

Review Article

Decoding Late Blight of Potato and Tomato: Insights into Pathogen Dynamics, Host Interactions and Emerging Solutions

Humayra Ferdus¹, Mahabuba Mostafa¹, Dodi Al Sharif² and Md. Motaher Hossain¹

¹Department of Plant Pathology, Gazipur Agricultural University, Gazipur, Bangladesh

²Department of Agroforestry and Environmental Science, Gazipur Agricultural University, Gazipur, Bangladesh

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Corresponding Author:

Md. Motaher Hossain

Department of Plant Pathology,
Gazipur Agricultural University,
Gazipur, Bangladesh

Email: hossainmm@gau.edu.bd

Abstract: The oomycete *Phytophthora infestans* is the source of late blight, a devastating disease that significantly impacts on tomato and potato cultivation worldwide, threatening food security and causing considerable economic losses. This review explores the epidemiological dynamics of late blight, focusing on the pathogen's life cycle, reproductive strategies, and molecular pathogenesis. Traditional management strategies, including cultural practices, host resistance, and biocontrol agents, are discussed alongside emerging sustainable technologies. Recent advancements such as CRISPR-Cas9 genome editing, RNAi (RNA interference), MAS (Marker-Assisted Selection), and biopesticides offer promising solutions to enhance resistance and reduce environmental impacts. IoT sensors and drones with thermal and multispectral imaging are highlighted for their role in real-time disease monitoring, along with the importance of integrating these tools with advanced forecasting models like BLITECAST and JHULSACAST for precision disease management. This comprehensive review offers insightful information about sustainable late blight management techniques, emphasizing the potential of combining innovative technologies with traditional practices to address this persistent agricultural challenge. It underscores the need for collaborative research, policy support, and continued investment in integrated approaches to ensure resilient potato and tomato cultivation in light of evolving threats.

Keywords: *Phytophthora infestans*, Molecular Pathogenesis, CRISPR-Cas9, RNAi, Marker-Assisted Selection, Forecasting Models

Introduction

Food security is a key component of the UN's 2030 Agenda for Sustainable Development, which acknowledges the pressing need for sustainable farming methods to satisfy the expanding world population (Ghufran *et al.*, 2024). Among the various crops crucial to global nutrition and economic stability, potato (*Solanum tuberosum*) holds immense importance. A staple crop with a phenomenal growth rate, potatoes are farmed in more than 150 countries and offer vital nutrients, including vitamins B6 and C, dietary fiber, and minerals like potassium and copper (Lamichhane *et al.*, 2024; Raigond *et al.*, 2024). Potatoes are rich in health-

promoting substances such as flavonoids, carotenoids, and polyphenols that enhance their antioxidant qualities (Bhutto *et al.*, 2024).

Despite their significance, potatoes are very susceptible to destructive diseases, including late blight, as was experienced in past agricultural catastrophes such as the Irish Famine (Singh *et al.*, 2023). Late blight induced by *Phytophthora infestans* is a highly virulent disease that spreads very rapidly in low temperatures and high humidity to destroy foliage in large areas, rot tubers, and, if not controlled, complete crop loss. Its economic global impact is significant, amounting to an estimated \$3 to \$5 billion annually in direct yield losses and the excessively costly fungicide treatment (Islam *et al.*, 2021).



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In addition to potatoes, tomatoes (*Solanum lycopersicum*) are another crop that is of primary global significance and in high demand for their dietary value in the form of beta-carotene, lycopene, vitamin A, and vitamin C (Saffan *et al.*, 2022). A global average annual production of almost to 177 million tons (Nkongho *et al.*, 2023) makes tomatoes critical for both direct human consumption and industrial processing applications. However, tomato cultivation is also most vulnerable to late blight, adding to challenges in sustainable crop management (Lacaze *et al.*, 2023).

Control of late blight needs excessive amounts of fungicides, posing risks such as environmental contamination, pathogen resistance, and human health concerns (Bouket *et al.*, 2022). However, recent innovations in plant biotechnology, such as CRISPR-Cas9 (Angmo *et al.*, 2023), RNAi (RNA interference) (Zhao *et al.*, 2021), and MAS (marker-assisted selection) (Osei *et al.*, 2019) transforming late blight management. Additionally, precision agriculture technologies, including Internet of Things (IoT)-based sensors and drones equipped with thermal and multispectral imaging, enable real-time monitoring and early detection of late blight (Mothapo *et al.*, 2022; Sun *et al.*, 2023). These tools, combined with advanced disease forecasting models, allow for targeted interventions, reducing fungicide dependency and mitigating environmental impacts (Narouei-Khandan *et al.*, 2020).

This review seeks to explore the pathobiology of the devastating late blight disease, including the pathogen's life cycle and infection mechanisms, and to analyze the dynamics of disease outbreaks in relation to environmental factors. Additionally, it highlights innovative and sustainable management approaches aimed at reducing the consequences of late blight. By synthesizing current knowledge and identifying research gaps, the article seeks to support the development of effective and sustainable solutions to enhance global food security.

Agricultural and Economic Impact of Late Blight

Devastating plant diseases like late blight have serious negative effects on agriculture and the economy. The disease was first identified in the Andes of South America, and by the 1840s, it had spread to Europe and the US (Saville *et al.*, 2016). The Irish Potato starvation (1845–1852), in which late blight resulted in severe crop failures, widespread starvation, and a sharp population drop, is most famously associated with its historical significance (Powderly, 2019). Although *P. infestans* was thought to have originated in the Andes, new study indicates that it actually started in central Mexico, from where it traveled around the world (Duan *et al.*, 2021).

Late blight epidemics continue to occur in Peru, the origin of both crops (Majeed *et al.*, 2022).

The economic threat posed by late blight is immense, particularly to global tomato and potato production. It is one of the few plant diseases capable of completely destroying a crop, with losses reaching 100% in vulnerable cultivars. In addition to field crops, late blight also affects stored potatoes and tomatoes, causing rot and rendering them unsellable (Tsedaley, 2014). The disease thrives under conditions of high humidity and mild temperatures, spreading rapidly across fields and impacting large cultivation areas. This has made it a significant concern for regions heavily reliant on these crops, threatening food security and economic stability. Annual global losses resulting from late blight are estimated at \$12 billion, with developing nations bearing approximately \$10 billion of this burden (Haverkort *et al.*, 2009). In Bangladesh, annual losses of potato yield from late blight range from 25 to 57% (Kessel *et al.*, 2017), encouraging the adoption of decision support services such as GEOPOTATO that act to inform on the timing of fungicide applications to improve disease control and economic recovery. Moreover, a study conducted in Bangladesh from 2019 to 2021 showed that combining biological agents with the decreased use of fungicides controlled late blight and raised farmers' incomes by 7.19 and 10.98% per hectare (Islam *et al.*, 2022). Late blight has been reported to reduce potato production by 5 to 90% in India, depending on climate conditions, with 15% loss per annum (mean) across the country (Lal *et al.*, 2018). These region strategies show the importance of targeted approaches in mitigating the negative economic impact of late blight for both.

Geographical Distribution of Late Blight

P. infestans originated in Central and South America. Historical documentation suggests that the pathogen has been endemic to the Andes for an extensive duration & was acknowledged by indigenous populations (Austin Bourke, 1964). Mexico is esteemed as a focal point of pathogen diversity, and it was in this area that the sexual phase of the pathogen was first described. The pathogen disseminated from Mexico, culminating in outbreaks within the United States throughout the 20th century (Fry *et al.*, 2015).

Potatoes and tomatoes are geographically distributed across all continents. In Africa, they can be found in countries such as Cameroon, Egypt, Kenya, Nigeria, South Africa, and Ethiopia. In Asia, notable examples include China, India, Iran, Bangladesh, and Thailand. In Oceania, they are present in Australia, New Zealand, and Papua New Guinea. In Europe, these crops are cultivated in countries like France, Germany, Spain, and the United

Kingdom. In Central America and the West Indies, they are found in Costa Rica, Cuba, and the United States. Finally, in South America, they are grown in Argentina, Brazil, Colombia, and Peru (Arora *et al.*, 2014; Cooke *et al.*, 2012). A shared ancestor between groups of pathogens and hosts, first proposed in the 19th century soon after the Irish potato famine (de Bary 1876), has been supported by recent DNA evaluations and isozyme, and by the pathogenicity resemblance between *P. infestans* isolates from Peru, the US, and Europe (Nowicki *et al.*, 2012). CAB International (Anonymous, 2003) catalogued 122 nations where late blight was documented (Fig. 1), yet it undoubtedly manifested in additional countries without formal records.

Phytophthora Infestans as the Cause of Late Blight

In 1845, Montagne identified *Botrytis infestans* as the late blight pathogen, but De Bary reclassified them as *P. infestans* in 1846 (Ifeduba and Kwon-Ndung, 2021). The term "*Phytophthora*" derived from Greek, meaning "plant destroyer" (Rhouma *et al.*, 2024). Morphologically, *P. infestans* shows closer relations to brown algae than true fungi. It is characterized by a hyaline, coenocytic mycelium that is widely branched, with hyphae generally wider and growing more slowly than typical fungi. Unlike most fungi, *Phytophthora* species are diploid, a key feature that sets them apart (Chen *et al.*, 2009). Combined with their unique cell wall composition, primarily cellulose and glucan rather than chitin, this further distinguishes them from true fungi (Rhouma *et al.*, 2024).

P. infestans is considered as a hemibiotroph as it initially grows in a biotrophic phase, feeding on living host tissue, followed by a necrotrophic phase, killing the host tissue to spread and propagate (Perfect and Green, 2001). The pathogen affects a diverse array of plant tissues, including fruit, tubers, herbaceous stems, roots, foliage, and even woody trunks. Taxonomically, it belongs to the Kingdom Chromista, Order Peronosporales, and Phylum Oomycota, which places it in a distinct taxonomic group from true fungi. The genus *Phytophthora* includes around 60 species, some of which are significant pathogens of other plants.

These include *P. cactorum*, a major apple pathogen; *P. capsicum*, which affects peppers; *P. citrophthora*, known for infecting citrus plants; and *P. cinnamomi*, a pathogen that impacts many woody plants, including conifers (Lamichhane *et al.*, 2024).

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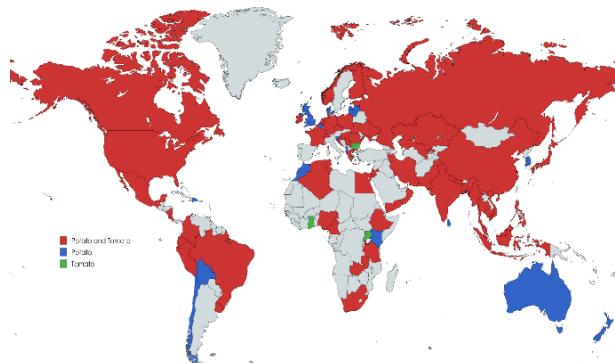


Fig. 1: Geographical distribution map of late blight affecting potatoes and tomatoes. (Red indicates regions where both potatoes and tomatoes are infected; Blue represents areas where only potatoes are infected; Green signifies regions where only tomatoes are infected)

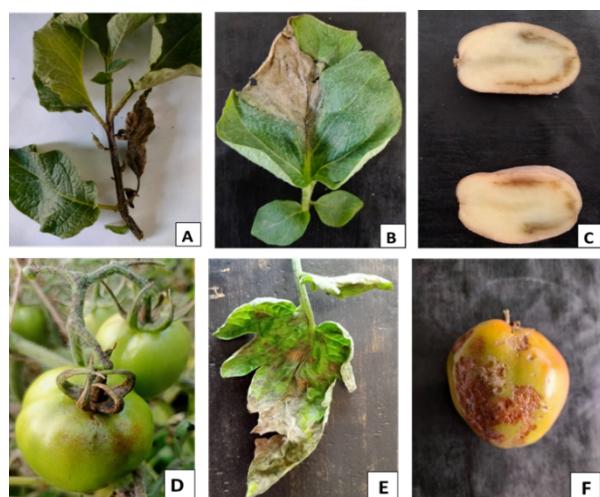


Fig. 2: Symptoms of late blight on various parts of potato and tomato plants. (A) Infected potato foliage, (B) Infected potato leaf and (C) Infected potato tuber; (D) Infected tomato fruit-bearing stem, (E) Spreading black lesions develop on tomato leaves and (F) Fruits of tomato become brown in appearance

Life Cycle and Reproductive Strategies of Phytophthora Infestans

P. infestans reproduces through both asexual and sexual mechanisms, with asexual reproduction being the dominant mode under most conditions. Asexual reproduction involves the production of distinctive, lemon-shaped sporangia formed at the tips of branched sporangiophores (Fig. 3) (Rhouma *et al.*, 2024). These sporangia can either release motile zoospores or germinate directly to produce infection hyphae. A key identifying feature of *P. infestans* sporangia is their papillate structure, which facilitates pathogen identification (Al-Adhaileh *et al.*, 2023). Morphological

variability has been observed in different regions, such as Cameroon, where sporangial forms include ellipsoid, pip-shaped, and lemoniform structures (Mugao, 2023).

Sporangia typically measure 60.5 μm in length and 31.7 μm in width, contributing to the white, fluffy appearance of the mycelium (Shimelash and Dessie, 2020). Under optimal environmental conditions, such as temperatures ranging from 20 to 25°C and adequate nutrient availability, sporangia can germinate directly to infect host plants. Conversely, less favorable conditions, including temperatures between 10°C and 15°C or limited nutrients, trigger the release of biflagellate zoospores. These motile zoospores are dispersed by wind and can encyst on the surface of host plants, initiating infection & completing the asexual cycle (Schiffer-Forsyth *et al.*, 2023). The rapidity of this cycle enables *P. infestans* to effectively colonize large areas under favorable conditions (Fig. 4).

Sexual reproduction in *P. infestans* occurs through the formation of oospores, which are generated in the presence of compatible mating types, 1 and A2. This heterothallic interaction is essential for oospore production (Tsedaley *et al.*, 2014). Oospores serve as a vital survival mechanism, enabling the pathogen to persist between growing seasons. Their thick, resistant walls allow them to endure harsh environmental conditions, including extended periods in soil.



Fig. 3: Microscopic view of *Phytophthora infestans* A) Sporangia on sporangiophores (B) Limoniform sporangia

However, they are sensitive to extreme heat, such as temperatures of 40°C sustained for 12 hours (Liang *et al.*, 2020). Upon germination, oospores produce sporangia that release zoospores, restarting the infection cycle. This dual capacity for sexual and asexual reproduction enhances the pathogen's adaptability to varying environmental conditions, ensuring its survival and spread (Tsedaley *et al.*, 2014). Environmental factors significantly affect the life cycle of *P. infestans* (Fig. 4). For instance, moist and temperate conditions promote zoospore development within two hours of sporangial formation. These motile zoospores utilize their

biflagellate structure to locate and infect host plants, leading to rapid disease progression. In highly susceptible potato or tomato crops, complete wilting of the leaf canopy can occur within a week (Giachero *et al.*, 2022; Rhouma *et al.*, 2016; Schiffer-Forsyth *et al.*, 2023). Sporangia are typically discharged during morning hours when temperatures rise, and humidity decreases, allowing them to spread across significant distances. However, their viability is compromised by desiccation and sunlight exposure.

Infected plant materials, such as discarded tubers or tomato fruits, act as sources of inoculum between cropping seasons. Proper management of these materials is crucial to reducing reinfection risks. The mycelium of *P. infestans* can persist in infected tubers, initiating new infection cycles in the spring when sporangia form on these tubers or on volunteer plants (Srisawad *et al.*, 2023). Integrated disease management approaches, including rotation of rotation, environmental monitoring, and the removal of infected plant debris, are essential for controlling the spread of this pathogen (Dufková *et al.*, 2021).

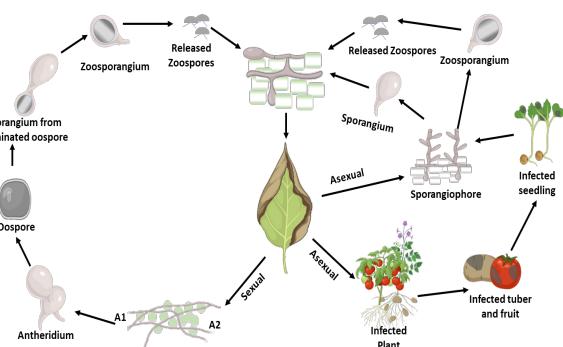


Fig. 4: Life cycle of *Phytophthora infestans*, illustrating key stages from spore release to plant infection. The diagram shows the formation of sporangia (top left), zoospore release (top center), germination and infection (center), colonization of plant tissues (bottom left), and eventual damage to the crops of tomatoes and potatoes (bottom right). The sequence demonstrates how quickly the disease spreads in favorable environmental circumstances

Population Structure of *Phytophthora Infestans*

P. infestans has a complex population structure influenced by its historical spread, genetic diversity, and migration patterns (Table 1). The population dynamics were profoundly influenced by the uncovering of the A2 mating type in Mexico, first reported outside its native range in Switzerland in 1981 (Dyer *et al.*, 1993). Genetic studies confirm that the global dissemination of A2 isolates in the 1980s was not a result of local evolution but rather international migration, emphasizing the need for stringent global biosecurity protocols (Goodwin and Drenth, 1997).

