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REVIEW

Erwinia psidii, an emergent pathogen in South America

Alice Maria Silva Carvalho[1] · Ian Carlos Bispo Carvalho[1] · Pollyane da Silva Hermenegildo[1] · Marisa Alvares da Silva Velloso Ferreira[1] · Maurício Rossato[1]

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Abstract

Erwinia psidii is an emerging bacterial phytopathogen of increasing concern in South America due to its ability to infect economically important hosts such as guava (*Psidium guajava*) and eucalyptus (*Eucalyptus* spp.). First reported in Brazil in the 1980s, affecting guava trees, the pathogen later emerged in commercial eucalyptus plantations, suggesting a recent host shift within the Myrtaceae family. This emergence may be attributed to the expansion of acreage into warmer and more humid regions, as these conditions favor novel pathogen-host interactions. Studies present contrasting perspectives regarding the genetic diversity of *E. psidii* and the hypotheses about how this expansion in host range occurred. Nevertheless, there is consensus that *E. psidii* exhibits cross-pathogenicity between guava and eucalyptus, with no evidence of host specialization or differentiation among isolates from different geographic origins. The pathogen's ability to survive on plant surfaces and debris, along with its dissemination through asymptomatic propagative material, highlights the importance of understanding disease epidemiology for effective monitoring and management. Advances in molecular diagnostics, including qPCR assays, have significantly improved early detection and surveillance. Currently, management relies on exclusion practices and cultural measures, although their effectiveness remains limited in large-scale forestry plantations. The identification of resistant genotypes, such as clones of *Eucalyptus urophylla* × *E. maidenii* and resistant guava varieties, offers potential strategies for control. The emergence of *E. psidii* as a multi-host pathogen highlights the importance of integrated strategies that combine surveillance, resistant germplasm, and diagnostic tools. Understanding the ecological and evolutionary mechanisms underlying host shifts is essential for anticipating disease dynamics and safeguarding guava and eucalyptus production systems.

Keywords Bacterial Blight · Brazil · *Eucalyptus* spp. · *Psidium guajava*

Introduction

Bacterial blight affects both guava (*Psidium guajava* L.) and eucalyptus (*Eucalyptus* spp.) and is caused by the Gram-negative bacterial species *Erwinia psidii* (Arriel et al. 2014; Coutinho et al 2011; Rodrigues Neto et al. 1987). Typical symptoms such as wilt and dieback directly affect fruits and stems, as well as other plant organs that indirectly influence yield, posing a threat to productivity in orchards and planted forest areas (Arriel et al. 2014; Resende et al. 2022; Rodrigues Neto et al. 1987). The bacterium typically induces symptoms in eucalyptus within the first two years after planting seedlings in the field (Mânica et al. 2000; Resende et al. 2022). After this period, symptoms can be more severe, leading to sudden wilting and plant death (Mânica et al. 2000; Resende et al. 2022). Asymptomatic young guava plants will show symptoms approximately two years after their establishment in the orchard, which is the time necessary for fructification (Gonzaga Neto et al. 2001).

Guava is a fruit of great importance in the Brazilian market, both for fresh consumption and to produce juices, sweets, preserves and pulps. On the other hand, eucalyptus (*Eucalyptus* spp.) species are used in Brazil's plantation tree industry, a sector that has been growing exponentially (Mânica et al. 2000; Resende et al. 2022). This fact has made the country the second-largest producer of cellulose in the world, as well as one of the top 10 paper producers globally (IBÁ, 2023). Despite the economic and social importance of these plant species, there are challenges affecting their productivity, particularly due to plant diseases.

This first review of the bacterial blight pathosystems addresses both historical and current information about the

✉ Maurício Rossato
mauricio.rossato@unb.br

[1] Universidade de Brasília, Brasília, Distrito Federal, Brazil

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pathogen and the diseases it causes in guava and eucalyptus, highlighting our current understanding of disease epidemiology and management, and the available tools for pathogen detection and identification.

Impact and economic relevance

The botanical family Myrtaceae comprises approximately 102 genera and 3,024 species distributed globally, with a predominance in the Americas and Oceania, especially the genera *Psidium* and *Eucalyptus* (Mânica et al. 2000). The genus *Psidium*, native to the Americas, features the guava (*Psidium guajava* L.) as its most prominent species due to its significant economic importance in fruit cultivation (Mânica et al. 2000). In this context, Brazil ranks as the third-largest fruit producer worldwide and the leading producer of red guavas, a sector that surpassed 550,000 tons in 2024 and reached a production value of approximately 1.3 billion reais (Freitas and Borém, 2021; EMBRAPA 2024; IBGE 2024). Despite its domestic prominence, guava exports remain constrained. International consumers, particularly in the European Union and North America, typically favor white-pulp varieties and perceive red guava as a high-priced exotic niche product (Freitas and Borém, 2021).

Concurrently, the genus *Eucalyptus*, native to Oceania, plays a fundamental role in the timber industry, with emphasis on the cultivation of species such as *E. grandis*, *E. saligna*, and hybrids like *E. urograndis* (IBÁ, 2022; Resende et al. 2022). Eucalyptus production has shown exponential growth to meet the demand for pulp, charcoal, and wood panels, being valued for its high productivity and versatility (IBÁ, 2022; Resende et al. 2022). This is reflected in the Brazilian forest-based industry, which comprises approximately 9.93 million hectares of planted trees, with eucalyptus accounting for 76% of this area (IBÁ, 2022, 2023). With projected investments of 60 billion reais by 2028, the planted tree segment grew by 6.3%, outperforming the national GDP and reaching a production value of R$ 260 billion, positioning Brazil as the world's largest pulp exporter (IBÁ, 2023).

However, the increased exploitation of these plantations and the expansion of cultivated areas into hot and humid locations contribute to the emergence of plant diseases caused by various phytopathogenic agents (Mânica et al. 2000; Resende et al. 2022). Among the diseases affecting guava and eucalyptus, bacterial blight is notable and highlighted as one of the main limiting factors for production, as it directly impacts the commercial use of the plant (Manica et al. 2000; Resende et al. 2022). Losses in eucalyptus are estimated to range between 30% and 50% of the stand, while in guava, it causes losses of around 60% to 85% (Romeiro et al. 1994; Oliveira et al. 2000). Although not yet described in other guava-producing countries, it is considered a potential risk for India, Egypt, Mexico, and Pakistan (Janse, 2012).

