae* has been observed in aerosolized debris generated by carrot seed threshers during field operations (du Toit et al., 2005). *X. hortorum* pv. *pelargonii* can be transmitted by greenhouse whiteflies (*Trialeurodes vaporariorum*) (Bugbee & Anderson, 1963), and insects were noted to be vectors for *X. hortorum* pv. *carotae* but no details (insect genus or species) were given (Gilbertson, 2002).

### IDENTIFICATION AND DETECTION

Visual symptom assessment is the first step to detect a suspected *X. hortorum* infection and subsequent identification is based on pathogen isolation. *X. hortorum* strains are readily isolated from infected plant tissue using serial dilution plating. Growth media used can be nonselective (e.g., nutrient agar, sucrose peptone, or yeast-dextrose-calcium carbonate [YDC] agar) or semiselective (Saddler & Bradbury, 2015). Irrespective of medium type, *X. hortorum* colonies are yellow, mucoid, and convex (Saddler & Bradbury, 2015).

Phenotypic profiles of this species, analysed using phenotype microarrays (e.g., Biolog, OMNILOG), remain too variable to provide an accurate identification at the species level (Akhtar & Aslam, 1990; Bouzar et al., 1999; Mirik et al., 2018; Morinière et al., 2020; Myung et al., 2010; Stoyanova et al., 2014; Trébaol et al., 2000; Uddin et al., 1996). Pathovars cannot be distinguished from one another by using such phenotypic profiling as no stable, discriminative traits exist (Morinière et al., 2020; Trébaol et al., 2000). Even though pathovar classification depends on host pathogenicity (see Taxonomy update), the identification of *X. hortorum* pathovars should not solely rely on the host range. Indeed, some strains of this species can naturally infect hosts other than their original host of isolation (see Host range).

STD-PAGE protein profiling and later DDHs (Stefani et al., 1994; Vauterin et al., 1991, 1995) were used to identify *X. hortorum* pv. *vitiens* “type B”, revealing the existence of aberrant strains (Table 2). Even though fatty acid profiling did not provide identification among pathovars and often remains inaccurate at the species level (Barak & Gilbertson, 2003; Mirik et al., 2018; Sahin et al., 2003; Sekiwoko et al., 2009; Uddin et al., 1996), it still distinguished between *X. hortorum* pv. *vitiens* “type B” and the unusual isolates (Sahin et al., 2003).

Furthermore, a panel of 16 xanthomonad-specific monoclonal antibodies (Table 2), used in enzyme-linked immunosorbent assays (ELISAs), distinguished two serovars of *X. hortorum* pv. *vitiens* isolates (Sahin et al., 2003).

Antibodies were used to detect *X. hortorum* pv. *pelargonii*. Pathovar-specific monoclonal antibodies (Benedict et al., 1990; Chittaranjan & De Boer, 1997) and polyclonal antibodies (Balaž et al., 2016; Mirik et al., 2018) were successfully used for serological identification of this pathogen (Table 2), using commercial double-antibody sandwich ELISA kits (LOEWE Biochemica GmbH and Agdia).

Several DNA-based molecular assays have been developed over recent decades to identify and detect *X. hortorum* strains (Table 2). The available methods are limited to four of the seven pathovars, as diagnostics methods are unavailable for *X. hortorum* pv. *hederae*, *taraxaci*, and *cynarae* at the time of writing. Several PCR detection protocols are available to amplify DNA from many *Xanthomonas* species, including one or more *X. hortorum* pathovars, by targeting the 16S rRNA gene (Maes, 1993), the hpr gene cluster (Leite et al., 2019), or *gumD*, *fyuA*, and the internal transcribed spacer (ITS) (Adriko et al., 2014). However, these general protocols are usually not implemented for the identification and detection of *X. hortorum* pathovars. Instead, targeted assays allowing specific detection and identification at the pathovar level are often preferred.

The first targeted detection DNA-based assays were mostly derived from DNA fingerprint methods, and were used to study the genetic diversity of *X. hortorum* pathovars (Barak & Gilbertson, 2003;
TABLE 2 Non-DNA and DNA-based identification methods for *Xanthomonas hortorum* pathovars. The detection targets, taxonomical level of detection, and primer sequence availability, when applicable, are also reported.