Table 1: Global distribution and year of revelation of *Phytophthora infestans* strains, types, and races

Country	Types, strains, or race	References
Mexico	A1 and A2	Dyer <i>et al.</i> (1993)
United States	US-1, US-6, US-7, US-8, US-21, US-22, US-23 and US-24	Goodwin <i>et al.</i> (1994) Deahl <i>et al.</i> (2012)
Canada	US-22, US-23 and US-24	Danies <i>et al.</i> (2013)
Ecuador	US-1 and EC-1	Forbes <i>et al.</i> (1997)
Brazil	US-1 and BR-1	Maziero <i>et al.</i> (2009)
Ireland	HERB-1 5_A1 and 8_A1 13_A1, 5_A1, 6_A1 and 8_A1 6_A1	Yoshida <i>et al.</i> (2013) Cooke <i>et al.</i> (2012) Rhouma <i>et al.</i> (2024) Cooke <i>et al.</i> (2012)
Great Britain and Ireland		
Britain, Netherlands, and France	EU13_A2, US-22, US-23, and US-24	Khalid Naveed <i>et al.</i> (2017)
Netherlands	NL-003 to NL-008, NL00-1, NL-002, EU13_A2	Rajputt <i>et al.</i> (2017)
Malawi, Burundi, Mozambique, Kenya, Uganda, South Africa and Tanzania	US-1.1 to US-1.11	Rajputt <i>et al.</i> (2017)
Kenya and Rwanda	KE-1	Pule <i>et al.</i> (2013)
East Africa	EU13-A2 and KE-1	Rajputt <i>et al.</i> (2017)
Japan	JP-3 and JP-4	Akino <i>et al.</i> (2014)
Korea	KR-1	Choi <i>et al.</i> (2020)
Taiwan	US-1.1, US-1.2, US-1.3 and US-1.4 US11 and TW-1	Chen <i>et al.</i> (2009)
China	SG-1, US-1, SIB-1, and EU-13	Guo <i>et al.</i> (2010)
India	13_A2-1, 13_A2-3a, 13_A2-3b, and 13_A2 3c	Rajputt <i>et al.</i> (2017)

The coexistence of A1 and A2 mating types in various regions has raised concerns about the potential for sexual reproduction, leading to the creation of oospores and isolates with novel genetic traits. Reports of oospore production have been documented in North America and Europe, although controlled experiments in Japan did not yield progeny production under artificial conditions (Kato *et al.*, 1993). These findings highlight the variability in reproductive success across different environmental contexts.

Recent surveys reveal alarming trends in *P. infestans* population dynamics. Between 2009 and 2011, multiple mating types such as US-8, US-21, US-22, US-23, and US-24 were identified in the Midwestern and Eastern United States (Deahl *et al.*, 2012). In Ireland, the previously dominant 13_A2 genotype saw a significant decline in 2011, replaced by genotypes 5_A1 and 8_A1, while the 6_A1 genotype gained prevalence in the United Kingdom (Cooke *et al.*, 2012). In China, a unique

coexistence of native genotypes with SIB-1 (JP-2) and the globally dominant US-1 strain was observed between 1998 and 2006 (Guo *et al.*, 2010). Similarly, Taiwan's potato crops have been found to harbor the US-11 genotype (Chen *et al.*, 2018). The rate of SIB-1 in eastern Russia and its potential for cross-border migration further underscore the dynamic nature of *P. infestans* populations (Guo *et al.*, 2010).

Strains of *P. infestans* exhibit varying levels of virulence, with some strains being more aggressive and capable of overcoming host resistance more effectively. This variability is partly driven by genetic diversity, including clonal lineages and different mating types. These genetic differences affect the pathogen's virulence, competence to cause significant damage, and ability to resist control measures, such as fungicides. Some strains can develop resistance through evolutionary processes. Although control strategies-including fungicide rotation, planting resistant cultivars, and implementing cultural

methods like crop rotation-are employed, they may be ineffective owing to the appearance of more virulent strains (Ludwiczewska et al., 2025).

Epidemiological Dynamics and Environmental Influences

The development and spread of *P. infestans* are highly dependent on specific temperature and humidity conditions. Sporulation occurs when relative humidity exceeds 90% (Fig.5), leading to the formation of sporangia on the undersides of leaves and infected stems, which facilitates reinfection cycles (Beninal et al., 2022). The mechanism of sporangial germination is influenced by temperature; at temperatures between 21°C and 26°C, germination occurs directly through the formation of a germ tube, bypassing the zoospore stage. In contrast, at temperatures below 18°C (65°F), 6 to 8 motile zoospores are released, which require water for movement and infection (Srisawad et al., 2023). The pathogen remains active within a temperature range of 3 to 26°C, although sporulation is most efficient between 18 and 22°C (64 to 72°F) (Cray et al., 2016).

Prolonged wet conditions, such as rain or fog, combined with alternating cool nights and warm days, create ideal environments for disease outbreaks. These conditions can rapidly devastate entire potato fields within two weeks (Giachero et al., 2022). High precipitation and low temperatures exacerbate the severity of late blight by promoting sporangial dispersal and infection cycles (Bhardwaj et al., 2019). Recent climate modeling studies project shifts in the geographic distribution of late blight outbreaks due to warming temperatures, which will impact sporulation and zoospore release mechanisms that depend on temperature (Hossain et al., 2024).

The disease typically begins in early January under cool, foggy conditions, with various races of the pathogen predominantly found in the northern part of Bangladesh (Dey et al., 2010). Late blight has been recorded in India since the late 19th century, with severe outbreaks documented in potato and tomato crops. Notably, a major epidemic in 2014 in West Bengal caused significant crop losses and socioeconomic distress among farmers (Guha Roy et al., 2021). In the United States, specific clonal lineages of the pathogen, such as US-23, responsible for late blight outbreaks, have been linked to the introduction of infected seed potatoes in states like Florida (Donahoo and Roberts, 2013). Baker et al. (2004) noted a probability of high late blight risk being greater in the U.S. upper Great Lakes region based on 1948 to 1999 climatic data. Also in Finland, 20th century documents showed higher spring (April and May), modestly warmer summers (June–August), temperatures and smaller diurnal temperature range (Tuomenvirta and Heino, 1996; Tuomenvirta et al., 2000; Tuomenvirta, 2004) also, particularly since 1980. In northern Europe and Finland, it has been attributed to an increase in cloud

cover and a strengthening of the westerly flow (Tuomenvirta et al., 2000).

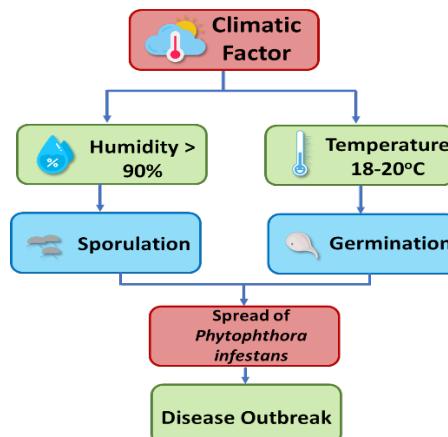


Fig. 5: Epidemiological dynamics and environmental influences on potato and tomato late blight

These climate changes may provide more favorable early season situation to potato growth, but they also provide more conditions that contribute to late blight disease. Model simulations have also indicated that in southern Finland, 10–20 days longer management time could be required to protect potato foliage against late blight, with a 1°C increase in the average temperature during the growing season, especially if soil-borne inoculum is low (Kaukoranta, 1996).

The risk of late blight extends beyond the field to storage facilities. Infected tubers and tomato fruits under high-moisture conditions provide a conducive environment for spore growth. Condensation on tuber surfaces facilitates sporangial production, contaminating adjacent tubers and triggering secondary infections, including soft rot caused by bacteria (Rogozina et al., 2023).

Molecular Pathogenesis of *Phytophthora Infestans*

P. infestans has developed to circumvent PAMP-Triggered Immunity (PTI) by secreting effector molecules that suppress plant defenses (Fig. 6). During the biotrophic phase, *P. infestans* suppresses host immune responses and apoptosis while developing haustoria or hyphae inside viable plant cells (Koeck et al., 2011). The pathogen releases a wide array of effectors, toxins like necrosis-inducing NLPs, and CWDEs, including glycosyl hydrolases, to facilitate host membrane damage and invasion. *P. infestans* secretes two kinds of effectors; intracellular (cytoplasmic) and extracellular (apoplastic) (Wang et al., 2017). Key extracellular effectors include protease inhibitors such as EPI1, EPI10, EPIC1, and EPIC2B, which inhibit host defensive proteases like Rcr3pim (Song et al., 2009). Intracellular effectors, particularly RXLR and CRN proteins, are critical in manipulating host immunity. RXLR effectors (Table 2) are secreted from haustoria and recognized by plant

resistance proteins, triggering effector-triggered immunity (ETI). These effectors have an N-terminal RXLR-dEER motif for targeting and secretion and a flexible C-terminal domain essential for their function (Van den Ackerveken, 2017). RXLR effectors like AVR3a and AVRblb2 act as avirulence factors recognized by R genes, initiating hypersensitive responses and programmed cell death. Host plants recognize PAMPs through surface-localized receptor kinases or receptor-like proteins, forming the first line of defense (Zipfel, 2014). PTI responses include ROS production, calcium ion signaling, MAPK activation, and defense gene transcription (Boller and Felix, 2009). R proteins, encoded by R genes, provide a secondary recognition mechanism against infections by detecting effectors directly, indirectly, or via decoy pathways (van der Hoorn and Kamoun, 2008). These proteins activate immune signaling through conserved domains such as NBS, TIR, or CC (Takken and Goverse, 2012). MAPK cascades are pivotal in host defense, mediating phosphorylation events that regulate transcription factors and enzymes responsible for ROS production (Murphy *et al.*, 2018).

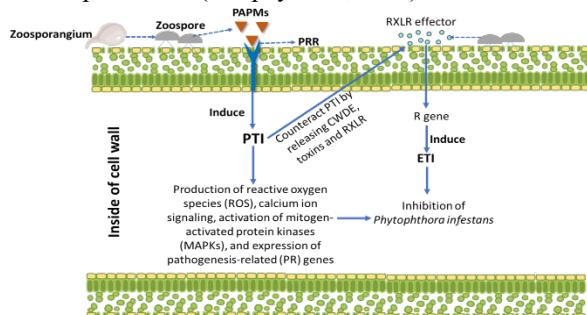


Fig. 6: Molecular pathogenesis of *Phytophthora infestans*. After sporangium encysted, zoospores were discharged and germinated. Host PRRs recognize the PAMPs released by *P. infestans*, which results in PAMP-triggered immunity. Toxins, RXLR, and CWDE are secreted by *P. infestans* to decrease PTI. ETI is triggered by certain RXLR effectors identified by the host resistance (R) gene

Sustainable Methods for Managing Late Blight

To effectively control late blight, a multimodal approach is essential. This strategy comprises three key components: the use of strategic chemical and biological controls, the cultivation of resistant plant varieties, and the adaptation of cultural practices. Furthermore, forecasting tools are available that aim to predict the optimal weather conditions for the pathogen, helping to determine the best timing for fungicide applications in the fields.

Cultural Practices

Cultural practices are a cornerstone of integrated disease management for late blight control in potato and tomato production. By preventing the establishment of *P. infestans*, cultural techniques play a crucial role in mitigating disease incidence and minimizing crop losses

(Schiffer-Forsyth *et al.*, 2023; Ivanov *et al.*, 2021). Among the most effective strategies is the use of disease-free seed tubers, which significantly reduces the introduction of pathogens into fields (Ivanov *et al.*, 2021). Additionally, preventing the accumulation of inoculum from nearby potato cull heaps or infected tomato transplants is vital for controlling late blight. Such cultural management practices focus on limiting inoculum introduction and reducing its buildup in the environment (Nowicki *et al.*, 2013). Several key cultural practices are commonly employed to manage late blight. Crop rotation and the implementation of fallow periods can help minimize the prevalence of *P. infestans* by breaking the pathogen's lifecycle and limiting its buildup in soil. Removing volunteer potato and tomato plants that may harbor the pathogen further diminishes inoculum sources (Giachero *et al.*, 2022). The management of cull piles is particularly crucial, as mycelia of *P. infestans* can persist in these heaps over winter and release large quantities of airborne spores at the start of the growing season, increasing the likelihood of disease outbreaks in subsequent crops. By removing infected plants and tubers, farmers reduce the potential for inoculum spread. Moreover, proper harvesting and storage techniques that regulate temperature and humidity also help limit pathogen survival and reproduction (Ivanov *et al.*, 2021).

In addition to removing infected material, maintaining strong soil coverage helps shield tubers from soil-borne inoculum, while drip irrigation and other optimized watering practices help reduce conditions conducive to infection (Schiffer-Forsyth *et al.*, 2023). Adequate plant nutrition is also critical, as a balanced diet can bolster the plant's natural defenses against the disease (Giachero *et al.*, 2022). Weed control is another important aspect, ensuring that fungicide coverage remains effective and preventing the formation of microclimates that favor the spread of *P. infestans* (Ivanov *et al.*, 2021).

Aligning row orientation with prevailing winds can facilitate the drying of foliage, further reducing the risk of infection. Regular monitoring of stored potatoes allows for early detection of disease and the removal of contaminated tubers, preventing the spread of the pathogen (Giachero *et al.*, 2022). Innovative cultural practices, such as intercropping, have also shown promise in controlling late blight. For example, in the central highlands of Ethiopia, a 3:1 intercropping arrangement of garlic and potatoes (75% garlic and 25% potato) reduced the growth of *P. infestans* and enhanced potato yield (Kassa and Sommartya, 2006). This practice suggests that specific intercropping techniques could provide additional disease suppression benefits, especially in elevated environments. The physical presence of the non-host crop, such as garlic, might act as a "bio-barrier," limiting pathogen spread via wind and precipitation and reducing the amount of inoculum available to infect

potato plants. Additionally, the "dilution effect" of non-host plants might lower the pathogen concentration, further reducing transmission and preventing localized outbreaks or focused epidemics (Skelsey *et al.*, 2005). These findings highlight the potential of integrating

diverse cultural practices to complement traditional disease management strategies and improve the sustainability of potato and tomato production systems.

Table 2: *Phytophthora infestans* genes encoding RxLR effectors and their functions in potato and tomato

Effectors	Function	References
* <i>Avr1</i>	Involved in the recognition of the host resistance responses	van der Lee <i>et al.</i> (2001)
<i>Avr2</i>	Contributes to suppressing host resistance	Aguilera-Galvez <i>et al.</i> (2020)
<i>Avr3a</i>	Plays a crucial part in virulence and immune evasion	Armstrong <i>et al.</i> (2005)
<i>Avr3b</i>	Interferes with the host's defense mechanisms, especially defense signaling pathways	Rietman <i>et al.</i> (2012)
<i>Avr4</i>	Implicated in virulence by suppressing or manipulating plant defense	Van Poppel <i>et al.</i> (2008)
<i>Avr8</i>	Participating in virulence and suppression of host immunity	Vossen <i>et al.</i> (2016)
<i>Avrblb1</i>	Contributes to host defense recognition	Song <i>et al.</i> (2003)
<i>Avrblb2</i>	Contributes to host defense recognition	van der Vossen <i>et al.</i> (2005)
<i>Avrvnt1</i>	Modulates virulence for infection success	Pais <i>et al.</i> (2018)
<i>AvrSmira1</i>	Targets specific host defense components to promote virulence	Rietman <i>et al.</i> (2012)
<i>AvrSmira2</i>	Possible involvement in the evasion of host immunity	
<i>Avrchc1.1</i>	Allows <i>P. infestans</i> to evade detection	Monino-Lopez <i>et al.</i> (2021)
<i>Avrchc1.2</i>	Likely contributes to pathogen virulence or immune suppression	
<i>Avramr1</i>	Interferes with host immunity by targeting defense signaling pathways	Witek <i>et al.</i> (2021)
<i>Avramr3</i>	Enhances pathogen survival and infection	Lin <i>et al.</i> (2021)

Host Resistance

Cultivating resistant potato and tomato cultivars reduces the need for fungicide applications, which not only lowers production costs but also helps mitigate the environmental impacts of pesticide use (Enciso-Maldonado *et al.*, 2022). Additionally, utilizing resistant cultivars helps limit changes in the population dynamics of *P. infestans*, thus reducing the risk of the pathogen developing resistance to fungicides (Rogozina *et al.*, 2023).

Currently, over 20 potato late blight resistance genes have been successfully isolated, primarily from the CC-NBS-LRR gene family, including genes such as *R1*, *R2*, *R3a*, *R3b*, *Rpi-blb2*, *Rpi-blb3*, and others (Table 3). Incorporating these genes into cultivated varieties remains environmentally friendly methods for managing late blight (Szajko *et al.*, 2020).

Late blight resistance in cultivars ranges from moderate to high, with varieties suitable for both mountainous and plains regions. Notable resistant varieties include *Kufri Giriraj*, *K. Himalini*, *K. Shailja*, and *K. Himsona* for mountainous areas, and *K. Anand*, *K. Sutlej*, *K. Badshah*, and others for plains (Central Potato Research Institute). Additionally, advanced hybrids such

as *Kufri Garima*, derived from the cross between PH/F-1045 and MS/82-638, exhibit enhanced resistance to late blight (Lal *et al.*, 2013a). Although *Rpi* genes are effective against *P. infestans*, their durability varies significantly. Some genes provide long-lasting immunity, while others can be quickly overcome by pathogen populations. The *Rpi-blb1* gene from *S. bulbocastanum* is considered one of the most durable due to its broad-spectrum resistance and conservation across the wild species in which it is found (van der Vossen *et al.*, 2005). In contrast, the resistance genes identified in *S. demissum*, such as *R1* and *R3a*, have proven to be vulnerable to the selection of adapted pathogens, leading to their classification as short-lived resistance options (Ballvora *et al.*, 2002; Huang *et al.*, 2004). Additionally, *Rpi-blb2* and *Rpi-blb3* provide resistance but are also susceptible to breakdown by certain strains of *P. infestans*. Therefore, gene pyramiding is essential to enhance durability (Lokossou *et al.*, 2009; van der Vossen *et al.*, 2005). Novel genes like *Rpi-edn2* (*R9a*) and *Rpi-hcb1.1* show promising resistance, but their long-term stability is still under evaluation (Keijzer *et al.*, 2022; Aguilera-Galvez *et al.*, 2020). Polygenic resistance, which involves multiple resistance genes such as *RGA2*, *RGA3*, *R3a*, and others, has shown considerable potential in providing more durable disease tolerance (Tiwari *et al.*, 2021).