History and geographical distribution

In 1982 a new bacterial disease of previously unknown etiology was observed in guava orchards in the municipalities of Valinhos and Pindamonhangaba in the state of São Paulo, Brazil (Fig. 1) (Rodrigues Neto et al. 1987). For the identification of the causal agent, phenotypic characterization including cultural, physiological and biochemical tests, as well as pathogenicity tests and hypersensitivity reaction in tobacco leaves was performed. The results supported the hypothesis that it was a new species in the "amylovora" group of the genus *Erwinia* (Rodrigues Neto et al. 1987) and the designation of *Erwinia psidii* sp. nov. was proposed for type strain IBSBF 435 (PDDCC 8426) (Rodrigues Neto et al. 1987). Subsequently, the occurrence of this new bacterial pathogen was reported in Minas Gerais (Romeiro et al. 1994), Espírito Santo (Oliveira et al. 2000), the Federal District (Uesugi et al. 2001), Paraná (Coelho et al. 2002), and Goiás (Coelho et al. 2002).

In 2009, eucalyptus plants in Brazil began to show symptoms of wilt, dieback, leaf death, and the presence of a whitish exudate when the stem was cut transversely (Alfenas et al. 2009). However, it was not possible to determine the etiology of the disease, and the cause was attributed to abiotic factors (Alfenas et al. 2009). Two years later, the same symptoms were reported in eucalyptus plants in Argentina and Uruguay (Coutinho et al. 2011). Bacteria were isolated from the exudate present in symptomatic plants of *Eucalyptus grandis, Eucalyptus dunnii, Eucalyptus globulus,* and *Eucalyptus maidenii*, and subsequently characterized with Gram staining, oxidative/fermentative metabolism test, hypersensitivity reaction in tobacco (*Nicotiana tabacum* cv. Samsun), pathogenicity test on seedlings of *E. grandis*, and sequencing of the 16S rRNA, *gyrB*, and *rpoB* genes (Coutinho et al. 2011). Results indicated that the pathogen responsible for the disease in eucalyptus was *E. psidii* (Coutinho et al. 2011).

In 2014, the occurrence of *E. psidii* was confirmed in eucalyptus crops in Três Lagoas (MS), Lençóis Paulistas (SP), Guaíba, and Rosário do Sul (RS) in Brazil (Arriel et al. 2014). Bacterial cultures from symptomatic plants were characterized for partial sequence of the 16S rRNA gene, phylogenetic analyses of the housekeeping genes *gapA, recA,* and *rpoB*, as well as biochemical tests, hypersensitivity reaction in tobacco (*N.tabacum*), and pathogenicity test on seedlings of the hybrid *E. grandis x E. urophylla* (Arriel et al. 2014).

Afterwards, the presence of *E. psidii* was reported in Malaysia associated with papaya dieback (Chai et al. 2017), although only the partial sequence of the 16S rRNA gene

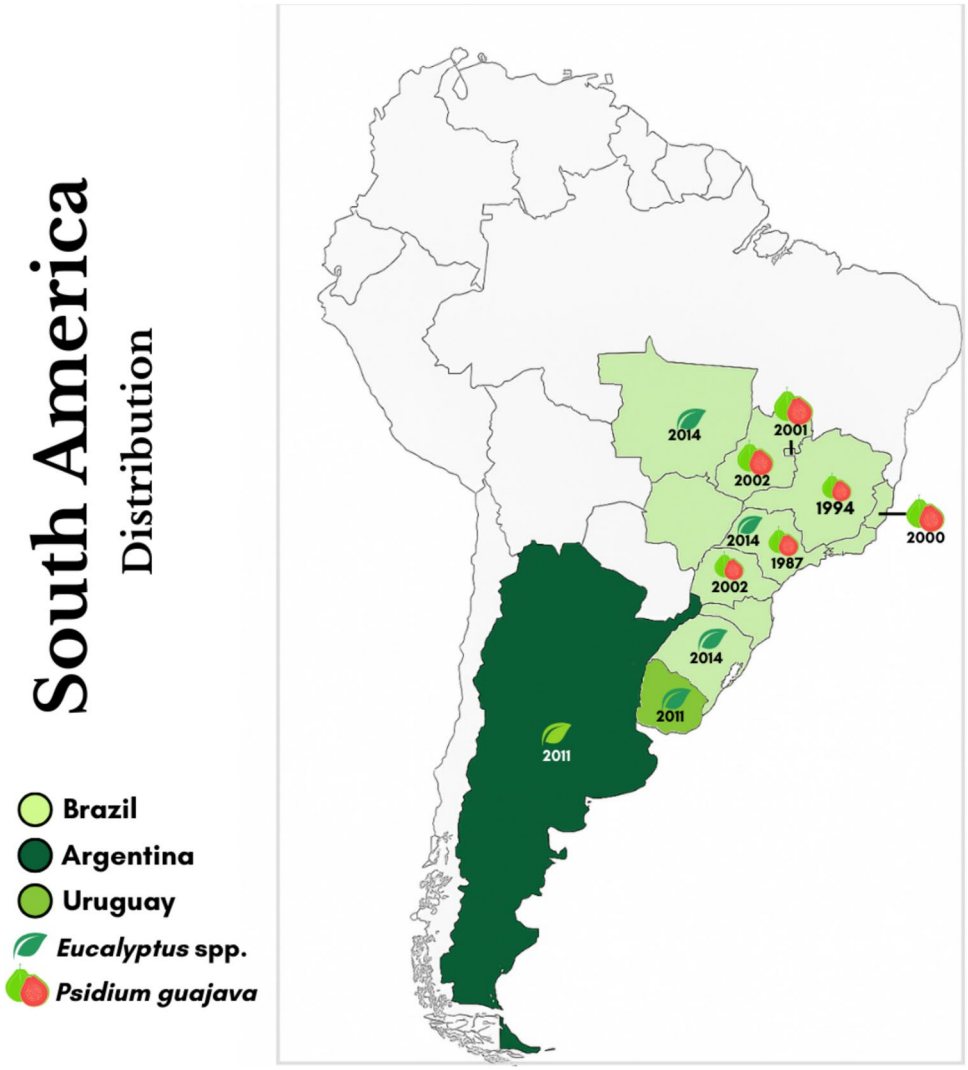


Fig. 1 Distribution of *Erwinia psidii* in South America, indicating the year of the first confirmed report in each location

was used for identification, an unreliable method for species determination (Gao et al. 2017). In addition, Caires et al. (2019) performed controlled artificial inoculation in seedlings of various botanical species and did not observe symptoms caused by *E. psidii* in papaya. Since there are other species of *Erwinia* that can infect papaya plants, such as *E. papaya* (Maktar et al. 2008) and *E. mallotivora* (Noriha et al. 2010), this might have been a case of misdiagnosis.