| Detection | Target(s) | Taxonomical level | Targeted pathovar | Specific for the targeted pathovar (antibody, primer, or probe name) | Reference(s) | Comments |
|-----------|-----------|-------------------|-------------------|-------------------------------------------------|--------------|----------|
| ELISA     | Non-DNA   | Polyclonal antibodies | Pathovar | *pv. pelargonii* | Yes | Balaz et al. (2016) | Commercial ELISA kit |
| ELISA     | Non-DNA   | Monoclonal antibodies | *Xanthomonas* species | *pv. pelargonii* | Yes (MAb Xpel-1) | Benedict et al. (1990) | NA |
| ELISA     | Non-DNA   | Monoclonal antibodies | Pathovar | *pv. pelargonii* | Yes (McAb 2H5) | Chittaranjan and De Boer (1997) | NA |
| ELISA     | Non-DNA   | Monoclonal antibodies | *Xanthomonas* species/pathovars | *pv. vitians* | No | Sahin et al. (2003) | Pattern-based discrimination |
| SDS-PAGE  | Non-DNA   | Various proteins | *Xanthomonas* species/pathovars | various: *pv. vitians* (cluster 7d), *hederae* (cluster 7e), *pelargonii* (cluster 12) | No | Vauterin et al. (1991) | Pattern-based discrimination |
| SDS-PAGE  | Non-DNA   | Various proteins | *Xanthomonas* species/pathovars | *pv. vitians* | No | Stefani et al. (1994) | Pattern-based discrimination |
| SDS-PAGE  | Non-DNA   | Various proteins | Pathovar | *pv. gardneri* | No | Quezado-Duval et al. (2004) | Pattern-based discrimination |
| DDH       | DNA       | DNA homology groups | *Xanthomonas* species/pathovars | various: *pv. pelargonii*, *hederae*, *vitians* (group 2) | No | Vauterin et al. (1995) | Clustering-based discrimination |
| MLSA/MLST | DNA       | Various housekeeping genes, including *gyrB* | *Xanthomonas* species | various *pv*s | No | Parkinson et al. (2007); Young et al. (2008); Parkinson et al. (2009) | Clustering-based discrimination |
| MLSA/MLST | DNA       | Various housekeeping genes, including *gyrB* | Pathovar | *pv. vitians* | No | Fayette et al. (2016) | Clustering-based discrimination |
| PCR       | DNA       | RAPD fragments | Pathovar | *pv. carotae* | Yes (3S/3SR and 9B/9BR) | Meng et al. (2004) | D.L.: 22 fg (3S) and 2 pg (9B) |
| PCR       | DNA       | CDS or intergenic regions | Pathovar | *pv. carotae* | Yes (Xhcpp02, PP03, PP04, and PP05) | Kimbrel et al. (2011) | NA |
| PCR       | DNA       | Based on the target of Xhcpp02 (Kimbrel et al., 2011) | Pathovar | *pv. carotae* | Yes (Xhc-q2) | Temple et al. (2013) | NA |
| PCR       | DNA       | AFLP fragments | BSX | *pv. gardneri* | Yes (Bs-XgF/Bs-XgR) | Koenraadt et al. (2009); Pereira et al. (2011) | NA |
| PCR       | DNA       | 1.2 kb DNA-fragment | Pathovar | *pv. pelargonii* | Yes | Manulis et al. (1994); Chittaranjan and De Boer (1997) | NA |
| PCR       | DNA       | ERIC, REP regions | Pathovar | *pv. pelargonii* | No | Sulzinski et al. (1995) | Pattern-based discrimination |
| PCR       | DNA       | ERIC fragment | Pathovar | *pv. pelargonii* | Yes (XcpM1/XcpM2) | Sulzinski et al. (1996); Sulzinski et al. (1997); Sulzinski et al. (1998); Sulzinski (2001) | NA |
| Detection | Type | Target(s) | Taxonomical level | Targeted pathovar | Specific for the targeted pathovar (antibody, primer, or probe name) | Reference(s) | Comments |
|-----------|------|-----------|-------------------|-------------------|------------------------------------------------------------------|--------------|----------|
| PCR       | DNA  | RAPD fragments | Pathovar          | pv. vitians       | Yes (B162)                                                        | Barak et al. (2001) | NA       |
| PCR       | DNA  | BOXA, ERIC, REP, and 16S-23S rDNA regions | Xanthomonas species/pathovars | pv. vitians | No                                                               | Sahin et al. (2003) | Pattern-based discrimination |
| PCR       | DNA  | SNP-based | Pathovar          | pv. vitians       | No                                                               | Hébert et al. (2021) | Cₜ values |
| Multiplex PCR | DNA | ERIC fragment | X. hortorum pv. pelargonii and Ralstonia solanacearum | pv. pelargonii | Yes (DG1/DG2)                                             | Glick et al. (2002) | NA       |
| PCR and multiplex PCR | DNA | AFLP fragments | BSX               | pv. gardneri      | Yes (Bs-XgF/Bs-XgR)                                             | Araújo et al. (2012) | D.L.: 50 pg/μl bacterial suspension; 5 × 10⁴ cfu/ml (100 bacterial cells per reaction) |
| Real-time PCR | DNA | ERIC fragment | Pathovar          | pv. pelargonii   | Yes (XhqF/XhqR)                                                  | Farahani and Taghavi (2016) | D.L.: 200 fg |
| Multiplex real-time PCR | DNA | lepA | BSX + Clavibacter michiganensis subsp. michiganensis, Pseudomonas syringae pv. tomato | pv. gardneri | No                                                               | Peňázová et al. (2020) | Cy5 was used for multiplex PCR that targeted BSX together |
| Multiplex real-time PCR | DNA | hrbB7 primers and probes | BSX               | pv. gardneri      | Yes, in combination with probe (FP2/RP2) | Strayer, Jeyaprakash, et al. (2016) | D.L.: 5 × 10⁶ cfu/ml |
| LAMP      | DNA  | Based on PCR product of 9B primer set (Meng et al., 2004) | Pathovar          | pv. carotae       | Yes (Lace primer set)                                           | Temple and Johnson (2009); Temple et al. (2013) | NA       |
| LAMP      | DNA  | hrbB6         | Pathovar          | pv. gardneri      | Yes                                                               | Stehlíková et al. (2020) | D.L.: 1 pg/μl |
| RPA       | DNA  | hrbB6         | Pathovar          | pv. gardneri      | No (XGF/XGR)                                                     | Strayer-Scherer et al. (2019) | D.L.: 5 × 10⁶ cfu/ml; amplified X. hortorum pv. cynarae CFBP 2044 |

*BSX, the Xanthomonas species causing bacterial spot of tomato and pepper: X. hortorum pv. gardneri, X. vesicatoria, and X. euvesicatoria pvs euvesicatoria and perforans.*

*Primer sequences are available in all the DNA-based detection methods.*

*D.L., reported detection limits; NA, not available.*
Hamza et al., 2012; Sahin et al., 2003; Sulzinski, 2001). For example, a PCR for *X. hortorum* pv. *carotae* was developed from random amplified polymorphic DNA (RAPD) analysis (Meng et al., 2004). Similarly, diagnostic PCR tests for *X. hortorum* pv. *pelargonii* were developed from specific DNA fragments identified by RAPD analysis, enterobacterial repetitive intergenic consensus (ERIC) PCR or repetitive extragenic palindromic (REP) PCR (Chittaranjan & De Boer, 1997; Manulis et al., 1994; Sulzinski, 2001; Sulzinski et al., 1995, 1996, 1997, 1998). A multiplex PCR scheme for the simultaneous detection of *X. hortorum* pv. *pelargonii* and members of the *Ralstonia solanacearum* species complex, the second major bacterial pathogen of geranium, was developed from one of the two previously identified ERIC-PCR fragments (Glick et al., 2002). The same molecular region was used to develop a real-time quantitative PCR (qPCR) assay, allowing quantification of the pathogen (Farahani & Taghavi, 2016).

For *X. hortorum* pv. *gardneri*, a marker identified using amplified fragment polymorphism (AFLP) was initially used to design a diagnostic PCR assay (Koenraadt et al., 2009). The assay was later adapted into a multiplex PCR targeting four *Xanthomonas* species associated with tomato bacterial spot (Araújo et al., 2012). A multiplex TaqMan qPCR assay differentiating these four species was based on *hrpB*, a less conserved gene within the *hrpB* operon (Strayer, Jeyaprakash, et al., 2016). A multiplex qPCR detecting these four *Xanthomonas* species, as well as tomato pathogens *Clavibactor michiganensis* subsp. *michiganensis* and *Pseudomonas syringae* syringae pv. *tomato*, has been recently developed by targeting lepA (Peňázová et al., 2020).