Table 3: Resistance genes against *Phytophthora infestans* (*Rpi* genes) in wild potato and wild tomato relatives

Gene	Species	Durability of Resistance	References
<i>Rpi-avl1</i>	<i>S. avilesii</i>	Moderate	Verzaux (2010)
<i>Rpi-ber1</i>		Narrow-spectrum	Park <i>et al.</i> (2009)
<i>Rpi-ber1.2</i>	<i>S. berthaultii</i>	Narrow-spectrum	Monino-Lopez <i>et al.</i> , (2021)
<i>Rpi-blb1</i>	<i>S. bulbocastanum</i>	Durable, broad-spectrum resistance	Naess <i>et al.</i> (2000)
<i>Rpi-blb2</i>		Durable	van der Vossen <i>et al.</i> (2005)
<i>Rpi-blb3</i>		High durability when stacked with <i>Rpi-blb1</i> or <i>blb2</i>	Lokossou <i>et al.</i> (2009)
<i>Rpi-bit1</i>		Moderate	Oosumi <i>et al.</i> (2009)
<i>Rpi-cap1</i>	<i>S. capsicibaccatum</i>	Moderate resistance	Verzaux <i>et al.</i> (2012)
<i>Rpi-qum1</i>	<i>S. circaeifolium</i> ssp. <i>quimense</i>	Durability unknown	
<i>R1</i>	<i>S. demissum</i>	Historically beneficial, but most contemporary races have overtaken	Ballvora <i>et al.</i> (2002)
<i>R3a; R3b</i>		<i>R3b</i> is moderately durable in pyramids, while <i>R3a</i> is frequently defeated	Huang <i>et al.</i> (2004)
<i>R4^{al}; R4^{MA}</i>		Weak durability	Van Poppel (2010)
<i>R5</i>		Race-specific	Huang (2005)
<i>R6; R7</i>		Limited durability	
<i>R11; R10</i>		Moderate durability	Bradshaw <i>et al.</i> (2006)
<i>Rpi-edn1.1</i>	<i>S. edinense</i>	Promising	Champouret (2010)
<i>Rpi-edn2 (R9a)^a</i>		High potential for long-lasting resistance; broad spectrum	Keijzer <i>et al.</i> (2022)
<i>Rpi-edn3</i>		Unknown durability	Verzaux (2010)
<i>Rpi-hjt1.1</i>	<i>S. hjertingii</i>	Under evaluation	Champouret (2010)
<i>Rpi-hcb1.1</i>	<i>S. huancabambense</i>	Broad resistance	Aguilera-Galvez <i>et al.</i> (2020)
Novel <i>Rpi</i> gene(s)	<i>S. jamesii</i>	Resistant in laboratory settings	Zheng <i>et al.</i> (2020)
<i>Rpi-mch1</i>	<i>S. michoacanum</i>	Moderate durability	Śliwka <i>et al.</i> (2012b)
<i>Rpi-nrs1</i>	<i>S. neorossii</i>	Moderate durability	Jones <i>et al.</i> (2009)
<i>Rpi-pcs</i>	<i>S. paucisectum</i>	Unknown	Villamón <i>et al.</i> (2005)
<i>Rpi-rzcl^a</i>	<i>S. ruiz-ceballosii</i>	Promising	Śliwka <i>et al.</i> (2012a)
<i>Rpi-snk1.1</i>	<i>S. schenckii</i>	Limited use	Champouret, (2010)
<i>Rpi-sto1^a</i>		Strong field resistance	Wang <i>et al.</i> (2008)
<i>Rpi-sto2</i>	<i>S. stoloniferum</i>	Moderate resistance	Champouret (2010)
<i>Rpi-pt2</i>		Promising in conjunction with <i>Rpi-blb2</i>	Wang <i>et al.</i> (2008)
<i>Rpi-tar1</i>	<i>S. tarjense</i>	Race-specific	Haverkort <i>et al.</i> (2016)
<i>Rpi-tar1.3</i>		Broader effect	Monino-Lopez <i>et al.</i> (2021)
<i>Rpi-Smira1</i>	<i>S. tuberosum</i> cv. Sárpo Mira	Durable in EU trials	Rietman <i>et al.</i> (2012)
Novel <i>Rpi</i> gene(s)	<i>S. tuberosum</i> subsp. <i>andigena</i>	Potential for resistance breeding in the future	Duan <i>et al.</i> , (2021)
<i>Rpi-ver1</i>	<i>S. verrucosum</i>	Broad-spectrum resistance	Chen <i>et al.</i> (2018)
** <i>Ph-1</i>	<i>S. pimpinellifolium</i>	Efficient in the initial phases	Bonde and Murphy (1952)
<i>Ph-2</i>		Partial resistance	Gallegly and Marvel (1955)
<i>Ph-3</i>		Durable	Chunwongse <i>et al.</i> (2002)
<i>Ph-5.1</i>		Potential additive resistance	Merk and Foolad 2012;
<i>Ph-5.2</i>		Investigation ongoing	Nowicki <i>et al.</i> 2012

To date, five main race-specific resistance genes that provide varying levels of resistance against tomato *P. infestans* strains *Ph-1*, *Ph-2*, *Ph-3*, *Ph-4*, and *Ph-5* have been discovered within *Solanum pimpinellifolium*, a closely related red-fruited wild relative of tomato (Table 3). The resistance gene to *P. infestans* race 0 shows very little resistance to race 1, the current dominant race

(Peirce, 1971). The other resistance gene, *Ph-2* which was first found in *S. pimpinellifolium* accession West Virginia 700 (Gallegly and Marvel, 1955), suppresses the development of the disease, but not resistant to *P. infestans* in all cases (Foolad *et al.*, 2008).

The best characterized resistance gene is *Ph-3*, which was initially found in a L3708 (also shown as LA1269 and

PI365957), and which displays incomplete dominant resistance to several *P. infestans* isolates (Chunwongse *et al.*, 2002). Until now, *Ph-3* has been the leading resistant gene against late blight in tomatoes and has been efficiently introgressed into several breeding lines and commercial hybrid varieties of both fresh-market and processing tomatoes in several breeding programs around the world. For example, fresh-market breeding lines such as NC1 CELBR (*Ph-2 + Ph-3*) and NC2 CELBR (*Ph-2 + Ph-3*), and hybrid cultivars such as Plum Regal (*Ph-3*), and Mountain Merit (*Ph-2 + Ph-3*) have been developed through the North Carolina State Tomato Breeding Program (Gardner and Panthee, 2010; Panthee *et al.*, 2015).

The gene *Ph-4* in *S. habrochaites* 'LA1033' has been proposed as a candidate region for quantitative trait locus (AVRDC, 1998; Lough, 2000). The *Ph-5* gene, identified in *S. pimpinellifolium* PI 270443, confers resistance to 7 race/species of the late blight pathogen (Foolad *et al.*, 2008). Nevertheless, *Ph-5* is regulated by two loci, one on chromosome 1 (*Ph-5-1*) and another on chromosome 10 (*Ph-5-2*) (Merk and Foolad, 2012; Nowicki *et al.*, 2012), which complicates its practical application.

However, introgression of other late blight resistance QTLs into cultivated tomato varieties is a labor-intensive task and several of them may even display undesirable characteristics (Brouwer *et al.*, 2004). However, these QTLs may provide a more durable solution than that based on major resistance genes alone. To counter the threat to established *P. infestans* resistance genes due to the appearance of new strains (Stellingwerf *et al.*, 2018), breeders are utilizing gene stacking approaches to stack more resistance genes together. This strategy increases the genetic barriers that the pathogen must overcome, as it requires mutations in several avirulence (Avr) loci for *P. infestans* to successfully evade this enhanced resistance.

Microbial Biocontrol

Microbial biocontrol is an important and sustainable strategy in managing the late blight disease of potato and tomato caused by *P. infestans*. For long-term disease control, it is essential to continue researching and developing alternative approaches, such as host resistance and biocontrol techniques. While *in vitro* studies help in understanding the mechanisms behind microbial biocontrol, translating these results to field applications remains a challenge. However, certain fungal species, such as *Trichoderma*, have demonstrated significant potential in combating late blight. *Trichoderma* spp., including *T. harzianum* and *T. asperellum*, exhibit various mechanisms, such as coiling around the pathogen and releasing enzymes, secondary metabolites, and toxins to inhibit pathogen growth (Kariuki *et al.*, 2020). Notably,

T. harzianum and *T. asperellum* have been shown to increase tomato plant growth by more than 30 and 19%, respectively, while also reducing late blight symptoms by up to 40% (Table 4) (Mollah and Hasan, 2023).

Despite their bioactive potential, bacterial and fungal Biocontrol Agents (BCAs) are not always effective under field conditions. For instance, *Trichodex*®, a commercial product containing *T. harzianum*, reduced *P. infestans* growth by 40% *in vitro* but had no significant effect on late blight in greenhouse and detached leaf tests (Stephan *et al.*, 2005). This highlights the need for new selection techniques, possibly focusing on the synthesis of siderophores and biosurfactants, which may enhance *in planta* efficacy (Bailly and Weisskopf, 2017).

Other microorganisms also play a significant role in microbial biocontrol of late blight. The antagonistic oomycete *Pythium oligandrum*, for instance, demonstrates mycoparasitism by secreting enzymes that degrade cell walls and consuming various fungi and oomycetes for nutrition. Interestingly, this mycoparasitic behavior may have evolved through gene duplication and horizontal gene transfer, further supporting its effectiveness as a biocontrol agent (Liang *et al.*, 2020). Numerous naturally occurring microorganisms, including *Penicillium aurantiogriseum*, *Myrothecium verrucaria*, *Acremonium strictum*, and various *Trichoderma* species, have also shown promising antagonistic effects (Lal *et al.*, 2013b). In addition to fungi, bacteria such as *Bacillus*, *Pseudomonas*, and *Streptomyces* exhibit significant biocontrol properties. For example, *Bacillus* species inhibit the growth of *P. infestans*, while *Pseudomonas* species produce Volatile Organic Compounds (VOCs) such as hydrogen cyanide and aldehydes, which contribute to disease suppression. Some *Pseudomonas* strains also generate cyclic lipopeptides that target the zoospores of *P. infestans* and compete for iron through siderophore production (Caulier *et al.*, 2018). *In vitro* studies, along with molecular and genomic research, offer valuable insights into the mechanisms of BCAs. For example, research on *Pseudomonas* has identified specific genetic loci that control aggression toward *P. infestans*, paving the way for the development of hyper-aggressive strains for future applications (De Vrieze *et al.*, 2020).

Moreover, understanding the evolutionary history of BCAs, such as the horizontal gene transfer events that enable *Pythium* spp. to acquire hyperparasitism, is crucial for the establishment of more effective biocontrol strategies (Caulier *et al.*, 2018). An important strategy in the biocontrol of *P. infestans* is the degradation of the pathogen's cell wall, which is composed primarily of β -D-glucans and cellulose. Many BCAs secrete enzymes that break down these cell wall components, and combining such agents may offer greater efficacy in managing late blight (Liang *et al.*, 2020).

Table 4: Microbial biocontrol agents and their role in late blight management

Agent	Effect	References
<i>Trichoderma harzianum</i>	40% less disease, and the release of cell wall-breaking enzymes	Chowdappa <i>et al.</i> (2013)
<i>Trichoderma asperellum</i>	Reduces late blight, enhances plant growth, and secretes secondary metabolites	Kariuki <i>et al.</i> (2020)
<i>Pythium oligandrum</i>	Exhibits mycoparasitism and produces cell wall-degrading enzymes	Liang <i>et al.</i> (2020)
<i>Trichoderma viride</i>	Inhibits growth through enzyme secretion and antagonistic interactions	Purwantisari <i>et al.</i> (2018)
<i>Penicillium</i> sp.	Demonstrates antagonistic effects	f <i>et al.</i> (1991)
<i>Chaetomium brasiliense</i>	Generates cell wall degrading enzymes	Gupta <i>et al.</i> (2004)
<i>Acremonium strictum</i>	Inhibits pathogen growth	
<i>Pseudomonas fluorescens</i>	Produces volatile organic compounds (VOCs), cyclic lipopeptides, and siderophores to inhibit pathogen growth	Slininger <i>et al.</i> (2007)
<i>Pseudomonas</i> sp.	Secretes VOCs like hydrogen cyanide, produces biosurfactants that impede <i>P. infestans</i> growth	Caulier <i>et al.</i> (2018)
<i>Bacillus subtilis</i>	Activates defense enzymes and reduces late blight	El-Naggar <i>et al.</i> (2016)
<i>Streptomyces</i> sp.	Secrets enzyme and competes for nutrients	Fu <i>et al.</i> (2022)
<i>Aspergillus flavus</i>	Behaves antagonistically with <i>P. infestans</i>	
<i>Aspergillus niger</i>	Shows inhibitory effects on the proliferation of pathogen	Lal <i>et al.</i> (2013b)

Furthermore, endophytic bacteria, which are naturally occurring antagonists in healthy plants, have shown promise in the biocontrol of late blight. For example, 2800 microorganisms resembling *Bacillus* and *Pseudomonas* were extracted from potato agroecosystems, and several of these strains significantly alleviated disease symptoms in greenhouse trials. One particular strain, *B. subtilis* 30B-B6, demonstrated effectiveness in a small-scale field trial (Caulier *et al.*, 2018).

Regulatory approval is necessary to get from lab-scale promise to real-world implementation. The European Protection Agency (EPA) and the European Food Safety Authority (EFSA) conduct thorough evaluations, including risk assessments to determine impacts on human health, non-target organisms, and the environment, and efficacy tests to confirm their capacity to disease control like late blight. The agencies also assess environmental factors, e.g., persistence and mobility of microbial compounds and their capacity to disrupt ecological balance (EFSA, 2019). Upon approval, BCAs must undergo commercialization in the form of labeling with proper directions, compatibility with existing agricultural practice, and training of farmers on safe handling. Post-marketing surveillance is currently monitoring the long-term safety and effectiveness of these agents. With growing demand for sustainable management, microbial BCAs are highly promising as a

substitute for chemical fungicide, provided they meet stringent regulatory standards (Ball, 2015).

When used as preventative measures, biocontrol agents like *Penicillium* sp., *T. viride*, *T. harzianum*, and *Chaetomium* sp. demonstrated promise against *P. infestans*; but, when used as curative measures, they were ineffective (Dey *et al.*, 2010). While *P. infestans* was present on potato plants seven days before the antagonist was applied in the therapeutic procedure, a spore suspension of antagonists was sprayed on the plants 7 days before the *P. infestans* inoculation as a preventive step.

Fungicidal Application

Strategic fungicide application can contribute importantly to plant protection in situations of high disease-induced stress or when new races of pathogens are emerging (Ivanov *et al.*, 2021). Fungicide use, ranging from early inorganic products such as Bordeaux mixture to advanced systemic fungicides such as Mandipropamid and Azoxystrobin, has been key in the management of late blight. Systemic fungicides like metalaxyl, mefenoxam, and newer chemicals inhibit pathogen growth through interference with essential metabolic processes, namely RNA polymerase-1 (Davidse *et al.*, 1983). However, resistance to them has been induced at a very rapid pace in agricultural ecosystems.