Pathogen taxonomy and genomics

The genus *Erwinia* is classified as one of the most recently evolved groups of microorganisms capable of causing plant diseases, having diverged from the genus *Pantoea* less than 1,000 years ago (Morris and Moury, 2019). Within this genus, *Erwinia psidii* belongs to a group of species found in association with guava and eucalyptus (Rodrigues Neto et al. 1987; Coutinho et al. 2011).

The bacterium *E. psidii* morphologically, the cells are rod-shaped with peritrichous flagella, and colonies appear whitish, circular, and shiny, with edges that may vary from smooth to rough (Fig. 2) (Rodrigues Neto et al. 1987). Biochemically, it is described as a Gram-negative, facultative anaerobe, and non-pectolytic species. The average time for the development of visible colonies on a Petri plate is between 48 and 72 hours (Rodrigues Neto et al. 1987). It is negative for urease activity, nitrate reduction, pectate degradation, produces acid from mannitol but not from raffinose. These few tests can differentiate *E. psidii* from other *Erwinia* species, and those which are currently assigned to other genera in the Enterobacterales order, such as *Brenneria*, *Pantoea* and *Lonsdalea* (Rodrigues Neto et al. 1987; Marques et al. 2007).

Four genomes of *E. psidii* were sequenced by Hermenegildo et al. 2019; currently, the genome drafts are available in GenBank (RHHM01, RQSA01, RQRZ01, RQSB01). The genome size averages around 4.5 Mb with a G+C content of

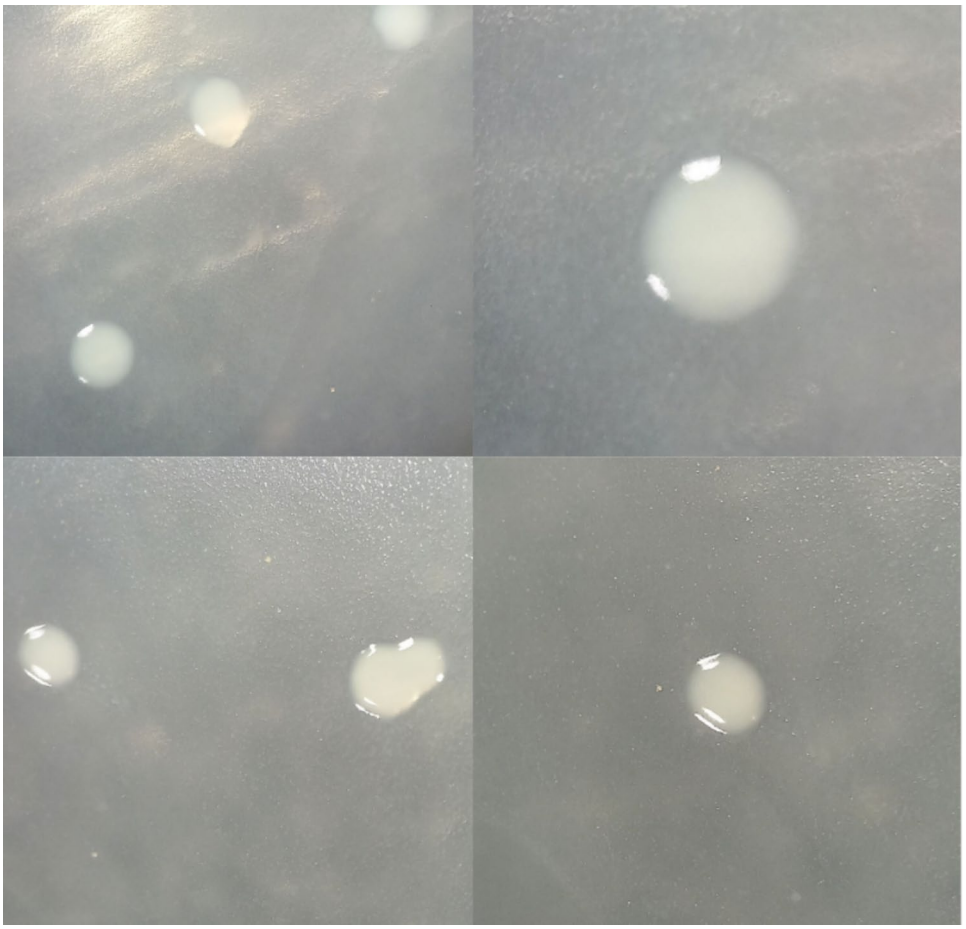


Fig. 2 Morphological characteristics of *Erwinia psidii* colonies grown on nutrient agar (isolate IBSBF 435). Colonies appear whitish, circular, and shiny, with edges that may vary from smooth to rough

approximately 51%, comprising a single chromosome with no plasmids (Hermenegildo et al. 2019).

Genomic analyses of four *Erwinia psidii* isolates (IBSBF435, LPF534, LPF640, and LPF681) indicated that the species pathogenicity may be associated with the presence of a type III secretion system (T3SS) and its corresponding type III effectors (T3SEs) (Pereira et al. 2021). A more recent study, using multiple bioinformatic approaches, predicted 18 distinct putative T3SEs. Among these, 11 (AvrB4, DspE1, Eop1, HopE1, HopG1, HopQ1, HopR1, HopV1, HopW1, HsvB, and HsvC) were predicted to be conserved across all analyzed isolates (Alves et al. 2023). Additionally, two novel effectors, Eps_EF1 and Eps_EF2, were predicted with no significant similarity to previously described T3SEs.

Comparative sequence analyses of the four isolates revealed extensive variation in the effectors AvrB4, DspE1, Eop1, Eps_EF1, HopAR1, and HopE1, suggesting that these differences may be associated with the observed variation in virulence among isolates (Alves et al. 2023). The low-virulence isolate LPF681 exhibited insertions and deletions in the coding region of *dspE* and multiple substitutions in *eop1*, including changes in the catalytic triad, which may be related to its attenuated virulence phenotype (Pereira et al. 2021). In contrast, Eps_EF2, HopO1, HopV1, HopZ2, and HsvC were highly conserved among isolates (Alves et al. 2023).