Two *X. hortorum* pv. *vitiens*-specific primer pairs, 9308B and B162, were developed from RAPD fragments (Barak et al., 2001), but their specificity to the target varied. Primer pair 9308B failed to amplify isolates recovered from lettuce and weeds around lettuce fields. On the other hand, primer pair B162 successfully detected *X. hortorum* pv. *vitiens* strains isolated over a 7-year period (Barak et al., 2001).

Partial gene sequence of *gyrB* offers a sufficient resolution for the identification of xanthomonad isolates at the species level (Parkinson et al., 2007, 2009). MLSA is preferred to single-gene (e.g., *gyrB*) to outline the precise phylogeny of *X. hortorum* (Morinière et al., 2020). However, MLSA schemes are based on different partial gene sequences, (sub)sets of partial genes, and trimming settings, which complicates the analysis by not allowing proper comparison between studies (Catara et al., 2021). The sequencing of the first draft genome of *X. hortorum* pv. *carotae* in 2011 allowed the first use of comparative genomics to develop two new diagnostics assays to detect this pathovar (Kimbrel et al., 2011; Temple et al., 2013). The first assay used a TaqMan qPCR, whereas the second relied on loop-mediated isothermal amplification (LAMP) (Temple et al., 2013). The latter method showed superior performance compared to qPCR because of its robustness in the presence of inhibitors, and its rapidity, versatility, and usefulness in facilities with limited resources (Kimbrel et al., 2011). Both assays were also the first ones to be used as viability assays (i.e., detection of viable bacterial cells) with a xanthomonad, by including a propidium monoazide treatment prior to DNA extraction.

Two other isothermal amplification methods were recently published for the in-field detection of *X. hortorum* pv. *gardneri* (Table 2), with an emphasis on differentiation from the other xanthomonad species responsible for tomato bacterial spot. The first method is based on recombine polymerase amplification (RPA) and targets *hrCN* (*hrpB*) (Strayer-Scherer et al., 2019). The second, based on LAMP, targets partial *hrpB* gene sequence (Stehlíková et al., 2020).

### 8 | Genomics

The genome of *X. hortorum* pv. *gardneri* ATCC 19865<sup>PT</sup> (Potnis et al., 2011) was the first *X. hortorum* genome publicly available in the National Center for Biotechnology Information (NCBI) database (accessed March 2021). At the time of writing, 35 *X. hortorum* genomes have been deposited in the database, and most (46%) were submitted in 2020 (Table 3). Their completeness varies, and 74% (*n* = 26) are incomplete (i.e., assembled at the scaffold or contig levels; Table 3). Eight of the nine complete *X. hortorum* genomes contain at least one plasmid sequence. The average genome size of *X. hortorum* is 5.26 Mb (4.92–5.68 Mb). The average G + C content is of 63.6% (63.2%–63.9%), and the average predicted coding sequence (CDS) number is 4260 (Table 3). The average size of *X. hortorum* plasmids is 86.90 kb (29.56–224.70 kb), and three plasmids in *X. hortorum* pvs *vitiens* and *gardneri* genomes are larger than 100 kb (Table 3). The average G + C content of plasmids is 60.30% (58.07%–62.18%), with an average of 94 predicted CDS.

The essential genome (genes required for growth and survival, irrespective of environmental conditions; Koonin, 2000) of *X. hortorum* pv. *vitiens* LM 16734 was recently characterized through saturated transposon insertion sequencing (Morinière et al., 2021) and included 370 protein-coding genes. These genes were mostly associated with critical cellular processes (e.g., translation, energy production, lipid transport), with 355 and 334 of them conserved within *X. hortorum* and the *Xanthomonadaceae* family, respectively.

#### 8.1 | Lipo- and exo-polysaccharides

Lipopolysaccharides (LPSs) are involved in biofilm formation and protecting pathogens from their environment (Corsaro et al., 2001; Newman et al., 2002, 2007). *X. hortorum* pv. *gardneri* ATCC 19865<sup>PT</sup> has a 17.7 kb ancestral-type LPS gene cluster, like that of *Pseudomonas aeruginosa* (Kimbrel et al., 2011). Both assays were the first ones to be used as viability assays (i.e., detection of viable bacterial cells) with a xanthomonad, by including a propidium monoazide treatment prior to DNA extraction.
### Table 3: Genome metrics of representative *Xanthomonas hortorum* strains