Table 5: Chemical management strategies and fungicide efficacy against late blight of potato and tomato

Category	Fungicide/ Strategy	Mode of action/Effectiveness	Comparative Efficacy (Multi-season)	References
First Generation Fungicides	Copper sulfate, hydrated lime, water (Bordeaux mixture)	Inorganic fungicide; prevents infection and disease spread	Moderately effective in the early stages of infection	Ryley and Drenth (2024);
Systemic Fungicides	Metalaxyl (Ridomil 2E), Mefenoxam (Ridomil Gold EC)	Decreases sporulation and mycelial development within tissues by inhibiting RNA polymerase-1	High efficacy at first, but after several seasons of use, resistance development was observed	Gisi and Cohen (1996); Davidse <i>et al.</i> (1983)
	Dimethomorph, Propamocarb	Affects pathogen growth and reproduction	In both early and late stages, dimethomorph is effective; in all seasons, propamocarb provides moderate protection	Alvarez-Romero <i>et al.</i> (2024)
Contact Fungicides	Mancozeb, Chlorothalonil (Bravo), Mancozeb + Cymoxanil (Curzate)	Broad-spectrum protectants; inhibits spore germination and disease spread	In heavy rain, effectiveness decreases	Lal <i>et al.</i> (2018);
Novel Fungicides	Fenamidone	Target cytochrome bc1 in mitochondrial complex III; interferes with respiration	Under moderate disease pressure, efficacy was maintained for two to three growing seasons	Kamel <i>et al.</i> (2024)
	Cymoxanil	Block cytochrome bc1 in mitochondrial complex III from exchanging electrons	Better in mixes for year-round effectiveness	Mahajan <i>et al.</i> (2024)
	Ametoctradin (Initium)	Non-systemic fungicide; inhibits ATP synthesis by affecting mitochondrial respiration	High effectiveness over several seasons when used in combination or rotation	Jackson <i>et al.</i> (2024)
Fungicide Mixtures	Metalaxyl + Mancozeb (Ridomil MZ), Cymoxanil + Mancozeb, Dimethomorph + Mancozeb	Combines systemic and contact fungicides to broaden activity spectrum and slow resistance development	Remains highly effective for more than three seasons.	Lal <i>et al.</i> (2018)
Alternative Strategies	β -Aminobutyric acid (BABA), Phosphoric acid	SAR (Systemic Acquired Resistance) activators; induce plant defense genes (e.g., PR-1 protein, β -1,3 glucanase,)	Year-to-year variations in performance; integrated programs are more successful	Lal <i>et al.</i> (2018)
Micronutrients	ZnSO ₄ , CuSO ₄ , Ferric chloride, Ferrous ammonium sulfate	Inhibit pathogen growth and spore germination; delay disease onset when used with resistant cultivars	Only supplemental control	Bhat <i>et al.</i> (2007)
Spray Schedules	Mancozeb 75% WP, Cymoxanil 8% + Mancozeb 64% WP, Dimethomorph 50% WP,	Scheduled prophylactic sprays followed by systemic fungicides effectively reduce terminal disease severity and yield loss	Following schedules results in a 30–40% increase in yield and a >60% decrease in disease in multi-season field experiments	Lal <i>et al.</i> (2017a)

Fungicide Efficacy Studies	Ametoctradin + Dimethomorph (w/w), Mandipropamid, Azoxystrobin	Efficient in combating novel <i>P. infestans</i> clonal lines (e.g., US-23, US-24)	Seasonally, Ametoctradin + Dimethomorph is quite successful	Seidl Johnson <i>et al.</i> (2015)
Environmental Concerns	Reduced fungicide use and EU delisting of products	Focus on integrated pest management (IPM), potato breeding, and forecasting models to reduce fungicide dependence	Long-term studies demonstrate that using integrated approaches reduces the use of fungicides by 40–50% while controlling disease	Fry (2007)
Prophylactic Strategies	Chlorothalonil, Mancozeb, or Dimethomorph mixtures	Preventative applications before disease onset followed by systemic fungicides for better control	Effective for several years when properly timed with disease predictions	Chakraborty and Mazumdar (2012)

Ofurace (Orafce 50WP), metalaxyl, and mancozeb (Ridomil MZ) have exhibited strong suppression of late blight (Lal *et al.*, 2018). A newly formed fungicide, fenamidone, targets *P. infestans*' cytochrome bc1 in mitochondrial complex III. Similarly, cymoxanil-type fungicides block electron transfer in mitochondrial complex III (Mahajan *et al.*, 2024). Dimethomorph and fenamidone proved to be the most potent in vitro treatments for late blight (Kamel *et al.*, 2024). Systemic fungicides supplemented with prophylactic sprays significantly decrease disease intensity and delay resistance development (Lal *et al.*, 2015). A new blend, dimethomorph (20.27% w/w) + ametoctradin (27%), was highly effective in controlling late blight of potatoes in studies carried out in India (Lal *et al.*, 2017b). Initium (ametoctradin) targets specifically *P. infestans* by inhibiting mitochondrial complex III, which blocks ATP synthesis (Jackson *et al.*, 2025). New molecular tools and fungicide classes, such as QoI fungicides such as ametoctradin, have been found to be effective in controlling resistant *P. infestans* populations (Jackson *et al.*, 2025).

Comparative studies have evaluated fungicide efficacy over different seasons. Earlier studies showed metals such as metalaxyl and mancozeb to perform well initially but in the third or fourth consecutive growing season there was partial or total resistance, especially in dense fungicide-applied areas (Fry *et al.*, 1993). Seidl Johnson *et al.* (2015) compared effectiveness of fungicides against three US clonal lines of *P. infestans* (US-22, US-23, US-24) in isolated tomato leaf tests. Preventive applications of these fungicides effectively managed late blight caused by novel *P. infestans* clonal lineages, with the US-24 lineage being managed by fewer applications of fungicides compared to US-23 or US-22. Field trials showed that combinations of fungicides, e.g., mandipropamid with cymoxanil or dimethomorph, were very effective in managing new clonal lineages, with disease severity reduced by over 80% (Alvarez-Romero *et al.*, 2024). A seven-spray regimen of three sprays of

Mandipropamid 23.4% SC and four sprays of Ametoctradin 27% + Dimethomorph 20.27% SC effectively managed late blight severity ($p < 0.05$) in India's North Eastern Himalayan region, increasing tuber yields from 21.58 t/ha to 21.86 t/ha with a BCR of ~1:1.97 (Dey *et al.*, 2024). Field tests in Nepal between 2015–2016 showed Dimethomorph, Fenamidone + Mancozeb, and Mancozeb reduced AUDPC by up to 90, 68, and 47%, respectively, with significantly superior improvements in tuber yields compared to non-treated controls (Khadka *et al.*, 2020).

Long-term fungicide efficacy was quantified using trials conducted in Europe and North America. Despite metalaxyl and mancozeb controlling late blight at first, repeated application led to resistance (Fry *et al.*, 2015). West Bengal experiments indicated that control of late blight was best when a prophylactic spray of mancozeb (0.25%) was supplemented with dimethomorph+mancozeb or cymoxanil+mancozeb (0.3%) at early infection stage, followed by a supplemental mancozeb spray (0.25%) seven days post-systemic fungicide application (Chakraborty and Mazumdar, 2012). Victory 72 WP was launched in West Shoa in Ethiopia to fight fungicide resistance in potato and tomato (Amin *et al.*, 2013). Studies showed that lower doses of systemic fungicides like Ridomil were economical without compromising efficacy (Tsedale, 2014). Preventative mancozeb and chlorothalonil sprays followed by systemic fungicides were superior to post-symptomatic application (Lal *et al.*, 2015). The result of a comparative trial of 12 fungicides with *P. infestans* clonal groups indicated that effective application of such fungicides in conventional and also organic crop management systems is feasible. Preventative sprays produced better control in contrast to curative sprays, where major focus was given to active management practices (Seidl Johnson *et al.*, 2015).

P. infestans resistance to fungicides is a result of primary genetic mutations at the target location, allowing

the pathogen to become tolerant to treatment. Quick emergence of metalaxyl-resistant isolates in Switzerland, Ireland, and the Netherlands has demonstrated *P. infestans*' ability to adapt rapidly (Gisi and Cohen, 1996). Resistance development is accelerated by excessive use of a single mode of action, which provokes increased selection pressure on the pathogen. Studies have demonstrated that metalaxyl-resistant isolates are more likely to produce oospores when subjected to fungicides, increasing further the cycles of resistance. New surveillance techniques revealed mutations in genes such as Cytochrome b and RNA polymerase I, responsible for lowered sensitivity to fungicides, showing the genetic nature of resistance mechanisms (Mahajan et al., 2024). Repeated application of the same mode of action fungicides induces selection for resistance strains, eventually reducing overall effectiveness. For example, resistance to traditional oomycete-targeting fungicides necessitated alternative mechanisms such as SDHI fungicides (fluopyram) (Kamel et al., 2024).

Fungicide resistance prevention involves integrating several management strategies. Preventative application of chlorothalonil and mancozeb followed by systemic or translaminar fungicides retarded the resistance more than curative spraying (Lal et al., 2015). A spraying programme beginning with mancozeb 75% WP (0.2%) before disease onset, followed by two sprays of dimethomorph 50% WP (0.2%) + mancozeb 75% WP (0.2%) at a gap of 7–10 days, recorded the lowest terminal severity of the disease (24.55%) and the maximum disease control (74.45%) (Lal et al., 2017a). Development of new fungicides such as QiI fungicides (ametoctradin) and SDHI fungicides (fluopyram) has facilitated resistance development ease to manage (Jackson et al., 2025). Genomic surveillance techniques now allow for real-time monitoring of resistance development, enhancing the precision of intervention methods (Mahajan et al., 2024). One of the most important ways to overcome resistance is fungicide rotation with different modes of action, and the use of fungicide mixtures. Blending mandipropamid with cymoxanil or dimethomorph has been effective in reducing disease severity and managing resistant *P. infestans* isolates (Alvarez-Romero et al., 2024) (Table 5). Integrated approaches incorporating new chemistries, resistant cultivars, and predictive modeling offer science-based solutions for sustainable late blight management.

Alternative Chemicals

Various alternative substances, aside from fungicides, have also been tested for their effectiveness in treating late blight in potatoes. Compounds such as FeCl_3 , $\text{NH}_4\text{Fe}(\text{SO}_4)_2 \cdot 12\text{H}_2\text{O}$, and zinc sulphate at a concentration of 10 mM demonstrated complete inhibition of both growth and spore germination of *P. infestans*. In contrast,

substances like $(\text{NH}_4)_2\text{MoO}_4$, CuSO_4 , and $\text{K}_2\text{S}_2\text{O}_4$ at a concentration of 1 mM achieved only partial inhibition of growth and spore germination (Bhat et al., 2007).

The use of micronutrient-based foliar sprays, such as zinc sulphate and copper sulphate (0.2%), in combination with host resistance, delayed the onset of late blight by 12 days, subsequently reducing disease severity and improving yield. Additionally, combining a sub-phytotoxic dose of boron with lower rates of propineb + iprovalidicarb proved more proficient than fungicide-only treatments (Frenkel et al., 2010).

Systemic acquired resistance (SAR) activators, such as phosphorous acid and β -aminobutyric acid (BABA), have also shown promise in controlling late blight. These activators reduced disease severity by 40% to 60% and stimulated the upregulation of defense-related genes and *P. infestans* effector proteins, including β -1,3-glucanase, protease inhibitors, PR-1 proteins, thaumatin proteins, xyloglucanase, and others (Lal et al., 2018).

Several factors determine the effectiveness of induced resistance (IR) including the plant genotype, environmental conditions, and application methods (Sharma et al., 2010; Liljeroth et al., 2010) (Fig. 7); therefore, IR alone does not provide full protection. However, IR can contribute to total protection when included in other disease control methods. For instance, the use of BABA in conjunction with fungicides is known to reduce fungicide application by up to 25%, which is an advantage in terms of sustainability for disease management (Liljeroth et al., 2010). Although many fungicides have been developed to control late blight throughout the past 15 years, there have been reports of fungicide resistance to fungicides, such as dimethomorph (Stein and Kirk, 2004).

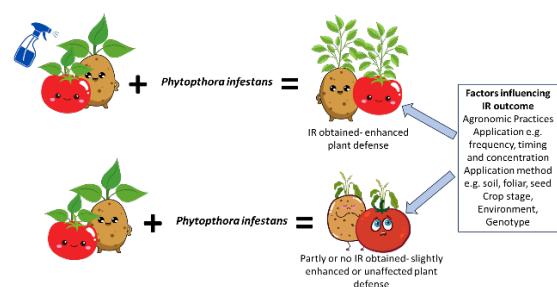


Fig. 7: Factors influencing the results of induced resistance (IR) in plants, late blight of potato and tomato as an example

A comprehensive study conducted between 1998 and 2000 evaluated 258 *P. infestans* isolates assembled from Brazilian potato and tomato fields including 87 isolates from potatoes to assess fungicide resistance (Reis et al., 2005). Statistical analysis of agar and leaf-disc sensitivity tests revealed a significant level of insensitivity to the

systemic fungicide metalaxyl among potato isolates. In the agar test, 35% of 210 isolates were found to be insensitive, 36% intermediately insensitive, and 29% sensitive, with US-1 and BR-1 genotypes showing similar resistance trends. Leaf-disc assays corroborated these results, indicating that 24.3% of 240 isolates were insensitive while 40.7% remained sensitive. In contrast, no resistance was observed against the protectant fungicides chlorothalonil and cymoxanil, as greater than 75% of the isolates exhibited ED50 values below 1.0 µg/ml. Further supporting this trend, European surveys conducted between 1996 and 1997 reported even higher levels of metalaxyl resistance in potato isolates, with 48% categorized as resistant, 18% as intermediate, and 34% as sensitive (Knapova *et al.*, 2002). Notably, only 2% of tomato isolates displayed resistance. Most resistant strains in these studies were associated with the A1 mating type, suggesting possible host-specific adaptation. These findings collectively underscore the widespread emergence of metalaxyl-resistant *P. infestans* strains, particularly in potato populations, and highlight the critical need for continuous resistance monitoring and the adoption of integrated fungicide management strategies to ensure effective and sustainable control of late blight. The integration of systemic fungicides with contact fungicides, exemplified by mancozeb, serves to mitigate the progression of resistance and enhance control efficacy. Numerous nations have enacted regulations aimed at limiting the frequency of fungicide applications. For example, within the European Union, it is advised that no singular fungicide be utilized more than twice consecutively to avert the accumulation of resistance (Fry, 2007).

Emerging Technologies in Late Blight Management

The prevalence of late blight worldwide today makes it clear that more work has to be done, despite the fact that a lot of effort has been made to combat *P. infestans* by employing pesticides and identifying resistance genes. Along with the ongoing enhancement of current methods to deal with late blight, new technologies have emerged (Fig. 8). The prevalence of late blight worldwide today makes it clear that more work has to be done, despite the fact that a lot of effort has been made to combat *P. infestans* by employing pesticides and identifying resistance genes.

Botanicals

A range of commercially available phytochemicals were assessed as potential environmentally acceptable biopesticides. Zeylenone, carvacrol, matrine, and eugenol were among those that demonstrated potential (Zhang *et al.* 2021; He *et al.* 2021). The use of 0.3 percent eugenol, for example, yielded a greater yield and demonstrated a protective effect on potato crops that was comparable to, if not superior to, that of conventional chemical pesticides

like mancozeb (80 percent WP) in a comparative field test (Dong and Zhou, 2022). They also discovered that eugenol may significantly slow down the growth of *P. infestans* on oatmeal agar. Eugenol's protective effects can be further enhanced by transporting it using nanomaterial carriers (Wang *et al.* 2021). Zeylenone, which was extracted from *Uvaria grandiflora*, influences the energy intake of *Phytophthora* and could eventually be employed for botanical fungicide (He *et al.* 2021).

CRISPR-Cas Genome Editing for Improving Resistance

With the advancement of CRISPR-Cas genome editing technology, precise alterations to plant genomes have been made possible, revolutionizing the process of creating resistant crop types. Through the introduction of resistance genes or mutations that strengthen innate immune responses, CRISPR-Cas9 enables the targeted editing of particular genes in tomatoes and potatoes. To increase ETI or the identification of PAMPs, for instance, genes linked to NLR proteins or PRRs can be altered. Stronger immune pathway activation brought on by these genetic changes may help the plants better resist *P. infestans* diseases (Li *et al.*, 2022; Angmo *et al.*, 2023). Moreover, susceptibility (S) genes that promote pathogen infection can be silenced using CRISPR-Cas9 (Zaidi *et al.*, 2018).

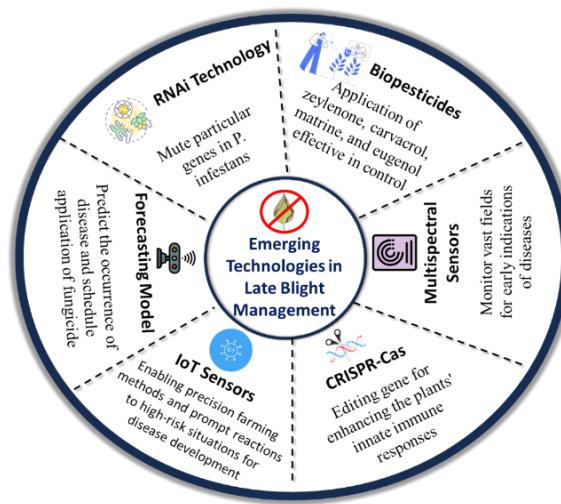


Fig. 8: Emerging technologies in late blight management. Innovations including remote sensing, pathogen monitoring, drones for crop surveillance, and advanced bioinformatics for managing potato late blight

The genes BSL1 and DMR6, for example, are known susceptibility (S) genes, and altering them may improve resistance to oomycete infections. Since DMR6 (Downy Mildew Resistance 6) functions as a negative regulator of plant defense mechanisms, mutations in this gene have

been linked to greater resistance in a number of plant species. Similarly, pathogen susceptibility has been linked to BSL1 (BSU-like 1), which interacts with the brassinosteroid signaling system. CRISPR Cas editing can effectively decrease disease vulnerability by disrupting these genes (Kraśniewska *et al.*, 2020). Editing genes that decrease host defense mechanisms, such as DMR6 or BSL1, has showed potential in boosting resistance against oomycete pathogens. It is possible to considerably lessen tomatoes' and potatoes' vulnerability to late blight by deleting or altering these genes. These illustrations demonstrate how CRISPR-Cas9 genome editing provides a potent, effective, and sustainable way to increase tomato and potato resistance to late blight. Researchers & breeders can expedite the creation of resilient cultivars by utilizing this technique, guaranteeing increased agricultural output and resistance to changing disease threats. Despite its promise, the CRISPR/Cas system faces several significant limitations in disease resistance breeding. One major challenge is the dynamic nature of pathogens, which continuously evolve to overcome existing resistance mechanisms. A notable example is the trade-off observed in disease resistance: disabling the StNRL1 gene enhanced resistance to late blight but simultaneously increased susceptibility to early blight, suggesting the gene plays a dual role in pathogen response. Another critical issue is the implicit for off-target mutations associated with CRISPR/Cas9, which, although minimized through bioinformatics tools, still necessitate extensive screening to ensure precision. Additional obstacles include low transformation efficiency and difficulties in in vitro plant regeneration, which hinder the broader application of this technology in potato breeding (Norouzi *et al.*, 2024). Furthermore, CRISPR/Cas9-mediated mutagenesis of the SIMYBS2 gene in tomatoes, aimed at combating *P. infestans*, revealed further drawbacks. The edited mutant plants (slmybs2-c) exhibited reduced resistance, characterized by increased necrosis, larger lesion sizes, suppressed expression of defense-related genes, and excessive accumulation of reactive oxygen species (ROS), which likely contributed to cellular damage rather than protection. These findings underscore the complexities and limitations of using CRISPR/Cas9 for durable disease resistance (Liu *et al.*, 2021).