Beyond T3SEs, 92 apoplastic effectors were predicted to be shared among all four strains, many with enzymatic or unknown functions, with oxidoreductases and peptidases being the most abundant (Alves et al. 2023). Phylogenetic analysis based on housekeeping genes showed that *E. psidii* is most closely related to *Erwinia tracheiphila* (Pereira et al. 2021). However, the *dspE* and *eop1* effector sequences exhibited greater similarity to their homologs in *Pantoea agglomerans*, suggesting that these genes may have been acquired through horizontal gene transfer (HGT). The authors hypothesize that the coexistence of *E. psidii* and *P. agglomerans* in host plant tissues could have facilitated this process, although this hypothesis still lacks experimental validation (Pereira et al. 2021).

Disease symptoms

Erwinia psidii can cause a variety of symptoms, typically observed on leaves, stems, shoots, floral buds, and young or

mature fruits. In guava trees, symptoms initially develop at the tips of new branches and shoots, which suddenly wilt, leading to a darkened coloration (Coelho et al. 2002). On leaves, symptoms begin with the darkening of the central vein (Fig. 3), which expands throughout the leaf, progressing to progressive drying. This symptom of darkening of the medulla, followed by tissue destruction and darkening in the stems, along with wilting, occurs when the bacterium enters, multiplies, and moves through the xylem vessels. Subsequently, dieback and loss of apical dominance occur (Rodrigues Neto et al. 1987).

Necrosis and mummification of flowers and fruits are typical symptoms on guava; however, the presence of mummified fruits can occur without the observation of symptoms on branches and leaves (Coelho et al. 2002). Guava plants affected by *E. psidii*, even severely, rarely die; however, the damage caused by fruit loss is significant (Oliveira et al. 2000; Uesugi et al. 2001).

In eucalyptus, initially, bronzing of the petiole and leaf veins is observed, culminating in the death of the infected leaves (Fig. 3). Water-soaked lesions adjacent to the central leaf veins are also observed. On recently infected young branches, macroscopic and microscopic bacterial exudate can be noted, as well as discoloration of the xylem. Death of the main shoot leads to loss of apical dominance, resulting in reduced growth. In highly susceptible clones, wilting of the entire canopy can occur due to intense colonization of the xylem vessels by the bacterium (Arriel et al. 2014) (Fig. 3).

Occasionally, wilting occurs, resulting in the death of field plants at 2 to 3 months of age (Arriel et al. 2014). It is also possible to observe plants with yellowing leaves, wilting, and upward defoliation at the baseline, progressing to drying and death of the trees (Arriel et al. 2014). Through cross-sections of the stem, darkening of the internal wood tissues resulting from the infection is observable, and after a few minutes of cutting, macroscopic bacterial exudate is observed (Arriel et al. 2014).

Host range and genetic diversity

The first comprehensive assessment of the host range of *E. psidii* was conducted by Rodrigues Neto et al. (1987) through artificial inoculation of a guava-derived strain onto eight plant species within the Myrtaceae family, as well as other plant species (peach, winter squash, papaya, sweet corn, and sugarcane). Symptoms were reproduced only in *Psidium cattleianum*, *Eugenia jambolana*, and *Melaleuca viridiflora*. Subsequent studies expanded this

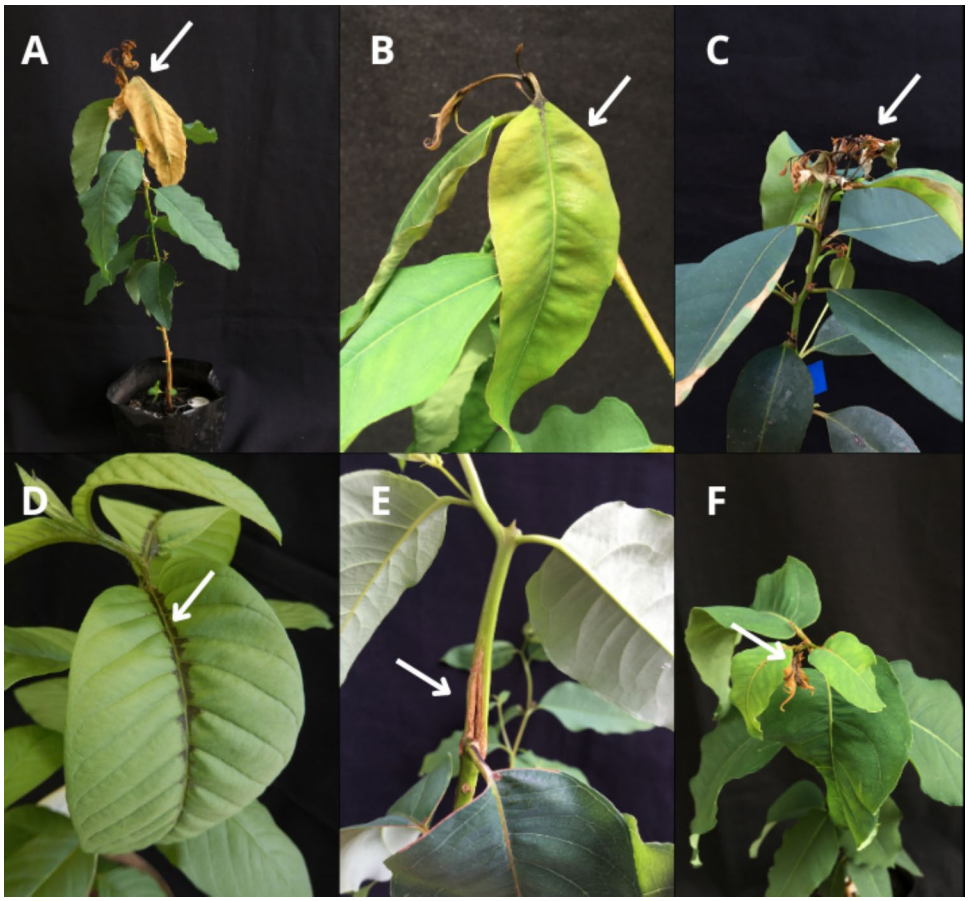


Fig. 3 Symptoms caused by *Erwinia psidii* in guava and eucalyptus seedlings. A, B, C, and F) Symptoms of drying, wilting of the youngest leaves in eucalyptus seedlings, and loss of apical dominance. D) Central vein with darkening and reddish-brown coloration in guava leaf. E) Necrotic lesion on the stem of a guava seedling. Photo: Pollyane da Silva Hermenegildo

list to include eight additional species within Myrtaceae: *Psidium guineense*, *Plinia edulis*, *Eugenia involucrata, Plinia cauliflora, Syzygium jambos, Siphoneugena densiflora, Eugenia uniflora*, and *Eugenia pyriformis*, as well as 28 species of the genus *Eucalyptus* and 4 species of the genus *Corymbia* (Caires et al. 2019). These species represent potential hosts for the pathogen under natural conditions.