| Organism          | Submission year | Strain      | GenBank assembly accession | Assembly level | Contigs/scaffolds | Size (Mb) | GC (%) | N<sub>50</sub> (bp) | CDS<sup>a</sup>                  | Plasmids (bp)                  |
|-------------------|-----------------|-------------|----------------------------|----------------|------------------|-----------|--------|---------------------|---------------------------------|------------------------------|
| *X. hortorum*     | 2017            | B07-007     | GCA_002285515.1            | Complete       | 2                | 5.25      | 63.6   | 5,175,249           | pB07007 (75,655 bp)             |                              |
| *X. hortorum*     | 2019            | VT 106      | GCA_008728175.1            | Complete       | 2                | 5.15      | 63.7   | 5,101,806           | pVT106 (44,015 bp)              |                              |
| *X. hortorum*     | 2020            | FPH2013-1   | GCA_011305375.1            | Scaffold        | 70               | 5.22      | 63.7   | 190,176             | –                               |                              |
| *X. hortorum*     | 2013            | M081        | GCA_000505565.1            | Chromosome      | 1                | 5.05      | 63.7   | 5,052,399           | –                               |                              |
| *X. hortorum*     | 2020            | MAFF 301101 | GCA_015726835.1            | Contig          | 423              | 5.10      | 63.7   | 20,618              | –                               |                              |
| *X. hortorum*     | 2018            | CFBP 4189<sup>PT</sup> | GCA_002939985.1       | Scaffold        | 102              | 5.06      | 63.7   | 145,505             | –                               |                              |
| *X. hortorum*     | 2020            | CFBP 2044   | GCA_903978235.1            | Complete       | 2                | 5.12      | 63.7   | 5,079,002           | CFBP2044_p40 (40,232 bp)        |                              |
| *X. hortorum*     | 2015            | SM234-10    | GCA_001009295.1            | Complete       | 179              | 5.33      | 63.5   | 49,361              | –                               |                              |
| *X. hortorum*     | 2015            | SM605-11    | GCA_001009325.1            | Complete       | 158              | 5.34      | 63.5   | 61,942              | –                               |                              |
| *X. hortorum*     | 2016            | JS749-3     | GCA_001908755.1            | Complete       | 3                | 5.42      | 63.5   | 5,158,913           | –                               |                              |
| *X. hortorum*     | 2015            | SM775-12    | GCA_001009625.1            | Complete       | 176              | 5.25      | 63.6   | 59,240              | –                               |                              |
| *X. hortorum*     | 2020            | CFBP 499    | GCA_012922125.1            | Complete       | 132              | 5.17      | 63.7   | 118,955             | –                               |                              |
| *X. hortorum*     | 2020            | NCPPB 940<sup>PT</sup> | GCA_903978185.1       | Complete        | 2                | 5.03      | 63.8   | 4,999,567           | NCPPB940_p30 (29,567 bp)        |                              |
| *X. hortorum*     | 2020            | LM 16735    | GCA_012922125.1            | Complete       | 138              | 5.19      | 63.7   | 118,265             | –                               |                              |
| *X. hortorum*     | 2020            | LMG 938<sup>PT</sup> | GCA_012922135.1       | Complete       | 119              | 5.03      | 63.8   | 141,718             | –                               |                              |
| *X. hortorum*     | 2020            | LM 16388    | GCA_012922175.1            | Complete       | 121              | 5.07      | 63.7   | 115,523             | –                               |                              |
| *X. hortorum*     | 2020            | CFBP 3978   | GCA_012922195.1            | Complete       | 131              | 5.13      | 63.7   | 141,718             | –                               |                              |
| *X. hortorum*     | 2020            | CFBP 499    | GCA_012922335.1            | Complete       | 132              | 5.17      | 63.7   | 118,955             | –                               |                              |
| *X. hortorum*     | 2020            | LM 16734    | GCA_014338485.1            | Complete       | 2                | 5.27      | 63.7   | 5,213,310           | –                               |                              |
| *X. hortorum*     | 2020            | CFBP 498    | GCA_903978195.1            | Complete       | 4                | 5.68      | 63.2   | 5,365,193           | –                               |                              |
| *X. hortorum*     | 2016            | ICMP 7383   | GCA_001908775.1            | Complete       | 4                | 5.63      | 63.3   | 5,313,102           | –                               |                              |

<sup>a</sup>The number of CDS is a direct output from NCBI and three numbers appear to overestimate the actual number.
stress (Kakkar et al., 2015; Kamoun & Kado, 1990; Sutherland, 1993). The EPS gene cluster of \textit{X. hortorum} \textit{pv. carotae} and \textit{vitiants} is arranged similarly to that of \textit{X. campestris} \textit{pv. campestris} and contains all 12 genes from the \textit{gumB-gumM} cluster (Kimbrel et al., 2011; Morinière et al., 2021). Unlike in other \textit{Xanthomonas} species (Katzen et al., 1998; Kim et al., 2008), only the mutations of \textit{gumE}, \textit{gumI}, and \textit{gumJ} were lethal in \textit{X. hortorum} \textit{pv. vitiants} LM 16734 (Morinière et al., 2021). The presence of a tRNA gene flanking the cluster in some \textit{Xanthomonas} genomes suggests a horizontal transfer acquisition (Lu et al., 2008). However, no evidence of insertion elements was found in the EPS gene cluster of \textit{X. hortorum} \textit{pv. carotae} and \textit{vitiants} (Kimbrel et al., 2011; Morinière et al., 2021).

### 8.2 | Secretion systems

Secretion systems and their effector proteins are crucial determinants of virulence in the \textit{Xanthomonas} genus (Büttner & Bonas, 2010). There are two types of type II secretion system (T2SS) clusters within \textit{Xanthomonas}: the T2SS-xps, directly involved in virulence, and the T2SS-xcs, which has seemingly no direct virulence function (Szczesny et al., 2010). The pathotype strains of \textit{X. hortorum} \textit{pv. hederae}, \textit{gardneri}, and \textit{cynarae}, in addition to strain B07-007, have complete T2SS-xps (xpsD-xpsN) and T2SS-xcs (xcsC-xcsN) clusters (Alvarez-Martínez et al., 2021; Timilsina et al., 2020). Unlike T2SS-xcs, the T2SS-xcs cluster is not conserved within \textit{Xanthomonas} spp. (Timilsina et al., 2020) but is conserved between the four \textit{X. hortorum} strains.

The type III secretion system (T3SS) delivers effector proteins that, in turn, can suppress or trigger plant defence mechanisms (Büttner, 2016; White et al., 2009). The T3SS is found in most \textit{Xanthomonas} strains, including \textit{X. hortorum} (Timilsina et al., 2020). The T3SS of \textit{X. hortorum} \textit{pv. gardneri} ATCC 19865\textsuperscript{PT} is a mosaic \textit{hrp} cluster, with elements like that of \textit{X. campestris} \textit{pv. campestris} ATCC 33913\textsuperscript{T}, but also including novel effectors (see Molecular host-pathogen interactions) (Potnis et al., 2011). \textit{X. hortorum} \textit{pv. carotae} M081 has a complete \textit{hrp} cluster and is predicted to be functional (Kimbrel et al., 2011). Furthermore, a recent study reported that the T3SS \textit{hrp} cluster in \textit{X. hortorum} \textit{pv. gardneri} ATCC 19865\textsuperscript{PT}, \textit{cynarae} CFBP 4188\textsuperscript{PT}, \textit{hederae} CFBP 4925\textsuperscript{T}, and \textit{carotae} M081 are similar, with some differences in the two 20 kb regions flanking the cluster (Merda et al., 2017).