RNA Interference (RNAi)

RNAi is a new and innovative technology that has recently been added to the potential toolkit of PLB (potato late blight) control. RNAi was initially discovered to be a part of the antiviral defense system of plants, but it is now believed to be essential for many other environmental adaptation mechanisms in plants, including defense against arthropod herbivores and fungal diseases (Zhao *et al.*, 2021). Some *Phytophthora* effectors can disrupt the

plant's RNA-silencing pathway, according to recent studies (Qiao *et al.*, 2013). The first proof of host-induced gene suppression in *P. infestans* by potatoes was presented by Jahan *et al.* (2015), indicating the necessity of the cross-kingdom molecular process. RNAi is a part of the potato-*Phytophthora* pathosystem. RNA interference (RNAi) technology can silence specific genes in *P. infestans* that are critical to its virulence, reducing the pathogen's ability to infect and providing a new method of biological control (Dong and Zhou, 2022). Recent advancements in RNA interference (RNAi) technology have facilitated the development of late blight-resistant potato cultivars by silencing genes encoding essential effector proteins used by *P. infestans* to suppress plant defenses. This approach has led to the creation of genetically engineered potato lines containing RNAi constructs, based on an inverted repeat strategy, specifically targeting the R3a homolog in *P. infestans*. This method has effectively reduced late blight severity by disrupting the pathogen's infection cycle and interfering with its molecular pathogenesis (Drozda *et al.*, 2022; Berindean *et al.*, 2024).

In parallel, the role of circular RNAs (circRNAs), particularly circRNA45 and circRNA47, has gained increasing attention for their involvement in plant defense responses. These circRNAs are upregulated during infection and act as molecular sponges for microRNAs such as miR477-3p, thereby modulating the expression of disease resistance genes. Transient overexpression of circRNA45 and circRNA47 in tomato plants has been shown to reduce lesion size, demonstrating their potential to enhance plant immunity (Hong *et al.*, 2020).

Small RNAs also play a pivotal role in plant-pathogen interactions. Notably, miR8788 targets the plant gene StABH1, which is involved in defense signaling. Downregulation of StABH1 by miR8788 facilitates pathogen infection; however, silencing miR8788 through miRNA target mimicry has produced knockdown strains with impaired growth on potato plants, leading to improved resistance. These findings were supported by transformation techniques using plasmid DNA and RNA extractions from *P. infestans* strains (Hu *et al.*, 2020).

Furthermore, the regulatory influence of microRNAs such as miR1918 has been underscored due to its association with genes linked to susceptibility. Transgenic tomato plants expressing specific small RNAs targeting *P. infestans* genes have shown enhanced resistance. qRT-PCR analyses have confirmed an inverse correlation between miR1918 levels and the expression of target genes, reinforcing its role in modulating plant defense responses (Jahan, 2015).

RNA interference (RNAi) technology presents promising potential for plant disease management, but it

is not without significant limitations. One of the primary drawbacks is the variability and instability of RNAi constructs, which can lead to inconsistent resistance across successive plant generations. Additionally, RNAi-mediated gene silencing may cause unintended off-target effects, impacting non-target genes and resulting in undesirable phenotypes (Dubrovina and Kiselev, 2019). Unlike gene knockout techniques, RNAi only downregulates gene expression, which may be insufficient when combating highly virulent *P. infestans* isolates. Moreover, the silencing effect can diminish over time due to epigenetic modifications or the plant's own defense mechanisms against foreign RNA, undermining its long-term effectiveness (Sun *et al.*, 2016). The efficacy of RNAi is also influenced by double-stranded RNA (dsRNA) concentrations—while certain levels inhibit pathogen growth, others might paradoxically promote it. Environmental factors such as growth medium and temperature further affect outcomes, complicating the extrapolation of laboratory results to field conditions. Most studies to date have been conducted in controlled environments using detached leaves or seedlings, which may not accurately represent the complex interactions in natural field settings. There is also concern that repeated RNAi applications could lead to resistance development in pathogens. Finally, regulatory hurdles and public apprehension surrounding genetically modified organisms pose additional barriers to the widespread adoption of RNAi-based approaches. Addressing these challenges through continued research is crucial for enhancing the viability of RNAi in sustainable agricultural disease management (Porwal *et al.*, 2020).

Molecular Breeding Through Marker-Assisted Selection (MAS)

The use of molecular breeding, such as MAS, has become essential for improving tomato and potato crops' resilience to late blight. MAS uses genetic markers associated with late blight resistance genes to enable the accurate identification and selection of resistance characteristics. With the help of this technology, breeders can quickly introduce desired features into market cultivars, avoiding the time-consuming and frequently inaccurate traditional breeding procedures. MAS can be used to develop high-yielding, disease-resistant cultivars by introducing resistance genes, such as *Ph3* and *Ph5* from wild tomatoes or *Rpi-vnt1*, *Rpi-blb1*, and *Rpi-blb2* from wild potato species, into susceptible types (Angmo *et al.*, 2023; Osei *et al.*, 2019). Furthermore, MAS facilitates the pyramiding of several resistance genes into a single cultivar in order to produce long-lasting and universal resistance. The idea of combining several *Rpi* genes in potatoes or *Ph* genes in tomatoes to increase resistance to *P. infestans* is backed by research showing that these resistance (R) genes can identify various

pathogen effectors, offering a more comprehensive and long-lasting defense (Vossen *et al.*, 2016). Targeting different *P. infestans* effector proteins, pyramiding *Rpi-blb1*, *Rpi-blb2*, and *Rpi-vnt1* in potatoes has been demonstrated to increase resistance (Vossen *et al.*, 2016). MAS was used to identify the resistance genes *Rpi-abpt* and *Rpi-blb1* in a study that involved 72 potato lines that were produced by crossing the susceptible cultivar 'ACI Pakri-1' with a donor that was resistant to late blight. According to field assessments, the susceptible parent showed 100% foliage destruction at 63–65 days after planting (DAP), while the chosen resistant lines showed just 1–25% degradation at 85 DAP (Islam *et al.*, 2018). Likewise, tomatoes that have *Ph3* and *Ph5* genes combined have stronger defenses against different types of pathogens (Foster *et al.*, 2009). In tomato conducting MAS-based breeding with *Ph-3*, resistant cultivars demonstrated up to a 70% reduction in disease incidence in comparison with non-resistance (Foolad *et al.*, 2008). These statistical outcomes underscore the efficacy of MAS in generating long-lasting cultivars resistant to late blight, which mitigates the need for fungicides and improves the productivity of crops.

The MAS was effective in identifying recombinants with the desired resistance traits. Out of 1152 F2 plants screened, 11 were identified as having potential recombination events between *Ph-3* and *Sw-5*, and three of these were confirmed to have resistance to late blight pathogens (Robbins *et al.*, 2010). Similarly, the high saturation of the potato molecular map with over 350 uniformly distributed markers enables precise identification of resistance genes and QTLs. This robust genetic framework enhances the effectiveness of Marker-Assisted Selection (MAS) in breeding *P. infestans*-resistant potato cultivars, improving crop resilience and yield (Barone *et al.*, 2004). Additionally, MAS makes it easier to create resistant cultivars without sacrificing important agronomic characteristics like fruit quality, yield, or stress tolerance. The efficiency of MAS is further increased when combined with modern methods like high-throughput genotyping, which makes it a crucial tactic in late blight resistant breeding initiatives. Therefore, MAS is a revolutionary method for preventing tomato and potato late blight. MAS speeds up the creation of resilient cultivars, guaranteeing sustainable agricultural production and food security, by incorporating resistance traits from wild relatives and implementing them in commercial breeding programs.

Use of Sensors

By facilitating real-time monitoring and precise interventions, the incorporation of sensor technology has completely transformed the treatment of late blight in tomato and potato crops. Field-installed Internet of Things (IoT) sensors continuously gather information on

temperature, humidity, soil moisture, and plant health—all of which are important variables affecting the development of late blight. Real-time microclimate data from these sensors can be used to forecast times when disease outbreaks are most likely to occur. IoT technologies facilitate precision farming by enabling farmers to take targeted and timely measures, such as modifying irrigation schedules or optimizing fungicide applications to lessen the conditions that encourage the growth of pathogens.

In potato fields, hyperspectral imaging sensors were utilized in studies through Unmanned Aerial Vehicles (UAVs) for the detection of late blight. The sensitivity of the disease monitoring was remarkably improved with the proposed CropdocNet model having a detection rate of 98.6% (Shi *et al.*, 2022). Two-drone coordination was utilized in another study to track potato late blight severity. It improved disease severity monitoring accuracy through complete field coverage in addition to early data collection (Sun *et al.*, 2023). Environmental factors causing the outbreak of late blight have also been monitored through IoT-based models. To notify farmers in real time when the conditions are favorable for the development of the disease, one of the systems had wireless sensors for temperature, humidity, and leaf wetness (Wang *et al.*, 2024). These technologies do not only improve the speed and accuracy of late blight detection but also enable targeted intervention, which can mitigate crop loss and improve yield.

Drones with thermal and multispectral imaging sensors are effective instruments for monitoring potato and tomato farms on a wide scale. Frequently before visual symptoms manifest, these drones are able to identify early indicators of late blight, such as variations in canopy temperature or chlorophyll fluorescence. Farmers can reduce the need for widespread pesticide applications and conserve resources by using this data to detect diseased areas and implement tailored treatments (Sun *et al.*, 2023; Mothapo *et al.*, 2022).

LAMP can be utilized to develop web-based dashboards, databases, and APIs for visualizing and managing IoT sensor data. In the context of disease detection, the LAMP assay successfully identified *P. infestans* in asymptomatic potato leaves as early as 24 hours post-inoculation. This rapid detection capability is crucial for timely intervention and effective management of late blight (Si Ammour *et al.*, 2017). To sum up, sensor technologies such as Internet of Things systems and sensors installed on drones—offer revolutionary ways to control tomato and potato late blight. These tools promote sustainable agriculture by facilitating accurate, data-driven farming methods that improve crop health, resource efficiency, and disease detection.

Advanced Disease Forecasting Models

To anticipate the probability of late blight outbreaks, sensor data is frequently included into sophisticated disease forecasting models, including BLITECAST and JHULSACAST. By using these forecasts, farmers can minimize losses and lessen their effects on the environment by making well-informed decisions about crop management (Parola, 2022). To predict the presence of late blight disease, a number of forecasting models have been developed. Van Everdingen originally created "Dutch rules" (Van Everdingen, 1926) to predict the onset of late blight and to schedule fungicide applications under Holland conditions. Many forecasting systems, such as SIMCAST, BLITECAST, PhytoPre, NegFry, ProPhy, PROGEB, Web-Blight, China Blight, Bio-PhytoPre, Plant Plus, PhytoPRE + 2000, and others, have been developed for different regions of the world (Arora *et al.*, 2014). To predict the onset of potato late blight, the BLITE-SVR forecasting system was developed. This model was developed using 13 various kinds of meteorological data, and the effectiveness of BLITE-SVR was contrasted with that of linear regression, pace regression, and the conventional moving-average method. The prediction accuracy for the first instance of late blight in potatoes was 64.3% for BLITE-SVR, 42.9% for the conventional moving-average method, 35.7% for linear regression and 42.9% using pace regression (Gu *et al.*, 2016). An online Decision Support System (DSS) was developed to manage late blight in potatoes and tomatoes (Small *et al.*, 2015). To predict disease dynamics based on crop data, weather, and management strategies, this system combines several models. Subsequent to the ascertainment of the geographical coordinates applicable to their production unit, the system systematically collects meteorological data from the closest operational weather station, in conjunction with acquiring localized forecast data from the National Weather Service's National Digital Forecast Database (Small *et al.*, 2015). By predicting the frequency and severity of late blight using a range of meteorological variables, these models assist farmers in determining when to use fungicides (Henderson *et al.*, 2007). Forecasting is important in chemical control due to the potential to provide information about the spray application process, including optimum amount, timing, and frequency of treatment. A variety of approaches to predict the optimal timing for the first fungicide application, as well as for subsequent applications, are more convenient and reduce the number of sprays needed for good blight control (Litschmann *et al.*, 2020).

Conclusion and Future Perspectives

Late blight, caused by *P. infestans*, continues to threaten global food security by causing substantial losses in potato and tomato production. The pathogen's complex

epidemiology, characterized by adaptive reproductive strategies and potent virulence mechanisms, presents significant challenges for effective management. While traditional methods such as cultural practices, host resistance, and biocontrol have shown some success, the integration of innovative and sustainable technologies is critical for long-term control. Emerging tools like CRISPR-Cas9 genome editing, RNAi, molecular breeding through MAS, biopesticides, and IoT-enabled sensors are transforming late blight management strategies. Advanced disease forecasting models also enable precise, data-driven interventions, optimizing resource use and reducing environmental impacts.

Future research should focus on developing broad-spectrum resistance by pyramiding multiple resistance-associated genes into commercial cultivars using genome editing and MAS techniques. Enhancing the efficacy of natural biopesticides, such as zeylenone and carvacrol, through advanced delivery systems like nanomaterials could provide eco-friendly alternatives to chemical controls. The expanded use of digital agriculture tools, including IoT sensors, drones, and real-time analytics integrated with forecasting models, can further advance precision farming and disease management. A deeper understanding of the molecular mechanisms governing *P. infestans* pathogenesis and host-pathogen interactions will be instrumental in designing novel resistance strategies. Moreover, the effects of the disease progress on the progression of late blight in the context of climate change must be analyzed and climate-resilient management strategies must be implemented to secure future agriculture productivity.

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Mahabuba Mostofa: Drafting, data collection and data analysis.

Dodi Al Sharif: Drafting, data collection and data analysis.

Md Motaher Hossain: Conception, Research design, and draft reviewing.

Ethics

This paper is original and not submitted elsewhere. The corresponding author agrees that all authors have seen and approved the final version of the manuscript and there is no ethical problem to disclose.

References

Aguilera-Galvez, C., Chu, Z., Omy, S. H., Wouters, D., Gilroy, E. M., Vossen, J. H., ... & Vleeshouwers, V. G. 2020. The *Rpi-mcql* resistance gene family recognizes *Avr2* of *Phytophthora infestans* but is distinct from *R2*. *BioRxiv*. <https://doi.org/10.1101/2020.10.08.331181>

Akino, S., Takemoto, D., & Hosaka, K. (2014). *Phytophthora infestans*: a review of past and current studies on potato late blight. *Journal of General Plant Pathology*, 80(1), 24–37. <https://doi.org/10.1007/s10327-013-0495-x>

Al Hareethi, A. A., Abdullah, Q. Y. M., Al Jobory, H. J., Al Aquil, S. A., & Arafa, R. A. (2023). First report of molecular identification of *Phytophthora infestans* causing potato late blight in Yemen. *Scientific Reports*, 13(1). <https://doi.org/10.1038/s41598-023-43510-2>

Al-Adhaileh, M. H., Verma, A., Aldhyani, T. H. H., & Koundal, D. (2023). Potato Blight Detection Using Fine-Tuned CNN Architecture. *Mathematics*, 11(6), 1516. <https://doi.org/10.3390/math11061516>

Alvarez-Romero, P. I., Robalino, D. A. R., Cabrera, C. E. M., Cordova, V. L., & Sánchez, L. A. H. (2024). *Optimizing Late Blight Management in Ecuadorian Tomato Crops through Potassium Phosphate and Integrated Fungicide Strategies*. <https://doi.org/10.20944/preprints202411.1780.v1>

Amin, M., Mulugeta, N., & Selvaraj, T. (2013). Field Evaluation of New Fungicide, Victory 72 WP for Management of Potato and Tomato Late Blight (*Phytophthora infestans* (Mont) de Bary) in West Shewa Highland, Oromia, Ethiopia. *Journal of Plant Pathology & Microbiology*, 04(08), 1–6. <https://doi.org/10.4172/2157-7471.1000192>

Angmo, D., Sharma, S. P., & Kalia, A. (2023). Breeding strategies for late blight resistance in potato crop: recent developments. *Molecular Biology Reports*, 50(9), 7879–7891. <https://doi.org/10.1007/s11033-023-08577-0>

Armstrong, M. R., Whisson, S. C., Pritchard, L., Bos, J. I. B., Venter, E., Avrova, A. O., Rehmany, A. P., Böhme, U., Brooks, K., Cherevach, I., Hamlin, N., White, B., Fraser, A., Lord, A., Quail, M. A., Churcher, C., Hall, N., Beriman, M., Huang, S., ... Birch, P. R. J. (2005). An ancestral oomycete locus contains late blight avirulence gene *Avr3a*, encoding a protein that is recognized in the host

cytoplasm. *Proceedings of the National Academy of Sciences*, 102(21), 7766–7771.
<https://doi.org/10.1073/pnas.0500113102>

Arora, R. K., Sharma, S., & Singh, B. P. (2014). Late blight disease of potato and its management. *Potato Journal*, 41(1).