However, discrepancies were observed regarding the results for *Corymbia citriodora* and *Eugenia uniflora*. In the report by Rodrigues Neto et al. (1987), these two species did not exhibit symptoms when artificially inoculated with *E. psidii*. Subsequently, in the study conducted by Caires et al. (2019), the same species developed typical symptoms following inoculation with *E. psidii*.

These differences may be attributed to intraspecific variation of the pathogen, differences in inoculation protocols, or the origin of the isolates used, which were obtained from *P. guajava* and *Eucalyptus* spp. (Caires et al. 2019). Although this pathogen has also been associated with papaya decline in Malaysia (Chai et al. 2017), this association was not confirmed by inoculation tests conducted by Rodrigues Neto et al(1987).

The expansion of a pathogen's host range occurs when it begins to colonize new species without a significant change in its genetic diversity. A typical example is the infection of exotic plants by pathogens already present in the area (Vági et al. 2006; Telle et al. 2011). In contrast, host jumping occurs when an organism colonizes a new species in such a way that genetic isolation from the original population leads to genetic differentiation and, eventually, the emergence of a new pathogen species (Choi and Thines 2015). It is important to note that these two evolutionary processes may become interconnected at later stages of pathogen evolution (Thines 2019).

Several factors may be involved in these events. Host range expansion can result from the colonization of introduced hosts and broad beneficial innovation (Thines 2019). The colonization of introduced hosts occurs when host species are introduced into new geographic areas, where indigenous pathogens prevailing in the region may efficiently colonize the new host (Thines 2019).

Host expansion or host jumping are common events in pathogen evolution and generally occur in three phases:

(1) Exposure of the new plant host to the pathogen,
(2) Successful infection, which depends on the compatibility between the two organisms, and
(3) Efficient transmission of the pathogen within the new plant population (Morris and Moury, 2019).

The likelihood of these events increases when plants are phylogenetically related, as they share similar resources and defense mechanisms, facilitating pathogen adaptation (Morris and Moury 2019).

The occurrence of host expansion of *E. psidii* to eucalyptus (Eucalyptus spp.) is a clear example of the ability of plant pathogens to broaden their host range (Morris and Moury 2019). The expansion of eucalyptus plantations beyond the natural distribution range of this tree species in Brazil revealed the ability of *E. psidii* to also infect eucalyptus (Arriel et al. 2014).

It is important to note that this shift from guava to eucalyptus was not caused by any apparent specialization of the bacterial strains involved in the epidemics, but rather by cross-contamination (Arriel et al. 2014; Morris and Moury 2019; Hermenegildo et al. 2021). The emergence of *E. psidii* as a significant pathogen of eucalyptus in Brazil is attributed to factors such as intensified production and the use of more susceptible hybrids in large-scale cultivation areas located outside the tree's natural environment (Morris and Moury 2019). The prevailing hypothesis suggests that the disease in eucalyptus originated from bacterial reservoirs in native plants of the Myrtaceae family (Morris and Moury 2019).

In the first study on the genetic diversity of *E. psidii*, data obtained through rep-PCR analysis indicated low genetic diversity among Brazilian populations of *Erwinia psidii*, showing greater than 87% similarity among strains (Teixeira et al. 2009). The low genetic diversity and high similarity among *E. psidii* strains found in the Federal District, Paraná, Espírito Santo, and São Paulo suggest that the pathogen may have been transported from São Paulo, where it was first identified in 1982, to other regions through contaminated propagative material (Teixeira et al. 2009). This genetic homogeneity also indicates a limited recombination rate within the population, a pattern similar to that observed in global strains of *E. amylovora* (Teixeira et al. 2009). Genetic homogeneity may reflect pathogen specialization to a specific plant host or a narrow ecological niche, given that *E. psidii* has a limited host range restricted to a few species of the Myrtaceae family (Teixeira et al. 2009).

Using molecular markers, Montoya-Estrada et al. (2019a, b, c) analyzed 101 isolates from *Eucalyptus* spp. and 5 from guava (*Psidium guajava*), observing low genetic variability among the *E. psidii* samples. The authors suggested that this low diversity may be associated with the pathogen's recent adaptation to eucalyptus and noted that similar results had previously been reported in studies with guava isolates, indicating a low frequency of recombination (Montoya-Estrada et al. 2019a, b, c).

Subsequently, a study using microsatellite markers on isolates from guava and eucalyptus demonstrated that the *E. psidii* population exhibits significant genetic diversity, an observation that contrasts sharply with previous studies employing the repetitive sequence-based PCR (rep-PCR) technique (Hermenegildo et al. 2021). The study also found

that the oldest strain, IBSBF 435 (isolated from guava), grouped genetically closer to some eucalyptus strains than to other guava strains, supporting the previously reported lack of host specificity (Hermenegildo et al. 2021).

Similarly, Arriel et al. (2014) also observed that the type strain IBSBF 435 exhibited equal aggressiveness when inoculated onto eucalyptus clones, and that isolates derived from guava and eucalyptus were clustered together. The results suggest that the pathogenicity of *E. psidii* in *Eucalyptus* spp. is more closely associated with the introduction of new eucalyptus species and hybrids than with pathogen speciation. This study identified *E. psidii* as pathogenic to the *Eucalyptus saligna* clone #34039, in contrast with the findings reported by Rodrigues Neto et al. (1987), in which *E. psidii* was not pathogenic to *Corymbia citriodora* or *Eucalyptus saligna*.

A recent genetic study using MLVA (Multilocus Variable Number of Tandem Repeat Analysis) suggests that the adaptation of *E. psidii* in eucalyptus may be a more complex process than previously thought (Hermenegildo et al. 2021). The authors point to an absence of pathogen specificity and suggest that the disease in eucalyptus may have been underdiagnosed in the past. The main evidence supporting this hypothesis is that the historical strain IBSBF435, isolated from guava in the 1980 s, was found to be genetically closer to certain eucalyptus strains than to those from guava (Hermenegildo et al. 2021).