The type IV secretion system (T4SS) is involved in protein transfer as well as bacterial conjugation (Guglielmi et al., 2014; Lawley et al., 2003; Lloia et al., 2002). \textit{X. hortorum} \textit{pv. gardneri} ATCC 19865\textsuperscript{PT} has two plasmidborne and one chromosomal T4SS clusters (Potnis et al., 2011). The chromosomal cluster of \textit{X. hortorum} \textit{pv. gardneri} is complete and similar to that of \textit{X. campestris} \textit{pv. campestris} ATCC 33913\textsuperscript{T}. One of the two \textit{X. hortorum} \textit{pv. gardneri} plasmidborne clusters is 98% and 89% identical to the T4SS clusters of \textit{Burkholderia multivorans} ATCC 17616 and \textit{Acidovorax avenae} subsp. \textit{citrulli} AAC001, respectively. The other plasmidborne cluster is similar to the one found in \textit{X. vesicatoria} ATCC 35937\textsuperscript{T} and \textit{X. euvesicatoria} \textit{pv. perforans} 91-118 (Potnis et al., 2011). The presence of a T4SS cluster in \textit{X. hortorum} \textit{pv. carotae} M081 was suggested by the detection of \textit{virB} genes scattered over three different contigs but its functionality was inconclusive (Kimbrel et al., 2011).

The type V secretion system (T5SS) is responsible for the secretion of various proteins, including adhesins, which are important for host colonization as they are among the first contact points between pathogen and host (Meukens et al., 2019). The members of T5SS are autotransporters, with the exception of type 5b, which is formed of two proteins (Guérin et al., 2017). In \textit{Xanthomonas} spp., T5SS clusters belong to categories 5a, 5b, and 5c (Alvarez-Martínez et al., 2021). \textit{X. hortorum} \textit{pv. gardneri} ATCC 19865\textsuperscript{PT} and \textit{X. hortorum} B07-007 have three types of T5SS (types 5a, 5b, and 5c) (Alvarez-Martínez et al., 2021).

The type VI secretion system (T6SS) is mostly responsible for bacterial antagonism, thus playing an important role in competition (Bayer-Santos et al., 2019; Russell et al., 2014). In \textit{Xanthomonas} spp., three subclasses of T6SSs have been reported (T6SS-I, T6SS-II, and T6SS-III) (Alvarez-Martínez et al., 2021; Bayer-Santos et al., 2019; Timilsina et al., 2020). \textit{X. hortorum} \textit{pv. hederae} WHRI 7744, \textit{gardneri} ATCC 19865\textsuperscript{PT}, and \textit{cynarae} CFBP 4188\textsuperscript{PT} do not possess T6SS-I and T6SS-III clusters. A complete T6SS-II cluster was detected in \textit{X. hortorum} \textit{pv. hederae} WHRI 7744, but not in strains CFBP 4188\textsuperscript{PT} and ATCC 19865\textsuperscript{PT} (Timilsina et al., 2020). However, two different studies reported that no T6SS was found in \textit{X. hortorum} \textit{pv. gardneri} and \textit{X. hortorum} (unspecified pathovar). In one study, strain numbers were not specified (Bayer-Santos et al., 2019), while in the other, the two strains were \textit{X. hortorum} \textit{pv. gardneri} ATCC 19865\textsuperscript{PT} and \textit{X. hortorum} B07-007 (Alvarez-Martínez et al., 2021).

### 8.3 | Copper resistance and homeostasis

Copper resistance is attributed to the acquisition of a copper resistance gene cluster through horizontal gene transfer (Behlau et al., 2008; Bender et al., 1990; Cooksey, 1994). Copper resistance is usually plasmid encoded (Stall et al., 1986) and can thus be acquired via conjugation by other bacteria (Basim et al., 1999). Because copper-based solutions have been extensively used for controlling bacterial spot diseases, with recommendations going back to the 1920s (Abrahamian et al., 2020; Higgins, 1922; Obradovic et al., 2008), copper-resistant strains pose a challenge for disease management (see Disease control and management).

\textit{X. hortorum} \textit{pv. gardneri} strains differed in their response to copper. For example, strain ATCC 19865\textsuperscript{PT} has copLAB homologs on the chromosome (cohLAB) and is homeostatic to copper, growing in copper concentrations up to 75 mg/L (Potnis et al., 2011). In contrast, strains JS749-3 and ICMP 7383 have plasmidborne copLAB and copMGCDF genes (Richard, Boyer, et al., 2017; Richard, Ravné, et al., 2017), as well as \textit{cusAB}/smmD systems, involved in heavy metal efflux resistance and originally described in \textit{Stenotrophomonas maltophilia} (Crossman et al., 2008). Strains JS749-3 and ICMP 7383 are copper-resistant and can grow in copper concentrations up to 470 mg/L (Richard, Ravné, et al., 2017).
9 | MOLECULAR HOST–PATHOGEN INTERACTIONS

The interactions of Xanthomonas species with their plant hosts involve the coordinated expression of various virulence factors (e.g., quorum sensing, effectors, avirulence genes) (Alvarez-Martinez et al., 2021; Ryan et al., 2011; Timilsina et al., 2020). Quorum sensing, a chemical communication mechanism allowing bacteria to regulate group behaviours in response to stimulus, involves the production, release, and detection of auto-inducers (Bassler, 1999; von Bodman et al., 2003; Miller & Bassler, 2001; Ng & Bassler, 2009; Whitehead et al., 2001). In Xanthomonas, the production and sensing of diffusible signal factors (DSF, e.g., α,β-unsaturated fatty acids) (Wang et al., 2004) are regulated by genes within the regulation of the pathogenicity factors (rpf) cluster.

Knocking out rpfF and rpfC in X. hortorum pv. pelargonii Xhp305 altered in planta motility, decreased disease severity on pelargonium plants, and disrupted the plant colonization pattern (Barel et al., 2015). The resulting inability of X. hortorum pv. pelargonii to switch back and forth between biofilm and planktonic lifestyles is thus DSF-dependent (Barel et al., 2015), and this shift is essential for pathogenicity (He & Zhang, 2008). Furthermore, in the rpfF and rpfC mutants, genes gumM, pilC, and pilT were down-regulated compared to the wild type, suggesting that gumM expression and biofilm production, and the type 4 pilus apparatus are DSF-dependent in X. hortorum pv. pelargonii (Barel et al., 2015).