Bailly, A., & Weisskopf, L. (2017). Mining the Volatilomes of Plant-Associated Microbiota for New Biocontrol Solutions. *Frontiers in Microbiology*, 8, 1638. <https://doi.org/10.3389/fmicb.2017.01638>

Baker, K. M., Kirk, W. W., Andresen, J., & Stein, J. M. (2004). A Problem Case Study: Influence of Climatic Trends on Late Blight Epidemiology in Potatoes. *Acta Horticulturae*, 638, 37–42.
<https://doi.org/10.17660/actahortic.2004.638.3>

Ball, A. S. (2015). *Biosafety and the Environmental Uses of Micro-Organisms*.
<https://doi.org/10.1787/9789264213562-en>

Ballvora, A., Ercolano, M. R., Weiß, J., Meksem, K., Bormann, C. A., Oberhagemann, P., Salamini, F., & Gebhardt, C. (2002). The *R1* gene for potato resistance to late blight (*Phytophthora infestans*) belongs to the leucine zipper/NBS/LRR class of plant resistance genes. *The Plant Journal*, 30(3), 361–371.
<https://doi.org/10.1046/j.1365-313x.2001.01292.x>

Barone, A. (2004). Molecular marker-assisted selection for potato breeding. *American Journal of Potato Research*, 81(2), 111–117.
<https://doi.org/10.1007/bf02853608>

Beninal, L., Bouznad, Z., Corbière, R., Belkhirer, S., Mabon, R., Taoutaou, A., Keddad, A., Runno-Paurson, E., & Andrivon, D. (2022). Distribution of major clonal lineages EU_13_A2, EU_2_A1, and EU_23_A1 of *Phytophthora infestans* associated with potato late blight across crop seasons and regions in Algeria. *Plant Pathology*, 71(2), 458–469.
<https://doi.org/10.1111/ppa.13471>

Berindean, I. V., Taoutaou, A., Rida, S., Ona, A. D., Stefan, M. F., Costin, A., Racz, I., & Muntean, L. (2024). Modern Breeding Strategies and Tools for Durable Late Blight Resistance in Potato. *Plants*, 13(12), 1711.
<https://doi.org/10.3390/plants13121711>

Bhardwaj, V., Salej, S., Ashwani, K., Vanishree, G., Sanjeev, S., & Sundaresha, S. (2019). Efficiency and reliability of marker assisted selection for resistance to major biotic stresses in potato. *Potato J*, 46(1), 56–66.

Bhat, M. N., Rani, A., & Singh, B. P. (2007). Efficacy of inorganic salts against potato late blight. *Potato Journal*, 34(1,2), 101–102.

Bhutto, R. A., Bhutto, N. ul ain H., Khanal, S., Wang, M., Iqbal, S., Fan, Y., & Yi, J. (2024). Potato protein as an emerging high-quality: Source, extraction, purification, properties (functional, nutritional, physicochemical, and processing), applications, and challenges using potato protein. *Food Hydrocolloids*, 157, 110415.
<https://doi.org/10.1016/j.foodhyd.2024.110415>

Boller, T., & Felix, G. (2009). A Renaissance of Elicitors: Perception of Microbe-Associated Molecular Patterns and Danger Signals by Pattern-Recognition Receptors. *Annual Review of Plant Biology*, 60(1), 379–406.
<https://doi.org/10.1146/annurev.arplant.57.032905.105346>

Bonde, R., & Murphy, E. F. (1952). Resistance of certain Tomato varieties and crosses to late blight. *Phytopathology*, 497, 15.

Bouket, A. C., Narmani, A., Tavasolee, A., Elyasi, G., Abdi, A., Naeimi, S., Sharifi, K., Oszako, T., Alenezi, F. N., & Belbahri, L. (2022). In Vitro Evaluation of Wood Vinegar (Pyroligneous Acid) VOCs Inhibitory Effect against a Fungus-like Microorganism *Ovatisporangium (Phytophytium)* Isolate Recovered from Tomato Fields in Iran. *Agronomy*, 12(7), 1609. <https://doi.org/10.3390/agronomy12071609>

Bradshaw, J. E., Bryan, G. J., Lees, A. K., McLean, K., & Solomon-Blackburn, R. M. (2006). Mapping the R10 and R11 genes for resistance to late blight (*Phytophthora infestans*) present in the potato (*Solanum tuberosum*) R-gene differentials of Black. *Theoretical and Applied Genetics*, 112(4), 744–751.
<https://doi.org/10.1007/s00122-005-0179-9>

Brouwer, D. J., Jones, E. S., & Clair, D. A. S. (2004). QTL analysis of quantitative resistance to *Phytophthora infestans* (late blight) in tomato and comparisons with potato. *Genome*, 47(3), 475–492.
<https://doi.org/10.1139/g04-001>

Caulier, S., Gillis, A., Colau, G., Licciardi, F., Liépin, M., Desoignies, N., Modrie, P., Legrèvre, A., Mahillon, J., & Bragard, C. (2018). Versatile Antagonistic Activities of Soil-Borne *Bacillus* spp. and *Pseudomonas* spp. against *Phytophthora infestans* and Other Potato Pathogens. *Frontiers in Microbiology*, 9, 143.
<https://doi.org/10.3389/fmicb.2018.00143>

Chakraborty, A., & Mazumdar, D. (2012). Development of effective spray schedule for the management of late blight of potato in plains of West Bengal. *Potato Journal*, 39(1), 92–94.

Champouret, N. (2010). *Functional genomics of Phytophthora infestans effectors and Solanum resistance genes*.

Chen, C., Wang, T., Black, L., Sheu, Z., Perez, F., & Deahl, K. (2009). Phenotypic and Genotypic Changes in the *Phytophthora infestans* Population in Taiwan – 1991 to 2006. *Journal of Phytopathology*, 157(4), 248–255.
<https://doi.org/10.1111/j.1439-0434.2008.01483.x>

Chen, X., Lewandowska, D., Armstrong, M. R., Baker, K., Lim, T.-Y., Bayer, M., Harrower, B., McLean, K., Jupe, F., Witek, K., Lees, A. K., Jones, J. D., Bryan, G. J., & Hein, I. (2018). Identification and rapid mapping of a gene conferring broad-spectrum late blight resistance in the diploid potato species *Solanum verrucosum* through DNA capture technologies. *Theoretical and Applied Genetics*, 131(6), 1287–1297. <https://doi.org/10.1007/s00122-018-3078-6>

Choi, J., Hong, S., Kessel, G. J. T., Cooke, D. E. L., Vossen, J. H., Cho, J., Im, J., Park, Y., & Cho, K. (2020). Genotypic and phenotypic characterization of *Phytophthora infestans* in South Korea during 2009–2016 reveals clonal reproduction and absence of EU_13_A2 genotype. *Plant Pathology*, 69(5), 932–943. <https://doi.org/10.1111/ppa.13178>

Chowdappa, P., Mohan Kumar, S. P., Jyothi Lakshmi, M., & Upreti, K. K. (2013). Growth stimulation and induction of systemic resistance in tomato against early and late blight by *Bacillus subtilis* OTPB1 or *Trichoderma harzianum* OTPB3. *Biological Control*, 65(1), 109–117. <https://doi.org/10.1016/j.biocontrol.2012.11.009>

Chunwongse, J., Chunwongse, C., Black, L., & Hanson, P. (2002). Molecular mapping of the *Ph-3* gene for late blight resistance in tomato. *The Journal of Horticultural Science and Biotechnology*, 77(3), 281–286. <https://doi.org/10.1080/14620316.2002.11511493>

Cooke, L. R., Kildea, S., Mehenni-Ciz, J., Quinn, L., Little, G., Hutton, F., & Griffin, D. (2012). Ongoing changes in the Irish potato late blight population. *Proceedings of the 13th EuroBlight Workshop*. 13th EuroBlight Workshop, St. Petersburg, Russia.

Cray, J. A., Connor, M. C., Stevenson, A., Houghton, J. D. R., Rangel, D. E. N., Cooke, L. R., & Hallsworth, J. E. (2016). Biocontrol agents promote growth of potato pathogens, depending on environmental conditions. *Microbial Biotechnology*, 9(3), 330–354. <https://doi.org/10.1111/1751-7915.12349>

Danies, G., Small, I. M., Myers, K., Childers, R., & Fry, W. E. (2013). Phenotypic Characterization of Recent Clonal Lineages of *Phytophthora infestans* in the United States. *Plant Disease*, 97(7), 873–881. <https://doi.org/10.1094/pdis-07-12-0682-re>

Davidse, L. C., Hofman, A. E., & Velthuis, G. C. M. (1983). Specific interference of metalaxyl with endogenous RNA polymerase activity in isolated nuclei from *Phytophthora megasperma* f. sp. *medicaginis*. *Experimental Mycology*, 7(4), 344–361. [https://doi.org/10.1016/0147-5975\(83\)90019-1](https://doi.org/10.1016/0147-5975(83)90019-1)

De Vrieze, M., Varadarajan, A. R., Schneeberger, K., Bailly, A., Rohr, R. P., Ahrens, C. H., & Weisskopf, L. (2020). Linking Comparative Genomics of Nine Potato-Associated *Pseudomonas* Isolates With Their Differing Biocontrol Potential Against Late Blight. *Frontiers in Microbiology*, 11, 857. <https://doi.org/10.3389/fmicb.2020.00857>

Deahl, K. L. (2012). Characterization of *Phytophthora infestans* populations in North America from the 2009–2011 late blight epidemics. *American Journal of Potato Research*. EuroBlight Workshop, St. Petersburg, Russia (EuroBlight Workshop 2011, published 2012).

Dey, U., Sarkar, S., Sehgal, M., Awasthi, D. P., De, B., Dutta, P., Majumdar, S., Pal, P., Chander, S., Sharma, Ph. R., & Mohanty, A. K. (2024). Integrating weather indices with field performance of novel fungicides for management of late blight of potato (*Phytophthora infestans*) in North Eastern Himalayan Region of India. *PLOS ONE*, 19(12), e0310868. <https://doi.org/10.1371/journal.pone.0310868>

Donahoo, R., & Roberts, P. (2013). Late Blight of Potato and Tomato. *EDIS*, 2013(1), 1–4. <https://doi.org/10.32473/edis-pp301-2012>

Dong, S., & Zhou, S. (2022). Potato late blight caused by *Phytophthora infestans*: From molecular interactions to integrated management strategies. *Journal of Integrative Agriculture*, 21(12), 3456–3466. <https://doi.org/10.1016/j.jia.2022.08.060>

Drozda, A., Kurpisz, B., Guan, Y., Arasimowicz-Jelonek, M., Plich, J., Jagodzik, P., Kuźnicki, D., & Floryszak-Wieczorek, J. (2022). Insights into the expression of DNA (de)methylation genes responsive to nitric oxide signaling in potato resistance to late blight disease. *Frontiers in Plant Science*, 13. <https://doi.org/10.3389/fpls.2022.1033699>

Duan, Y., Duan, S., Xu, J., Zheng, J., Hu, J., Li, X., Li, B., Li, G., & Jin, L. (2021). Late Blight Resistance Evaluation and Genome-Wide Assessment of Genetic Diversity in Wild and Cultivated Potato Species. *Frontiers in Plant Science*, 12, 710468. <https://doi.org/10.3389/fpls.2021.710468>

Dubrovina, A. S., & Kiselev, K. V. (2019). Exogenous RNAs for Gene Regulation and Plant Resistance. *International Journal of Molecular Sciences*, 20(9), 2282. <https://doi.org/10.3390/ijms20092282>

Dufková, H., Berka, M., Greplová, M., Shejbalová, Š., Hampejsová, R., Luklová, M., Domkářová, J., Novák, J., Kopačka, V., Brzobohatý, B., & Černý, M. (2021). The Omics Hunt for Novel Molecular Markers of Resistance to *Phytophthora infestans*. *Plants*, 11(1), 61. <https://doi.org/10.3390/plants11010061>

El-Naggar, M. A., Abouleid, H. Z., El-Deeb, H. M., Abd-El-Kareem, F., & Elshahawy, I. E. (2016). Biological control of potato late blight by means of induction systemic resistance and antagonism. *Research Journal of Pharmaceutical Biological and Chemical Sciences*, 7(1), 1338–1348.

Enciso-Maldonado, G. A., Lozoya-Saldaña, H., Colinas-Leon, M. T., Cuevas-Sánchez, J. A., Sanabria-Velázquez, A. D., Bamberg, J., & Raman, K. V. (2022). Assessment of Wild Solanum Species for Resistance to Phytophthora infestans (Mont.) de Bary in the Toluca Valley, Mexico. *American Journal of Potato Research*, 99(1), 25–39.
<https://doi.org/10.1007/s12230-021-09856-x>

Foolad, M. R., Merk, H. L., & Ashrafi, H. (2008). Genetics, Genomics and Breeding of Late Blight and Early Blight Resistance in Tomato. *Critical Reviews in Plant Sciences*, 27(2), 75–107.
<https://doi.org/10.1080/07352680802147353>

Forbes, G. A., Escobar, X. C., Ayala, C. C., Revelo, J., Ordoñez, M. E., Fry, B. A., Doucett, K., & Fry, W. E. (1997). Population Genetic Structure of *Phytophthora infestans* in Ecuador. *Phytopathology*, 87(4), 375–380.
<https://doi.org/10.1094/phyto.1997.87.4.375>

Foster, S. J., Park, T.-H., Pel, M., Brigneti, G., Śliwka, J., Jagger, L., van der Vossen, E., & Jones, J. D. G. (2009). *Rpi-vnt1.1*, a *Tm-2²* Homolog from *Solanum venturii*, Confers Resistance to Potato Late Blight. *Molecular Plant-Microbe Interactions*, 22(5), 589–600.
<https://doi.org/10.1094/mpmi-22-5-0589>

Frenkel, O., Yermiyahu, U., Forbes, G. A., Fry, W. E., & Shtienberg, D. (2010). Restriction of potato and tomato late blight development by sub-phytotoxic concentrations of boron. *Plant Pathology*, 59(4), 626–633.
<https://doi.org/10.1111/j.1365-3059.2010.02301.x>

Fry, W. E. (1993). Historical and Recent Migrations of *Phytophthora infestans*: Chronology, Pathways, and Implications. *Plant Disease*, 77(7), 653.
<https://doi.org/10.1094/pd-77-0653>

Fry, W. E. (2007). Phytophthora: Late blight on Ireland. *Microbiology Today*, 13–14.

Fry, W. E., Birch, P. R. J., Judelson, H. S., Grünwald, N. J., Danies, G., Everts, K. L., Gevens, A. J., Gugino, B. K., Johnson, D. A., Johnson, S. B., McGrath, M. T., Myers, K. L., Ristaino, J. B., Roberts, P. D., Secor, G., & Smart, C. D. (2015). Five Reasons to Consider *Phytophthora infestans* a Reemerging Pathogen. *Phytopathology*, 105(7), 966–981.
<https://doi.org/10.1094/phyto-01-15-0005-fi>

Fu, X., Liu, S., Ru, J., Tang, B., Zhai, Y., Wang, Z., & Wang, L. (2022). Biological control of potato late blight by *Streptomyces* sp. FXP04 and potential role of secondary metabolites. *Biological Control*, 169, 104891.
<https://doi.org/10.1016/j.biocontrol.2022.104891>

Gallegly, M. E., & Marvel, M. E. (1955). Inheritance of resistance to Tomato race 0 of *Phytophthora infestans*. *Phytopathology*, 45(2), 103–109.
<https://doi.org/10.5555/19551101759>

Gardner, R. G., & Panthee, D. R. (2010). NC 1 CELBR and NC 2 CELBR: Early Blight and Late Blight-resistant Fresh Market Tomato Breeding Lines. *HortScience*, 45(6), 975–976.
<https://doi.org/10.21273/hortsci.45.6.975>

Ghufran, M., Aldieri, L., Pyka, A., Ali, S., Bimonte, G., Senatore, L., & Vinci, C. P. (2024). Food security assessment in the light of sustainable development goals: a post-Paris Agreement era. *Environment, Development and Sustainability*, 27(2), 4541–4569.
<https://doi.org/10.1007/s10668-023-04089-w>

Giachero, M. L., Declerck, S., & Marquez, N. (2022). Phytophthora Root Rot: Importance of the Disease, Current and Novel Methods of Control. *Agronomy*, 12(3), 610.
<https://doi.org/10.3390/agronomy12030610>

Gisi, U., & Cohen, Y. (1996). Resistance to Phenylamide Fungicides: A Case Study with *Phytophthora infestans* Involving Mating Type and Race Structure. *Annual Review of Phytopathology*, 34(1), 549–572.
<https://doi.org/10.1146/annurev.phyto.34.1.549>

Goodwin, S. B., & Drenth, A. (1997). Origin of the A2 Mating Type of *Phytophthora infestans* Outside Mexico. *Phytopathology*, 87(10), 992–999.
<https://doi.org/10.1094/phyto.1997.87.10.992>

Goodwin, S. B., Cohen, B. A., & Fry, W. E. (1994). Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. *Proceedings of the National Academy of Sciences*, 91(24), 11591–11595.
<https://doi.org/10.1073/pnas.91.24.11591>

Gu, Y. H., Yoo, S. J., Park, C. J., Kim, Y. H., Park, S. K., Kim, J. S., & Lim, J. H. (2016). BLITE-SVR: New forecasting model for late blight on potato using support-vector regression. *Computers and Electronics in Agriculture*, 130, 169–176.
<https://doi.org/10.1016/j.compag.2016.10.005>

Guha Roy, S., Dey, T., Cooke, D. E. L., & Cooke, L. R. (2021). The dynamics of *Phytophthora infestans* populations in the major potato-growing regions of Asia – A review. *Plant Pathology*, 70(5), 1015–1031. <https://doi.org/10.1111/ppa.13360>

Guo, L., Zhu, X.-Q., Hu, C.-H., & Ristaino, J. B. (2010). Genetic Structure of *Phytophthora infestans* Populations in China Indicates Multiple Migration Events. *Phytopathology*, 100(10), 997–1006. <https://doi.org/10.1094/phyto-05-09-0126>

Gupta, H., Singh, B. P., & Mohan, J. (2004). Bio-control of late blight of potato. *Potato Journal*, 31(1,2), 39–42.