Thus, it is suggested that *E. psidii* may occur in eucalyptus in an asymptomatic or endophytic state. The association between the bacterium and symptoms of shoot dieback and wilting may have been underestimated over the years due to their similarity to symptoms caused by *Ralstonia* spp. (Arriel et al. 2014; Freitas et al. 2020; Hermenegildo et al. 2021). This host-shift highlights the importance of phytosanitary surveillance, genetic monitoring of the bacterium, and the implementation of integrated management strategies, since these host species may serve as potential sources of inoculum.

Disease cycle and epidemiology

The primary source of inoculum is contaminated but asymptomatic propagative material, especially seedlings that are transported for orchard establishment and planted forest areas (Teixeira et al. 2009; Montoya-Estrada et al. 2019b). Once the bacterium is established in the field, in the case of guava, short-distance dissemination occurs between organs of the same plant, from one plant to neighboring ones, and between orchards of neighboring properties, mainly using pruning shears (Romeiro et al. 1994). For eucalyptus, the main form of dissemination is the use of cuttings for clonal propagation. The sharing of agricultural implements between neighboring properties favors long-distance dissemination (Mânica et al. 2000) (Fig. 4A).

Conditions that favor the dissemination and penetration of the pathogen are temperatures between 32 °C and 33 °C and high humidity (Rodrigues Neto et al. 1987; Marques et al. 2007). In guava trees, the pathways of penetration are wounds caused by cultural practices such as pruning and fruit harvesting operations, or through natural openings (Barbosa and Lima 2010). In eucalyptus, bacterial entry may occur through wounds resulting from pruning operations, via primary and secondary roots, and through the process of clonal propagation of eucalyptus seedlings (Montoya-Estrada et al. 2019a) (Fig. 4B). It is known that in eucalyptus, it can invade both the xylem and the parenchyma, forming an organized biofilm that influences the development of disease symptoms (Caires et al. 2020). The presence of bacterial exudate is observed when making a cross-section of the stem (Arriel et al. 2014).

Regarding movement, studies have shown that *E. psidii* can move both upward and downward from the point of infection, both in guava seedlings and eucalyptus (Macagnan and Ferreira 2018; Caires et al. 2020; Hermenegildo et al. 2022) (Fig. 4C). Additionally, confocal microscopy analyses using a transformed isolate expressing the green fluorescent protein (GFP) revealed that when the bacterium is inoculated via root, it can penetrate primary and secondary roots and reach the xylem, although typical disease symptoms were not observed (Montoya-Estrada et al. 2019a).

An evaluation of the bacterium's survival on the phylloplane, in soil, and on leaf litter showed that it remained viable for approximately 40 to 60 days on the eucalyptus phylloplane (Lanna-Filho et al. 2021). For the soil survival assessment of *Erwinia psidii*, the bacterium was inoculated into both non-sterilized and sterilized soil. In non-sterilized soil, its persistence was only 15 days, whereas in sterilized soil, the bacterium was detected for 135 days. As for the survival in leaf litter, the bacterium remained viable for 90 days. Between 5 to 15 cm depth, *E. psidii* was detected for 75 days in sterilized soil and 45 days in non-sterilized soil (Lanna-Filho et al. 2021). These findings indicate an epiphytic phase for E. psidii, which potentially serves as a reservoir for secondary inoculum within eucalyptus plantations (Lanna-Filho et al. 2021) (Fig. 4E).

In the study conducted by Cortivo et al. (2025), the epiphytic persistence of *Erwinia psidii* on different plant species was evaluated. The bacterium survived between 35 and 56 days on the phylloplane of eucalyptus genotypes, whereas in species belonging to the Myrtaceae family, such as Surinam cherry (*Eugenia uniflora*) and guava (*Psidium guajava*), survival was even longer, reaching 77 and 85 days, respectively. However, persistence on grasses such as *Brachiaria decumbens* and *Digitaria insularis* was limited to 7 days,