Effectors are used by Xanthomonas species to trigger or suppress host defence mechanisms. Repertoires of effectors (effectomes) have been suggested to play a role determining host specificity (Hajri et al., 2009). Within X. hortorum, effector-related work is mainly focused on pv. gardneri, but there are also reports on pv. carotae strains (more information below). The T3SS of X. hortorum pv. gardneri ATCC 19865PT was associated with hrpW (Potnis et al., 2011), a gene predicted to encode a pectate lyase (White et al., 2009), involved in plant tissue maceration and rotting (Collmer & Keen, 1986). The function of effector gene xopZ2, located downstream of hrpW, was suggested by avrBs2 reporter gene fusion (Potnis et al., 2011). Other T3SS effectors (T3Es) in X. hortorum pv. gardneri strains were also reported: XopAM, XopAO (homolog of AvrRpm1 from P. syringae), XopAQ (homolog of Rip6/Rip11 from R. solanacearum), and XopAS (homolog of HopAS1 from P. syringae). Effectors XopAM and XopAO were demonstrated to be dependent on the T3SS using the AvrBs2 reporter system (Potnis et al., 2011). In addition, four novel T3Es were reported in multiple field strains of X. hortorum pv. gardneri: a second XopE2 paralog, in addition to XopJ and two predicted effectors, named T3EP and PTP, with homologs in R. solanacearum and X. campestris pv. campestris, respectively (Schwartz et al., 2015).

Effector AvrHah1, a transcription activator-like (TAL) effector of the AvrBs3/PthA family (Schornack et al., 2008), was the first characterized effector of X. hortorum pv. gardneri. AvrHah1 was able to trigger a Bs3-dependent hypersensitive response (HR) on pepper plants (Schornack et al., 2008). Gain-of-function experiments with a X. euvesicatoria pv. euvesicatoria strain revealed that avrHah1 is responsible for enhanced water-soaking in pepper leaves, a phenotype typical for the compatible interaction of X. hortorum pv. gardneri, the donor pathogen (Schornack et al., 2008). The virulence function of AvrHah1, triggering enhanced water-soaking in its known hosts tomato, pepper, and Nicotiana benthamiana, was attributed to the movement of water into the infected apoplast (Schwartz et al., 2017). Gene avrBs7 was also identified in X. hortorum pv. gardneri as another avirulence gene as its product triggered an HR in Capsicum baccatum var. pendulum (Potnis et al., 2012). When the corresponding single dominant resistance gene Bs7 was introgressed into C. annuum ‘Early Calwonder’ (ECW), the resulting near-isogenic line ECW-70R was resistant to strains harbouring avrBs7.

Twenty-one candidate T3E genes were identified in X. hortorum pv. carotae MO81, and the products of two of them, AvrBs2 and XopQ, were found to elicit effector-triggered immunity (Kimbre et al., 2011). Using Agrobacterium-mediated transient expression of avrBs2 from X. hortorum pv. carotae in transgenic N. benthamiana triggered an HR in a Bs2-dependent manner. In contrast, no phenotypes were visible in wild-type N. benthamiana lacking Bs2 on delivery of the same DNA construct. Transient expression of xopQ also resulted in strong and rapid HRs in most of the infiltrated leaves of wild-type Nicotiana tabacum, perhaps mediated by another resistance gene. These observations indicated a possibility for resistance gene-mediated control of X. hortorum pv. carotae (Kimble et al., 2011). A core Xanthomonas effectome of nine effectors, including AvrBs2, XopQ, and XopZ previously described, was reported in the tested strains of a study including X. hortorum B07-007 and X. hortorum pv. gardneri ATCC 19865PT.

10 | DISEASE CONTROL AND MANAGEMENT

An integrated control programme that focuses on excluding, reducing, or eradicating the pathogen, in combination with various methods like biological control and host resistance breeding, is the most suitable to manage bacterial spot pathogens like X. hortorum (Agrios, 2005; Marin et al., 2019). Preventing X. hortorum infections by excluding the pathogen from its hosts is crucial, especially because global trade of plants, seeds, and other propagating material plays an important role in the dissemination of this species (see Epidemiology).

Because X. hortorum pv. gardneri is locally present in the territory of the European and Mediterranean Plant Protection Organization (EPPO), the pathogen is on the EPPO A2 list and is recommended for regulation as a quarantine pest (EPPO, 2021). Since 2020, the EU (European Union) Plant Health Law regulates this pathovar as a nonquarantine pest (RNQP; Picard et al., 2018) on seeds, propagating, and planting material of tomato and peppers as well as propagating material of ornamental peppers (EU Commission, 2019). Other Regional Plant Protection Organizations (RPOs) can implement regional phytosanitary regulations. For
example. *X. hortorum pv. carotae* is considered an A1 plant pest by the Caribbean Plant Protection Commission (CPPC) and is under strict quarantine control there. Certification programmes propose requirements for production of disease-free plants. For example, certification scheme EPPO PM4/3 outlines various testing methods for *X. hortorum pv. pelargonii* on different propagation materials (nuclear, basic stock, and certified cuttings). Because cool temperatures during propagation suppress symptom expression, methods to detect low pathogen numbers in asymptomatic tissue are thus crucial (see Identification and detection).

Physical or chemical treatment of the planting material can decrease pathogen inoculum (Janse & Wenneker, 2002). Hot-water seed treatment reduced *X. hortorum pv. carotae* and *gardneri* infections. However, hot-water seed treatment can sometime be unsuitable. For example, a treatment at 50°C for 2 h of lettuce seeds against *X. hortorum pv. vitians* significantly reduced seed germination (Carisse et al., 2000). Some chemical seed treatments against this pathovar, such as soaking in 1% sodium hypochlorite for 5 min (Carisse et al., 2000), in 3% hydrogen peroxide for 5 min, or in suspensions of copper hydroxide plus mancozeb (Pernezny et al., 2002), were more effective in reducing seed contamination than others (copper hydroxide alone, benzoil peroxide, or calcium peroxide). The seed treatments described above are limited to university or extension research and, to the best of our knowledge, are not found in official documents by the National Seed Health System (NSHS) or the International Seed Federation (ISF-ISHI). The use of seed treatments remains at the discretion of seed production companies, which must indicate what treatment was used on each seed lot.