Haverkort, A. J., Struik, P. C., Visser, R. G. F., & Jacobsen, E. (2009). Applied Biotechnology to Combat Late Blight in Potato Caused by *Phytophthora Infestans*. *Potato Research*, 52(3), 249–264. <https://doi.org/10.1007/s11540-009-9136-3>

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Vossen, J. H., & Visser, R. G. F. (2016). Durable Late Blight Resistance in Potato Through Dynamic Varieties Obtained by Cisgenesis: Scientific and Societal Advances in the DuRPh Project. *Potato Research*, 59(1), 35–66. <https://doi.org/10.1007/s11540-015-9312-6>

He, J., Dou, M., Xie, J., Hou, S., Liu, Q., Hu, Z., Zhang, B., Zheng, S., Yin, F., Zhang, M., Xie, C., Lu, D., Ding, X., Zhu, C., & Sun, R. (2021). Discovery of zeylenone from *Uvaria grandiflora* as a potential botanical fungicide. *Pest Management Science*, 77(12), 5407–5417. <https://doi.org/10.1002/ps.6580>

Henderson, D., Williams, C. J., & Miller, J. S. (2007). Forecasting Late Blight in Potato Crops of Southern Idaho Using Logistic Regression Analysis. *Plant Disease*, 91(8), 951–956. <https://doi.org/10.1094/pdis-91-8-0951>

Hong, Y.-H., Meng, J., Zhang, M., & Luan, Y.-S. (2020). Identification of tomato circular RNAs responsive to *Phytophthora infestans*. *Gene*, 746, 144652. <https://doi.org/10.1016/j.gene.2020.144652>

Hossain, Md. M., Sultana, F., Mostafa, M., Ferdus, H., Rahman, M., Rana, J. A., Islam, S. S., Adhikary, S., Sannal, A., Al Emran Hosen, Md., Nayeema, J., Emu, N. J., Kundu, M., Biswas, S. K., Farzana, L., & Al Sabbir, Md. A. (2024). Plant disease dynamics in a changing climate: impacts, molecular mechanisms, and climate-informed strategies for sustainable management. *Discover Agriculture*, 2(1). <https://doi.org/10.1007/s44279-024-00144-w>

Hu, X., Persson Hodén, K., Liao, Z., Åsman, A., & Dixelius, C. (2022). *Phytophthora infestans* Ago1-associated miRNA promotes potato late blight disease. *New Phytologist*, 233(1), 443–457. <https://doi.org/10.1111/nph.17758>

Huang, S., Van Der Vossen, E. A. G., Kuang, H., Vleeshouwers, V. G. A. A., Zhang, N., Borm, T. J. A., Van Eck, H. J., Baker, B., Jacobsen, E., & Visser, R. G. F. (2005). Comparative genomics enabled the isolation of the *R3a* late blight resistance gene in potato. *The Plant Journal*, 42(2), 251–261. <https://doi.org/10.1111/j.1365-313x.2005.02365.x>

Huang, S., Vleeshouwers, V. G. A. A., Werij, J. S., Hutten, R. C. B., van Eck, H. J., Visser, R. G. F., & Jacobsen, E. (2004). The *R3* Resistance to *Phytophthora infestans* in Potato is Conferred by Two Closely Linked *R* Genes with Distinct Specificities. *Molecular Plant-Microbe Interactions*, 17(4), 428–435. <https://doi.org/10.1094/mpmi.2004.17.4.428>

Ifeduba, A. M., & Kwon-Ndung, E. H. (2021). Mechanisms of disease resistance to late blight disease of potato. *Direct Research Journal of Biology and Biotechnology*, 7, 37–46.

Islam, Md. H., Masud, Md. M., Jannat, M., Hossain, M. I., Islam, S., Alam, Md. Z., Serneels, F. J. B., & Islam, Md. R. (2022). Potentiality of Formulated Bioagents from Lab to Field: A Sustainable Alternative for Minimizing the Use of Chemical Fungicide in Controlling Potato Late Blight. *Sustainability*, 14(8), 4383. <https://doi.org/10.3390/su14084383>

Islam, S., Azad, Md. A. K., Islam, Md. R., Sultana, Mst. S., Khatun, J. A., & Islam, Md. H. (2021). Efficacy of Some Botanical Extracts on the Control of Late Blight Disease in Experimental Potato Field. *Advances in Bioscience and Biotechnology*, 12(12), 426–435. <https://doi.org/10.4236/abb.2021.1212027>

Islam, S., Raihan, A., Nahiyah, A. S. M., Siddique, M. A., & Rahman, L. (2018). Field Screening and Marker Assisted Selection of Late Blight Resistant Potato Lines. *International Journal of Plant & Soil Science*, 25(5), 1–12. <https://doi.org/10.9734/ijpss/2018/45301>

Ivanov, A. A., Ukladov, E. O., & Golubeva, T. S. (2021). *Phytophthora infestans*: An Overview of Methods and Attempts to Combat Late Blight. *Journal of Fungi*, 7(12), 1071. <https://doi.org/10.3390/jof7121071>

Jackson, V., Sherer, C., Jordan, L., & Clohessy, T. (2025). Unveiling the potential: exploring the efficacy of complex III inhibitors in fungal disease control. *Pest Management Science*, 81(5), 2450–2456. <https://doi.org/10.1002/ps.8384>

Jahan, S. (2015). *Small RNAs in Phytophthora infestans and cross-talk with potato*.

Jahan, S. N., Åsman, A. K. M., Corcoran, P., Fogelqvist, J., Vetukuri, R. R., & Dixelius, C. (2015). Plant-mediated gene silencing restricts growth of the potato late blight pathogen *Phytophthora infestans*. *Journal of Experimental Botany*, 66(9), 2785–2794. <https://doi.org/10.1093/jxb/erv094>

K. Osei, M., Premeh, R., Adjepong-Danquah, J., A. Opoku, J., Danquah, A., Danquah, E., Blay, E., & Adu-Dapaah, H. (2019). Marker-Assisted Selection (MAS): A Fast-Track Tool in Tomato Breeding. *Tomato - From Genome to Environment*, 1–20. <https://doi.org/10.5772/intechopen.76007>

Kamel, S. M., Essa, T. A. E., Arafa, R., Elgobashy, S. F., Shebl, A., Ahmed, N., & Abd-Elsalam, K. A. (2024). Investigating the impact of commercial potato cultivars and fungicides on late blight disease control. *Egyptian Journal of Agricultural Research*, 102(3), 362–380.
<https://doi.org/10.21608/ejar.2024.291618.1545>

Kariuki, W. G., Mungai, N. W., Otaye, D. O., Thuita, M., Muema, E., Korir, H., & Masso, C. (2020). Antagonistic effects of biocontrol agents against Phytophthora infestans and growth stimulation in tomatoes. *African Crop Science Journal*, 28(s1), 55–70. <https://doi.org/10.4314/acsj.v28i1.5s>

Kato, M. (1993). Oospores of Phytophthora infestans found in the experimental field of potato. *Ann Phytopathol Soc Jpn*, 59, 568–571.

Kaukoranta, T. (1996). Impact of global warming on potato late blight: risk, yield loss and control. *Agricultural and Food Science*, 5(3), 311–327. <https://doi.org/10.23986/afsci.72749>

Keijzer, P., van Bueren, E. T. L., Engelen, C. J. M., & Hutten, R. C. B. (2022). Breeding Late Blight Resistant Potatoes for Organic Farming—a Collaborative Model of Participatory Plant Breeding: the Bioimpuls Project. *Potato Research*, 65(2), 349–377. <https://doi.org/10.1007/s11540-021-09519-8>

Kessel, G. E. E. R. T., Moene, A. R. N. O. L. D., Valkengoed, E. R. I. C., Voet, P. A. U. L., Michielsen, J. M., Ahsan, H., & Hengsdijk, H. (2017). May. Geodata to control potato late blight in Bangladesh. *Proceedings of the Sixteenth EuroBlight Workshop*, 14–17.

Khadka, R. B., Chaulagain, B., Subedi, S., Marasini, M., Rawal, R., Pathak, N., Gautam, I. P., Chapagain, T. R., Khatri, B. B., & Sharma-Poudyal, D. (2020). Evaluation of fungicides to control potato late blight (*Phytophthora infestans*) in the plains of Nepal. *Journal of Phytopathology*, 168(5), 245–253. <https://doi.org/10.1111/jph.12886>

Khalid, N., Rajput, N. A., Khan, S. A., & Ahmad, A. (2017). Population structure of Phytophthora infestans on worldwide scale: A review. *Pakistan Journal of Phytopathology*, 29(2), 281.

Knapova, G., & Gisi, U. (2002). Phenotypic and genotypic structure of *Phytophthora infestans* populations on potato and tomato in France and Switzerland. *Plant Pathology*, 51(5), 641–653. <https://doi.org/10.1046/j.1365-3059.2002.00750.x>

Koeck, M., Hardham, A. R., & Dodds, P. N. (2011). The role of effectors of biotrophic and hemibiotrophic fungi in infection. *Cellular Microbiology*, 13(12), 1849–1857.
<https://doi.org/10.1111/j.1462-5822.2011.01665.x>

Kraśniewska, K., Galus, S., & Gniewosz, M. (2020). Biopolymers-Based Materials Containing Silver Nanoparticles as Active Packaging for Food Applications—A Review. *International Journal of Molecular Sciences*, 21(3), 698. <https://doi.org/10.3390/ijms21030698>

Lacaze, A., Sormany, F., Judelson, H. S., & Joly, D. L. (2023). The Expression of Cytoplasmic Effectors by *Phytophthora infestans* in Potato Leaves and Tubers Is Organ-Biased. *PhytoFrontiers™*, 3(3), 559–568.
<https://doi.org/10.1094/phytofr-01-22-0004-r>

Lal, M. E. H. I., Yadav, S. A. U. R. A. B. H., Chand, S. U. B. H. A. S. H., Kaushik, S. K., Singh, B. P., & Sharma, S. A. N. J. E. E. V. (2015). Evaluation of fungicides against late blight (*Phytophthora infestans*) on susceptible and moderately resistant potato cultivars. *Indian Phytopathol*, 68, 345–347.

Lal, M., Luthra, S. K., Singh, B. P., & Yadav, S. (2013). Screening of genotypes against potato late blight. *Potato Journal*, 40(1), 80–83.

Lal, M., Sharma, S., Yadav, S., & Kumar, S. (2018). Management of Late Blight of Potato. *Potato - From Incas to All Over the World*, 1–20.
<https://doi.org/10.5772/intechopen.72472>

Lal, M., Singh, A. P., Tomar, S., Hussain, T., Sharma, S., Kaushik, S., & Singh, B. (2013). Antagonistic Effect of Bio-agents Against Three Potato Fungal Diseases and Their Fungicidal Sensitivity. *Vegetos- An International Journal of Plant Research*, 26(2), 362–367. <https://doi.org/10.5958/j.2229-4473.26.2.098>

Lal, M., Singh, B. P., Yadav, S., & Sharma, S. (2017). Ametoctradin 27%+ dimethomorph 20.27%(w/w) SC: A new molecule for management of late blight of potato in India. *Journal of Experimental Zoology of India*, 20(2), 1119–1123.

Lal, M., Yadav, S., & Singh, B. P. (2017). Efficacy of New Fungicides against Late Blight of Potato in Subtropical Plains of India. *Journal of Pure and Applied Microbiology*, 11(1), 599–603. <https://doi.org/10.22207/jpam.11.1.78>

Lamichhane, S., Neupane, S., Timsina, S., Chapagain, B., Paudel, P. P., & Rimal, A. (2024). Potato Late Blight Caused by *Phytophthora infestans*; an Overview on Pathology, Integrated Disease Management Approaches, and Forecasting Models. *SSRN*.

Li, R., Maioli, A., Yan, Z., Bai, Y., Valentino, D., Milani, A. M., Pompili, V., Comino, C., Lanteri, S., Moglia, A., & Acquadro, A. (2022). CRISPR/Cas9-Based Knock-Out of the PMR4 Gene Reduces Susceptibility to Late Blight in Two Tomato Cultivars. *International Journal of Molecular Sciences*, 23(23), 14542. <https://doi.org/10.3390/ijms232314542>

Liang, D., Andersen, C. B., Vetukuri, R. R., Dou, D., & Grenville-Briggs, L. J. (2020). Horizontal Gene Transfer and Tandem Duplication Shape the Unique CAZyme Complement of the Mycoparasitic Oomycetes *Pythium oligandrum* and *Pythium periplocum*. *Frontiers in Microbiology*, 11, 581698. <https://doi.org/10.3389/fmicb.2020.581698>

Liljeroth, E., Bengtsson, T., Wiik, L., & Andreasson, E. (2010). Induced resistance in potato to *Phytophthora infestans*—effects of BABA in greenhouse and field tests with different potato varieties. *European Journal of Plant Pathology*, 127(2), 171–183. <https://doi.org/10.1007/s10658-010-9582-4>

Lin, X., Olave-Achury, A., Heal, R., Witek, K., Karki, H. S., Song, T., & Jones, J. D. (2021). Rpi-amr3 confers resistance to multiple *Phytophthora* species by recognizing a conserved RXLR effector. *BioRxiv*. <https://doi.org/10.1101/2021.06.10.447899>

Litschmann, T., Ervin, H., & Petr, D. (2023). A new method of potato late blight forecasting in the Czech Republic. *Journal of Plant Protection Research*, 60(2), 134–140. <https://doi.org/10.24425/jppr.2020.133306>

Liu, C., Zhang, Y., Tan, Y., Zhao, T., Xu, X., Yang, H., & Li, J. (2021). CRISPR/Cas9-Mediated SLIMYBS2 Mutagenesis Reduces Tomato Resistance to *Phytophthora infestans*. *International Journal of Molecular Sciences*, 22(21), 11423. <https://doi.org/10.3390/ijms222111423>

Liu, Chunxin, Zhang, Yiyao, Tan, Yinxiao, Zhao, T., Xu, X., Yang, H., & Li, J. (2017). CRISPR/Cas9-Mediated SLIMYBS2 Mutagenesis Reduces Tomato Resistance to *Phytophthora infestans*. *Agronomy Journal*, 22(21), 11423. <https://doi.org/https://doi.org/10.3390/ijms222111423>

Lokossou, A. A., Park, T., van Arkel, G., Arens, M., Ruyter-Spira, C., Morales, J., Whisson, S. C., Birch, P. R. J., Visser, R. G. F., Jacobsen, E., & van der Vossen, E. A. G. (2009). Exploiting Knowledge of *R/Avr* Genes to Rapidly Clone a New LZ-NBS-LRR Family of Late Blight Resistance Genes from Potato Linkage Group IV. *Molecular Plant-Microbe Interactions*®, 22(6), 630–641. <https://doi.org/10.1094/mpmi-22-6-0630>

Lough, R. C., & Gardner, R. G. (2000). 551 Inheritance of Tomato Late Blight Resistance Derived from *Lycopersicon hirsutum* LA1033 and Identification of Molecular Markers. *HortScience*, 35(3), 490E–490. <https://doi.org/10.21273/hortsci.35.3.490e>

Ludwiczewska, M., Janiszewska, M., Yin, Z., & Śliwka, J. (2025). Populations of *Phytophthora infestans* in northern and eastern Europe. *European Journal of Plant Pathology*, 171(1), 81–95. <https://doi.org/10.1007/s10658-024-02933-x>

Mahajan, P. J., Deshmukh, M. R., Khamkar, M. B., & Bansod, R. D. (2024). Management of late blight disease (*Phytophthora infestans*) of potato in the plateau region of Maharashtra. *International Journal of Statistics and Applied Mathematics*, SP-9(1), 330–333.