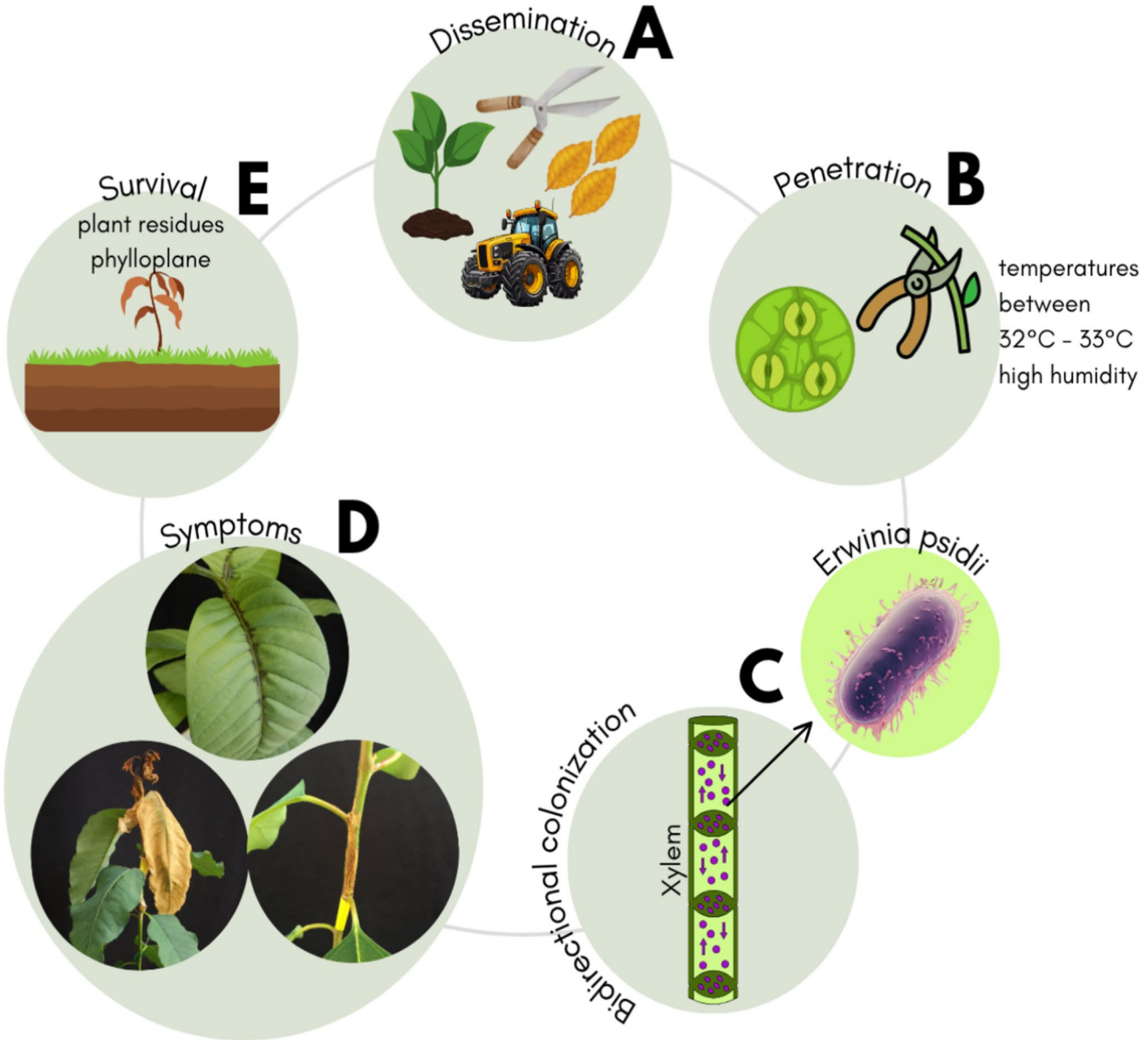


Fig. 4 Bacterial blight cycle caused by *Erwinia psidii*. A – The dissemination of the bacterium through contaminated tools, machinery, and propagative material. B – Penetration occurs through wounds caused by tools or the plant's natural openings. C – The bacterium colonizes the xylem vessels in a basipetal and acropetal manner. D – Symptoms caused by the colonization of the bacterium. E – *E. psidii* survives in crop residues and on the phylloplane

while on dicotyledonous species such as *Conyza bonariensis* and *Lantana camara*, it lasted for 21 days.

The bacterium was observed to survive longer on the leaves of plants from the Myrtaceae family, underscoring the role of the phylloplane of both native and cultivated species as a source of inoculum for the pathogen. These findings highlight the need for management strategies that include the removal of adjacent host plants and the implementation of detection protocols in asymptomatic seedlings, aiming to mitigate primary foci of bacterial blight in forest plantations (Cortivo et al. 2025).

Disease diagnosis

The primary sources of inoculum are contaminated propagative materials; therefore, the most effective control measure is the acquisition of healthy seedlings (Freitas and Borém, 2021). For this purpose, diagnostic tools have proven crucial for controlling and reducing the spread of *E. psidii*. Several biochemical, nutritional, serological, and molecular tests have been developed and employed over the years (Rodrigues Neto et al. 1987; Teixeira et al. 2008; Silva et al. 2015, 2016; Montoya-Estrada et al. 2019c; Hermenegildo et al.

2022). Among the biochemical and nutritional tests, there is a minimal set of procedures that assist in isolate identification, including Gram staining, oxidation–fermentation assays, catalase activity, pectate degradation, acid production from mannitol and raffinose, nitrate reduction to nitrite, and urease production (Rodrigues Neto et al. 1987; Marques et al. 2007).

A method for detecting *E. psidii* involving the enrichment of the bacterial population in guava leaf extract, followed by double radial immunodiffusion with the polyclonal antiserum As15-1, was developed (Teixeira et al. 2008). However, this method exhibited low sensitivity. In addition, the antiserum showed cross-reactivity with saprophytic isolates present on guava leaves, which could lead to false positives (Teixeira et al. 2008).

Subsequently, another serological method using a polyclonal antibody agglutination test was developed for the detection of *E. psidii* by Montoya-Estrada et al. (2019c). For *E. psidii* isolates associated with eucalyptus and guava, a polyclonal antibody, anti-EP, was produced. This method demonstrated remarkable specificity and sensitivity, being capable of identifying the presence of *E. psidii* without reacting with other pathogenic bacteria of eucalyptus (Montoya-Estrada et al. 2019c). However, its application is limited to pure or mixed cultures, requiring bacterial isolation from plant tissues (Montoya-Estrada et al. 2019c).

The Polymerase Chain Reaction (PCR), which exponentially amplifies a specific DNA region (Saiki et al. 1988), is a highly sensitive and specific method that is widely used for pathogen detection and disease diagnosis. From conventional PCR, several variations have been developed, including immunocapture PCR (IC-PCR) (Jansen et al. 1990; Wetzel et al. 1992), biological enrichment PCR (BIO-PCR) (Schaad et al. 1995), and quantitative real-time PCR (qPCR) (Higuchi et al. 1993).

For the identification of *E. psidii*, a pair of specific primers, Ep2L/Ep2R, was designed based on polymorphisms in the recombinase A (recA) gene sequences. These primers were employed in conventional PCR, BIO-PCR, and IC-PCR methods (Silva et al. 2015). In immunocapture PCR, a specific polyclonal antibody, As14.1, was used to perform a preliminary serological test that captures and increases the number of target cells subsequently used for conventional PCR (Silva et al. 2015). In BIO-PCR, a bacterial multiplication step was conducted through incubation in a culture medium before performing the conventional PCR (Schaad et al. 1995). However, this method is time-consuming due to the number of steps required (Silva et al. 2015).

Another PCR-based variation widely used for the detection of phytopathogenic bacteria is real-time PCR, commonly known as qPCR (Freitas et al. 2021; Eichmeier et al. 2019). In qPCR, the cycling steps of conventional PCR are combined with a detection and quantification system based on fluorescence emission (Livak et al. 2001). The primers Ep148_F/Ep148_R were also developed from the recA gene sequence to design a SYBR Green fluorescence-based qPCR method for the detection of *E. psidii* (Hermenegildo et al. 2022). The qPCR method enabled the detection of *E. psidii* in both symptomatic and asymptomatic guava samples (Hermenegildo et al. 2022).

Disease management

The primary control measure is based on the principle of exclusion, that is, preventing the entry of the pathogen into the area (Freitas and Borém, 2021). Given that *E. psidii* dissemination occurs through contaminated propagative material, obtaining healthy seedlings becomes crucial for disease management (Teixeira et al. 2009; Montoya-Estrada et al. 2019a). However, if the disease is already established in the orchard, control becomes more challenging. Nevertheless, there are preventive measures to reduce dissemination within orchards and nurseries. These include care for water quality and irrigation management, avoiding overhead irrigation systems, with micro-sprinklers or drip irrigation being preferable (Junqueira, 2002). Canopy management to allow good aeration, pruning all branches of affected plants followed by removal and burning in the orchard, and avoiding continuous pruning that induces sprouting during hot and humid periods are recommended (Tomita et al. 2016; Freitas and Borém, 2021).