Management of epiphytic *X. hortorum* (see Epidemiology) is challenging. Suppression methods of epiphytic *X. hortorum pv. carotae* on carrot foliage include sanitation and the use of drip irrigation to avoid wetting the phyllosphere during seed maturation (du Toit et al., 2005). Crop rotations or fallow periods could be used to eliminate contamination in plant debris by overwintering pathovars (Barak et al., 2001). In addition, good weed control and removing diseased plants can reduce inoculum amount (Barak et al., 2001; Toussaint et al., 2012), keeping in mind that some *X. hortorum* pathovars can survive epiphytically on weeds, and even infect them (see Epidemiology). Another good practice for decreasing the risk of disseminating *X. hortorum pv. pelargonii* involves not growing perennial *Geranium* spp. near greenhouse facilities producing *Pelargonium* spp. (Nameth et al., 1999).

Foliar applications of copper-based bactericides have been used for *X. hortorum pv. carotae* and *vitians* with variable efficacy depending on various factors (e.g., application time, disease development stage, and climate) (Bull & Koike, 2005; du Toit et al., 2005). Copper-based applications are unsustainable as they have adverse environmental effects, and because copper-induced resistant strains are problematic for sustainable, long-term control (Fishel, 2005; Husak, 2015; Willis & Bishop, 2016). For example, copper-induced resistance was reported in strains of *X. hortorum pv. gardneri* (Abbasi et al., 2015; Khanal et al., 2020). The use of nanoparticles was studied to manage copper-resistant and/or copper-tolerant strains. For example, silver (Ag) nanoparticles merged in a double-stranded DNA–graphene oxide matrix (Ag-dsDNA-GO) exhibited antibacterial activity against copper-tolerant *X. hortorum pv. gardneri* strains (Strayer, Oscy, et al., 2016).

Biological control solutions against some *X. hortorum* pathovars have been proposed. For example, alternative nontoxic compounds that induce a systemic acquired resistance (SAR) in the host plant can provide a more environmentally sustainable approach to disease management than pesticides. The compound acibenzolar-S-methyl (ASM), a benzothiadiazole, released in Europe as Bion (Syngenta Ltd) and in the United States as Actigard 50WG (Syngenta Crop Protection Inc.), has shown positive results for controlling bacterial spot caused by *X. hortorum pv. gardneri*, *pelargonii*, and *carotae* (regarding the latter, the application was only successful on seeds) (Blainski et al., 2018; Pontes et al., 2016; Simmons et al., 2010; Yellareddyari et al., 2013). However, a limitation of ASM is its adverse effect on tomato growth and yield, which may be attributed to the energy cost associated with resistance induction (Romero et al., 2001).

Treating geranium leaves with methyl jasmonate inhibited multiplication of *X. hortorum pv. pelargonii* (Zhang, Grefer, et al., 2009) and spraying leaves with EPSs from *Lactiplantibacillus plantarum* triggered a local induced resistance in tomato leaves against *X. hortorum pv. gardneri* (Blainski et al., 2018). When tested on agar plates, various essential oils inhibited *X. hortorum* pathovars. *Origanum compactum* (oregano) and *Thymus vulgaris* (thyme) inhibited *X. hortorum pv. pelargonii* (Kokoskova & Pavela, 2004), and three oregano species (*O. acutidens*, *O. rotundifolium*, and *O. vulgare*) seemed to inhibit the growth of *X. hortorum pv pelargonii* and *vitians* (Dadasoglu et al., 2011). Geraniin, a tannin extracted from sugar maple, resulted in high mortality of *X. hortorum pv. vitians* bacterial cells when tested by plate counting (Delisle-Houde et al., 2021).

Two *P. syringae* pv. *syringae* isolates, 422 and 17-049, decreased the colonization of *X. hortorum pv. carotae* on carrot leaves (Belvoir et al., 2019). Less virulent quorum-sensing mutants that elicit plant SAR might have a potential in management of *X. hortorum pv. pelargonii* (Barel et al., 2015). Bacteriophages applied as foliar sprays provided significant control of the disease caused by *X. hortorum pv. gardneri* in field trials (Balogh et al., 2003; Flaherty et al., 2000). However, bacteriophage effectiveness strongly depended on UV radiation and other environmental factors that affect their persistence in the phyllosphere (Iriarte et al., 2007). In greenhouse trials on potted geraniums, daily foliar sprays of bacteriophages significantly reduced disease caused by *X. hortorum pv. pelargonii* (Flaherty et al., 2001).

### 11 | HOST RESISTANCE

Resistance breeding research against *X. hortorum* has been focused on tomato, pepper, lettuce, carrot, and pelargonium, and multiple plant cultivars showed moderate to high resistance against the various pathovars. Wild tomatoes have a broad-spectrum resistance against multiple *X. hortorum pv. gardneri* strains (Liabef et al., 2015). Screening of *S. lycopersicum* and *Solanum pimpinellifolium* germplasm using HR identified partially resistant *S. lycopersicum* lines, as well
as three *S. pimpinellifolium* accessions (LA2533, LA1936, and PI 128,216) resistant against the pathovar. This resistance may be controlled by one to four loci with moderate heritability. The *S. pimpinellifolium* lines were also resistant under field conditions (Liabeuf et al., 2015). Another wild tomato genotype, *S. lycopersicum* var. *cerasiforme* line PI 114490, possessed broad-spectrum resistance to multiple xanthomonad pathogens, including *X. hortorum* pv. *gardneri*. Resistance in PI 114490 is quantitatively inherited, and QTL-3 locus and allele at QTL-11 are major contributors of resistance against *X. hortorum* pv. *gardneri* (Bernal et al., 2020).

A mutation in DMRI6 (downy mildew resistance 6) in *Arabidopsis*, conferring broad-spectrum resistance to various *Xanthomonas* and *Pseudomonas* phytopathogens, was tested in tomato (Thomazella et al., 2016). The stable transgenic tomato plants were resistant against *X. hortorum* pv. *gardneri* and were not compromised in their growth and development.

In pepper, two dominant resistance genes, Bs3 and Bs7, are known to confer resistance against *X. hortorum* pv. *gardneri* strains carrying avirulence genes *avrHah1* and *avrBs7*, respectively (Potnis et al., 2012; Schornack et al., 2008). However, the plasmidborne nature of both avirulence genes suggests vulnerability to resistance breakdown, so they have not been further considered in breeding programmes. Screening of core pepper germplasm collection against *X. hortorum* pv. *gardneri* revealed that more than 40 PI lines of *C. baccatum* in greenhouse conditions and multiple PI lines of *C. annum* showed promising resistance levels (Potnis et al., 2012). A total of 20 significant single nucleotide polymorphisms (SNPs), co-located within 150 kb of 92 unique genes, were recently identified against the pathovar (Potnis et al., 2019).