Other measures include the application of copper paste at branch cutting sites, pruning during the hottest hours of the day, during the dry season, the use of windbreaks around the area, disinfection of pruning tools in a solution of sodium hypochlorite or quaternary ammonia, application of nitrogen fertilizers according to soil and foliar analysis at the appropriate time, and avoiding planting in poorly drained soils or those prone to waterlogging (Junqueira, 2002).

Studies have been conducted regarding the use of copper fungicides in the control of bacterial plant diseases (Silva and Lopes 1995). However, these compounds can cause symptoms of phytotoxicity (Piccinin et al. 2005). Rezende et al. (2008) conducted studies on the phytotoxicity and control efficiency of *E. psidii* with copper sulfate, copper oxychloride, and copper hydroxide. Results showed that considering phytotoxicity and disease control, copper sulfate was not the best option, with copper oxychloride and copper hydroxide being preferable. However, spraying is not recommended when fruits reach about 3 cm due to its sensitivity to copper (Freitas and Borém, 2021).

Due to the size of the trees and the extensive cultivation areas, most of these cultural and chemical practices are unfeasible for eucalyptus cultivation (Arriel et al. 2014). The search for resistant plant material is a promising approach for disease control, despite the main varieties of guava trees

and eucalyptus species being highly susceptible (Caires et al. 2019). Caires et al. (2019) demonstrated the potential of *Corymbia henryi*, *Corymbia maculata*, *Eucalyptus thozetiana*,*Eucalyptus cloeziana*, *Eucalyptus viminalis*, *Eucalyptus dalrympleana*, and *Eucalyptus pilularis* as sources of resistance found, as these were highly resistant to *E psidii*. White-fleshed guava varieties show greater tolerance to dieback compared to red-fleshed varieties, which may indicate a possible source of resistance (Piccinin et al. 2005).

Future challenges

Determining the host range of a pathogen is essential for the development of effective plant disease management strategies (Garret and Mundt, 1999). As previously mentioned, the host range of *E. psidii* extends beyond the genera *Psidium* and *Eucalyptus*. Considering that the emergence of *Eucalyptus* as a host is a relatively recent event (Arriel et al. 2014; Coutinho et al. 2011), it is important to assess the potential for this pathogen to infect additional species within the Myrtaceae family under natural conditions. This could have a direct impact on disease epidemiology, as these species may serve as inoculum reservoirs for the pathogen. Moreover, natural infections in native Myrtaceae species may go unnoticed, since these plants are not commonly monitored.

Deployment of genetic resistance sources represents a valuable strategy for disease control. Currently, there are no resistant guava cultivars available; however, some producers in the state of São Paulo have reported that the 'Kumagai' cultivar exhibits tolerance to the disease (Freitas and Borém, 2021). Furthermore, inoculation assays showed that this variety remained symptomless despite the presence of *E. psidii* above and below the inoculation point. (Macagnan and Ferreira 2018). A study conducted by Caires et al. (2019) on sources of resistance in eucalyptus revealed that accessions of *E. thozetiana*, *E cloeziana*, *E viminalis*, *E. dalrympleana*, and *E. pilularis* showed resistance to infection by *E. psidii*. *E. urophylla* also exhibited potential resistance to the pathogen (Caires et al. 2019). This finding is particularly relevant for disease management, as *E. urophylla*, along with *E. grandis*, is one of the most widely used eucalyptus species in Brazil, especially in hybrids with *E. grandis* (Resende et al. 2022). However, it is important to note that further research is required to evaluate the use of *E. urophylla* and its hybrids prior to large-scale commercial planting, given the potential variability in resistance and the current lack of comprehensive understanding of the underlying resistance mechanisms (Caires et al. 2019).

Studies conducted by Caires et al. (2025) demonstrate that resistant plants showed no significant changes in physiological parameters and exhibited no visual symptoms of the disease. This stability in the photosynthetic processes of resistant plants, even under *E. psidii* inoculation, reinforces the importance of genetic resistance as a primary barrier against bacterial infection, preserving the functional integrity of the photosynthetic metabolism (Caires et al. 2025).

These findings are highly relevant for breeding programs, as they indicate that the selection of resistant genotypes not only mitigates the visual effects of the disease but also prevents physiological losses related to photosynthesis, which are directly linked to forest productivity (Caires et al. 2025).

Considering the challenges associated with disease management and the fact that its primary mode of dissemination is through asymptomatic, infected propagative material, effective monitoring is a critical tool for minimizing damage. Techniques such as loop-mediated isothermal amplification (LAMP) and hyperspectral imaging combined with artificial intelligence offer promising, precise, cost-effective, and rapid methods for detecting the presence of the pathogen in plants and propagative material (Martinelli et al. 2015; Whetton et al. 2018; Feng et al. 2019; Abdulridha et al. 2020; Panno et al. 2020; Carvalho et al. 2024).

The use of biocontrol agents, such as bacteria from the genera *Bacillus*, *Pseudomonas*, *Streptomyces*, and *Paenibacillus*, represents a sustainable alternative for the management of plant diseases. These microorganisms can suppress pathogens and promote plant growth, thereby contributing to global food security (Dimkić et al. 2022). Studies have demonstrated the potential of *Bacillus velezensis*, *Pseudomonas poae*, and *Pantoea agglomerans* in controlling *Erwinia amylovora* through the production of inhibitory metabolites (Dagher et al. 2021). Despite their potential, challenges such as formulation, regulatory approval, and field efficacy still need to be addressed. The advancement of biocontrol strategies relies on technologies such as genetic engineering and plant microbiome research, as well as policies that promote their adoption in agriculture (Collinge et al. 2022).

The pathogen's recent expansion, coupled with the inherent complexities of its management, creates an urgent need for research that can provide a solid foundation for developing effective, integrated control strategies. Furthermore, it highlights the importance of highly sensitive and specific detection methods capable of delivering rapid and accurate information to support decision-making in the cultivation of eucalyptus and guava.

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Ian C. B. Carvalho: Original Draft Preparation, Visualization
Pollyane S. Hermenegildo: Review & Editing, Validation
Marisa A. S. V. Ferreira: Review & Editing, Conceptualization
Maurício Rossato: Review & Editing, Conceptualization, Supervision
All authors participated in the writing and discussion of the manuscript.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest/Competing interest The authors declare no conflict of interest.

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