Regarding *X. hortorum* pv. *vitians*, different lettuce genotypes (*L. sativa*) show differential responses to the pathogen. For example, romaine and butterhead lettuce cultivars are among the highly susceptible ones (Pernezny et al., 1995). Moderately resistant cultivars include both green-leaf (e.g., Waldmann’s Green and Grand Rapids) and red-leaf (e.g., Red Line) cultivars (Carisse et al., 2000), although other studies have noted their susceptibility (Bull et al., 2007). Such discrepancy could be due to differences in the experimental setups of the studies, such as using different strains for the pathogenicity tests. Other moderately resistant cultivars include Little Gem and Reine des Glaces (Batavia crisphead) (Bull et al., 2007). These two latter cultivars were deemed to be promising in breeding resistant cultivars against *X. hortorum* pv. *vitians* (Hayes, Trent, Mou, et al., 2014; Hayes, Trent, Truco, et al., 2014). However, undesirable traits (e.g., small size and low yield) associated with cv. Little Gem are of concern. Furthermore, this cultivar has also shown variable resistance in separate studies, making it an unattractive candidate (Bull et al., 2007; Lu & Raid, 2013). This difference could be due either to virulence dissimilarities at the strain level or to host susceptibility variation as a result of different environmental conditions at the cultivar evaluation locations (Lu & Raid, 2013). In addition, resistance of cv. Reine des Glaces was also highly dependent on environmental conditions (Bull et al., 2007).

Genetic maps of various wild lettuce species like *L. serriola*, *L. saligna*, and *L. virosa*, have revealed multiple genes conferring broad resistance (McHale et al., 2009; Truco et al., 2013). However, *L. saligna* and *L. virosa* have compatibility issues, making hybridization difficult. The broad resistance in wild lettuce species have yet to be tested against *X. hortorum* pv. *vitians*.

The high genetic variability of the pathogen population is a challenge for breeding cultivars with durable resistance. Resistance against MLSA-based groups B, D, and E of *X. hortorum* pv. *vitians* was identified to be controlled by a single dominant locus, *Xanthomonas* resistance 1 (*Xar1*), in the Batavia heirloom cv. La Brillante (Bull et al., 2016; Hayes, Trent, Mou, et al., 2014; Hayes, Trent, Truco, et al., 2014). Two other cultivars, Little Gem and Pavane, carry Xar1 alleles and are resistant to Californian isolates of *X. hortorum* pv. *vitians*. Another locus identified as *X. campestris* vitians resistance (*Xcvr*) was found in the same linkage group (LG2) during the mapping of a PI 358001-1 × Tall Guizmaine population. The durability of *Xar1* and *Xcvr* resistances in cv. La Brillante and PI 358001-1 raised concerns because of the high variability in the pathogen population (Hayes, Trent, Mou, et al., 2014; Hayes, Trent, Truco, et al., 2014). Major and minor quantitative trait loci (QTLs) controlling this resistance were identified and co-located in the same region of LG2 as previously identified with *Xar1* and *Xcvr* (Sandoya et al., 2019).

A germplasm screening of carrot species (e.g., PI lines, public inbred lines, commercial cultivars, and wild varieties) indicated four PI lines (PI 263601, PI 418967, PI 432905, and PI 432906) and two of the wild relatives, Ames 7674 and SS10 OR, were the most resistant against *X. hortorum* pv. carotae (Christianson et al., 2015). The resistant PI lines are promising for use in commercial breeding programmes (Christianson et al., 2015).

In the genus *Pelargonium*, only a small number of pelargonium and geranium species have been screened for resistance against *X. hortorum* pv. *pelargonii* based on symptom expression alone after pathogen inoculation (Griesbach & Olbricht, 2002; Zhang, Sairam, et al., 2009). Five resistant pelargonium species were identified (Griesbach & Olbricht, 2002; Zhang, Sairam, et al., 2009), but most commercially important cultivars of *Pelargonium zonale* hybrids were highly susceptible (Griesbach & Olbricht, 2002; Zhang, Sairam, et al., 2009).

### 12 RESEARCH PERSPECTIVES

Several advances improving our understanding of the *X. hortorum* species have recently been published. However, some knowledge gaps remain, mainly related to extent of host range, detection, and control methods, including host resistance. Given the broad and diverse host range described for this species, it is likely that unreported hosts remain to be identified in various ecosystems. Further investigation of the natural and experimental host ranges of *X. hortorum* could provide insight into its evolutionary history and determine if plant domestication influenced host specialization of the pathovars of *X. hortorum*.

The recent increased availability of genomic data for *X. hortorum* will help in the identification of novel isolates from new natural hosts through establishing quick, field-deployable detection methods. Such
tools will also be very beneficial for phytosanitary control, especially as prevention strategies are preferred to formulation applications and are less costly than containment and eradication measures.

There is a significant need to conduct a comprehensive comparative genomics analysis of this species, especially in view of the recent taxonomical changes. Because plasmids offer a potentially large source of variation in the species, determining the plasmid content of strains and their contribution to pathogenicity is highly relevant. The recent application of a TnSeq analysis in X. hortorum pv. vitians paves the way to functional genomics analysis of other X. hortorum members. Aside from providing insights into essential bacterial genes in different in vitro and in planta conditions, TnSeq would also considerably improve our understanding of X. hortorum biology.

Most important commercial varieties are still highly susceptible to diseases caused by X. hortorum. The inefficiency of application-based control strategies further consolidates host resistance as a promising area for devising practical and durable disease control solutions against X. hortorum. Because nonhost resistance is more durable than host resistance, screening more nonhost species for their disease response to X. hortorum could uncover broad, nonhost resistance genes against the pathovars. Furthermore, exploring recent advancements in the field of host resistance against bacteria, such as CRISPR/Cas9-mediated gene mutations, also sound promising for breeding X. hortorum-resistant plant cultivars. However, as highlighted throughout this pathogen profile, the high genetic variability of these phytopathogens affecting several plant families represents a real challenge for long-term resistance.

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CONFLICT OF INTEREST
The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article as no new data were created or analysed in this study.

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