Majeed, A., Siyar, S., & Sami, S. (2022). Late blight of potato: From the great Irish potato famine to the genomic era – An overview. *Hellenic Plant Protection Journal*, 15(1), 1–9. <https://doi.org/10.2478/hppj-2022-0001>

Maziero, J. M. N., Maffia, L. A., & Mizubuti, E. S. G. (2009). Effects of Temperature on Events in the Infection Cycle of Two Clonal Lineages of *Phytophthora infestans* Causing Late Blight on Tomato and Potato in Brazil. *Plant Disease*, 93(5), 459–466. <https://doi.org/10.1094/pdis-93-5-0459>

Mazumdar, P., Singh, P., Kethiravan, D., Ramathani, I., & Ramakrishnan, N. (2021). Late blight in tomato: insights into the pathogenesis of the aggressive pathogen *Phytophthora infestans* and future research priorities. *Planta*, 253(6), 119. <https://doi.org/10.1007/s00425-021-03636-x>

Merk, H. L., & Foolad, M. R. (2012). Parent–offspring correlation estimate of heritability for late blight resistance conferred by an accession of the tomato wild species *Solanum pimpinellifolium*. *Plant Breeding*, 131(1), 203–210. <https://doi.org/10.1111/j.1439-0523.2011.01898.x>

Mollah, Md. M. I., & Hassan, N. (2023). Efficacy of *Trichoderma harzianum*, as a biological fungicide against fungal diseases of potato, late blight and early blight. *Journal of Natural Pesticide Research*, 5, 3618–3620. <https://doi.org/10.1016/j.napere.2023.100047>

Monino-Lopez, D., Nijenhuis, M., Kodde, L., Kamoun, S., Salehian, H., Schentsnyi, K., & Vossen, J. H. (2021). Allelic variants of the NLR protein Rpi-chc1 differentially recognize members of the *Phytophthora infestans* PexRD12/31 effector superfamily through the leucine-rich repeat domain. *The Plant Journal*, 107(1), 182–197. <https://doi.org/10.1111/tpj.15284>

Mothapo, M. C., Dube, T., Abdel-Rahman, E., & Sibanda, M. (2022). Progress in the use of geospatial and remote sensing technologies in the assessment and monitoring of tomato crop diseases. *Geocarto International*, 37(16), 4784–4804. <https://doi.org/10.1080/10106049.2021.1899303>

Mugao, L. (2023). Morphological and Molecular Variability of *Alternaria solani* and *Phytophthora infestans* Causing Tomato Blights. *International Journal of Microbiology*, 2023, 1–8. <https://doi.org/10.1155/2023/8951351>

Murphy, F., He, Q., Armstrong, M., Giuliani, L. M., Boevink, P. C., Zhang, W., Tian, Z., Birch, P. R. J.,

& Gilroy, E. M. (2018). The Potato MAP3K StVIK Is Required for the *Phytophthora infestans* RXLR Effector Pi17316 to Promote Disease. *Plant Physiology*, 177(1), 398–410.
<https://doi.org/10.1104/pp.18.00028>

Narouei-Khandan, H. A., Shakya, S. K., Garrett, K. A., Goss, E. M., Dufault, N. S., Andrade-Piedra, J. L., Asseng, S., Wallach, D., & Bruggen, A. H. C. van. (2020). BLIGHTSIM: A New Potato Late Blight Model Simulating the Response of *Phytophthora infestans* to Diurnal Temperature and Humidity Fluctuations in Relation to Climate Change. *Pathogens*, 9(8), 659.
<https://doi.org/10.3390/pathogens9080659>

Naess, S. K., Bradeen, J. M., Wielgus, S. M., Haberlach, G. T., McGrath, J. M., & Helgeson, J. P. (2000). Resistance to late blight in *Solanum bulbocastanum* is mapped to chromosome 8. *Theoretical and Applied Genetics*, 101(5–6), 697–704.
<https://doi.org/10.1007/s001220051533>

Nkongho, R. N., Ndam, L. M., Akoneh, N. N., Tongwa, Q. M., Njilar, R. M., Agbor, D. T., Sama, V., Ojongakpa, O. T., & Ngone, A. M. (2023). Vegetative propagation of F1 tomato hybrid (*Solanum lycopersicum* L.) using different rooting media and stem-nodal cuttings. *Journal of Agriculture and Food Research*, 11, 100470.
<https://doi.org/10.1016/j.jafr.2022.100470>

Norouzi, M., Nazarain-Firouzabadi, F., Ismaili, A., Ahmadvand, R., & Poormazaheri, H. (2024). CRISPR/Cas StNRL1 gene knockout increases resistance to late blight and susceptibility to early blight in potato. *Frontiers in Plant Science*, 14, 1278127. <https://doi.org/10.3389/fpls.2023.1278127>

Nowicki, M., Foolad, M. R., Nowakowska, M., & Kozik, E. U. (2012). Potato and Tomato Late Blight Caused by *Phytophthora infestans*: An Overview of Pathology and Resistance Breeding. *Plant Disease*, 96(1), 4–17.
<https://doi.org/10.1094/pdis-05-11-0458>

Nowicki, M., Kozik, E. U., & Foolad, M. R. (2013). Late blight of tomato. *Translational Genomics for Crop Breeding: Biotic Stress*, 1, 241–265.
<https://doi.org/10.1002/9781118728475.ch13>

Oosumi, T., Rockhold, D. R., MacCree, M. M., Deahl, K. L., McCue, K. F., & Belknap, W. R. (2009). Gene Rpi-bt1 from *Solanum bulbocastanum* Confers Resistance to Late Blight in Transgenic Potatoes. *American Journal of Potato Research*, 86(6), 456–465.
<https://doi.org/10.1007/s12230-009-9100-4>

Pais, M., Yoshida, K., Giannakopoulou, A., Pel, M. A., Cano, L. M., Oliva, R. F., Witek, K., Lindqvist-Kreuze, H., Vleeshouwers, V. G. A. A., & Kamoun, S. (2018). Gene expression polymorphism underpins evasion of host immunity in an asexual lineage of the Irish potato famine pathogen. *BMC Evolutionary Biology*, 18, 93.
<https://doi.org/10.1186/s12862-018-1201-6>

Panthee, D. R., Gardner, R. G., Ibrahem, R., & Anderson, C. (2015). Molecular Markers Associated with *Ph-3* Gene Conferring Late Blight Resistance in Tomato. *American Journal of Plant Sciences*, 06(13), 2144–2150.
<https://doi.org/10.4236/ajps.2015.613216>

Park, T.-H., Foster, S., Brigneti, G., & Jones, J. D. G. (2009). Two distinct potato late blight resistance genes from *Solanum berthaultii* are located on chromosome 10. *Euphytica*, 165(2), 269–278.
<https://doi.org/10.1007/s10681-008-9784-4>

Parola, C. M. (2022). Comparison of Multispectral and Hyperspectral UAV Imagery for Late Blight (*Phytophthora infestans*) detection in a potato.

Peirce, L. C. (1971). Linkage tests with *Ph* conditioning resistance to race 0, *Phytophthora infestans*.

Perfect, S. E., & Green, J. R. (2001). Infection structures of biotrophic and hemibiotrophic fungal plant pathogens. *Molecular Plant Pathology*, 2(2), 101–108.
<https://doi.org/10.1046/j.1364-3703.2001.00055.x>

Porwal, V., Sharma, A., & Kant, A. (2020). Efficacy of dsRNA in late blight (*Phytophthora infestans*) of tomato.

Powderly, W. G. P. (2019). How infection shaped history: lessons from the Irish famine. *Transactions of the American Clinical and Climatological Association*, 130, 127.

Pule, B. B., Meitz, J. C., Thompson, A. H., Linde, C. C., Fry, W. E., Langenhoven, S. D., Meyers, K. L., Kandolo, D. S., van Rij, N. C., & McLeod, A. (2013). *Phytophthora infestans* populations in central, eastern and southern African countries consist of two major clonal lineages. *Plant Pathology*, 62(1), 154–165.
<https://doi.org/10.1111/j.1365-3059.2012.02608.x>

Purwantisari, S., Priyatmojo, A., Sancayaningsih, R. P., Kasiandari, R. S., & Budihardjo, K. (2018). Systemic inducing resistance against late blight by applying antagonist *Trichoderma Viride*. *Journal of Physics: Conference Series*, 1025, 012053.
<https://doi.org/10.1088/1742-6596/1025/1/012053>

Qiao, Y., Liu, L., Xiong, Q., Flores, C., Wong, J., Shi, J., Wang, X., Liu, X., Xiang, Q., Jiang, S., Zhang, F., Wang, Y., Judelson, H. S., Chen, X., & Ma, W. (2013). Oomycete pathogens encode RNA silencing suppressors. *Nature Genetics*, 45(3), 330–333. <https://doi.org/10.1038/ng.2525>

Rraigond, P., Singh, B., Jayanty, S. S., & Luthra, S. K. (2024). Nutritional Significance of Potato and Its Biofortification. In: *Potato: Nutrition, Consumption, and Health*, 10.1007/978-981-97-1223-6_12, 349–367. https://doi.org/10.1007/978-981-97-1223-6_12

Reis, A., Ribeiro, F. H. S., Maffia, L. A., & Mizubuti, E. S. G. (2005). Sensitivity of Brazilian Isolates of *Phytophthora infestans* to Commonly Used Fungicides in Tomato and Potato Crops. *Plant Disease*, 89(12), 1279–1284.
<https://doi.org/10.1094/pd-89-1279>

Rhouma, A., Hajji-Hedfi, L., & Atallaoui, K. (2024). Potato late blight: the pathogen, the menace, the sustainable control. *DYSONA-Life Science*, 5(1), 37–51. <https://doi.org/10.30493/dls.2024.445326>

Rhouma, A., Salem, I. B., Hamdi, N. B. M., & Gomez, J. I. R. G. (2016). Efficacy of two fungicides for the management of *Phytophthora infestans* on potato through different applications methods adopted in controlled conditions. *International Journal of Applied and Pure Science and Agriculture*, 2(12), 39–45.

Rietman, H., Bijsterbosch, G., Cano, L. M., Lee, H.-R., Vossen, J. H., Jacobsen, E., Visser, R. G. F., Kamoun, S., & Vleeshouwers, V. G. A. A. (2012). Qualitative and Quantitative Late Blight Resistance in the Potato Cultivar Sarpo Mira Is Determined by the Perception of Five Distinct RXLR Effectors. *Molecular Plant-Microbe Interactions®*, 25(7), 910–919.
<https://doi.org/10.1094/mpmi-01-12-0010-r>

Robbins, M. D., Masud, M. A. T., Panthee, D. R., Gardner, R. G., Francis, D. M., & Stevens, M. R. (2010). Marker-assisted Selection for Coupling Phase Resistance to Tomato spotted wilt virus and *Phytophthora infestans* (Late Blight) in Tomato. *HortScience*, 45(10), 1424–1428.
<https://doi.org/10.21273/hortsci.45.10.1424>

Rogozina, E. V., Gurina, A. A., Chalaya, N. A., Zoteyeva, N. M., Kuznetsova, M. A., Beketova, M. P., Muratova, O. A., Sokolova, E. A., Drobayazina, P. E., & Khavkin, E. E. (2023). Diversity of Late Blight Resistance Genes in the VIR Potato Collection. *Plants*, 12(2), 273.
<https://doi.org/10.3390/plants12020273>

Roy, S., Singh, B. P., & Bhattacharyya, S. K. (1991). Biocontrol of late blight of potato. *Phytophthora Newslett.*

Ryley, M. J., & Drenth, A. (2024). A matter of where and when—the appearance of Late Blight of potato in Australia. *Historical Records of Australian Science*, 35(2), 213–222.
<https://doi.org/10.1071/hr23009>

Saffan, M. M., Koriem, M. A., El-Henawy, A., El-Mahdy, S., El-Ramady, H., Elbehiry, F., Omara, A. E.-D., Bayoumi, Y., Badgar, K., & Prokisch, J. (2022). Sustainable Production of Tomato Plants (*Solanum lycopersicum* L.) under Low-Quality Irrigation Water as Affected by Bio-Nanofertilizers of Selenium and Copper. *Sustainability*, 14(6), 3236.
<https://doi.org/10.3390/su14063236>

Saville, A. C., Martin, M. D., & Ristaino, J. B. (2016). Historic Late Blight Outbreaks Caused by a Widespread Dominant Lineage of *Phytophthora infestans* (Mont.) de Bary. *PLOS ONE*, 11(12), e0168381.
<https://doi.org/10.1371/journal.pone.0168381>

Schiffer-Forsyth, K., Frederickson Matika, D. F., Hedley, P. E., Cock, P. J. A., & Green, S. (2023). *Phytophthora* in Horticultural Nursery Green Waste—A Risk to Plant Health. *Horticulturae*, 9(6), 616.
<https://doi.org/10.3390/horticulturae9060616>

Seidl Johnson, A. C., Jordan, S. A., & Gevens, A. J. (2015). Efficacy of Organic and Conventional Fungicides and Impact of Application Timing on Control of Tomato Late Blight Caused by US-22, US-23, and US-24 Isolates of *Phytophthora infestans*. *Plant Disease*, 99(5), 641–647. <https://doi.org/10.1094/pdis-04-14-0427-re>

Sharma, K., Butz, A. F., & Finckh, M. R. (2010). Effects of host and pathogen genotypes on inducibility of resistance in tomato (*Solanum lycopersicum*) to *Phytophthora infestans*. *Plant Pathology*, 59(6), 1062–1071.
<https://doi.org/10.1111/j.1365-3059.2010.02341.x>

Shi, Y., Han, L., Kleerekoper, A., Chang, S., & Hu, T. (2022). Novel CropdocNet Model for Automated Potato Late Blight Disease Detection from Unmanned Aerial Vehicle-Based Hyperspectral Imagery. *Remote Sensing*, 14(2), 396.
<https://doi.org/10.3390/rs14020396>

Shimelash, D., & Dessie, B. (2020). Novel characteristics of *Phytophthora infestans* causing late blight on potato in Ethiopia. *Current Plant Biology*, 24, 100172. <https://doi.org/10.1016/j.cpb.2020.100172>

Si Ammour, M., Bilodeau, G. J., Tremblay, D. M., Van der Heyden, H., Yaseen, T., Varvaro, L., & Carisse, O. (2017). Development of Real-Time Isothermal Amplification Assays for On-Site Detection of *Phytophthora infestans* in Potato Leaves. *Plant Disease*, 101(7), 1269–1277.
<https://doi.org/10.1094/pdis-12-16-1780-re>

Singh, S. S., Mer, R., & Renu. (2023). Field evaluation of combination fungicides against late blight disease in potato (*Solanum tuberosum*). *The Indian Journal of Agricultural Sciences*, 93(2), 215–219.
<https://doi.org/10.56093/ijas.v93i2.128888>

Skelsey, P., Rossing, W. A. H., Kessel, G. J. T., Powell, J., & van der Werf, W. (2005). Influence of Host Diversity on Development of Epidemics: An Evaluation and Elaboration of Mixture Theory. *Phytopathology®*, 95(4), 328–338.
<https://doi.org/10.1094/phyto-95-0328>

Slininger, P. J., Schisler, D. A., Ericsson, L. D., Brandt, T. L., Jo Frazier, M., Woodell, L. K., Olsen, N. L., & Kleinkopf, G. E. (2007). Biological control of post-harvest late blight of potatoes. *Biocontrol Science and Technology*, 17(6), 647–663.
<https://doi.org/10.1080/09583150701408881>

Śliwka, J., Jakuczun, H., Chmielarz, M., Hara-Skrzypiec, A., Tomczyńska, I., Kilian, A., & Zimnoch-Guzowska, E. (2012). Late blight resistance gene from *Solanum ruiz-ceballosii* is located on potato chromosome X and linked to violet flower colour. *BMC Genetics*, 13(1), 11.
<https://doi.org/10.1186/1471-2156-13-11>

Śliwka, J., Jakuczun, H., Chmielarz, M., Hara-Skrzypiec, A., Tomczyńska, I., Kilian, A., & Zimnoch-Guzowska, E. (2012). A resistance gene against potato late blight originating from *Solanum × michoacanum* maps to potato chromosome VII. *Theoretical and Applied Genetics*, 124(2), 397–406.
<https://doi.org/10.1007/s00122-011-1715-4>

Small, I. M., Joseph, L., & Fry, W. E. (2015). Development and implementation of the BlightPro decision support system for potato and tomato late blight management. *Computers and Electronics in Agriculture*, 115, 57–65.
<https://doi.org/10.1016/j.compag.2015.05.010>

Small, I. M., Joseph, L., & Fry, W. E. (2015). Evaluation of the BlightPro Decision Support System for Management of Potato Late Blight Using Computer Simulation and Field Validation. *Phytopathology*, 105(12), 1545–1554.
<https://doi.org/10.1094/phyto-05-15-0117-r>

Song, J., Bradeen, J. M., Naess, S. K., Raasch, J. A., Wielgus, S. M., Haberlach, G. T., Liu, J., Kuang, H., Austin-Phillips, S., Buell, C. R., Helgeson, J. P., & Jiang, J. (2003). Gene *RB* cloned from *Solanum bulbocastanum* confers broad spectrum resistance to potato late blight. *Proceedings of the National Academy of Sciences*, 100(16), 9128–9133.
<https://doi.org/10.1073/pnas.1533501100>

Song, J., Win, J., Tian, M., Schornack, S., Kaschani, F., Ilyas, M., van der Hoorn, R. A. L., & Kamoun, S. (2009). Apoplastic effectors secreted by two unrelated eukaryotic plant pathogens target the tomato defense protease *Rcr3*. *Proceedings of the National Academy of Sciences*, 106(5), 1654–1659.
<https://doi.org/10.1073/pnas.0809201106>

Srisawad, N., Petchaboon, K., Sraphet, S., Tappiban, P., & Triwitayakorn, K. (2023). Possible Reasons Affecting Different *Phytophthora infestans* Populations in Tomato and Potato Isolates in Thailand. *Diversity*, 15(11), 1121.
<https://doi.org/10.3390/d15111121>

Stein, J. M., & Kirk, W. W. (2004). The Generation and Quantification of Resistance to Dimethomorph in *Phytophthora infestans*. *Plant Disease*, 88(9), 930–934. <https://doi.org/10.1094/pdis.2004.88.9.930>

Stellingwerf, J. S., Phelan, S., Doohan, F. M., Ortiz, V., Griffin, D., Bourke, A., Hutten, R. C. B., Cooke, D. E. L., Kildea, S., & Mullins, E. (2018). Evidence for selection pressure from resistant potato genotypes but not from fungicide application within a clonal *Phytophthora infestans* population. *Plant Pathology*, 67(7), 1528–1538.
<https://doi.org/10.1111/ppa.12852>

Stephan, D., Schmitt, A., Carvalho, S. M., Seddon, B., & Koch, E. (2005). Evaluation of biocontrol preparations and plant extracts for the control of *Phytophthora infestans* on potato leaves. *European Journal of Plant Pathology*, 112(3), 235–246. <https://doi.org/10.1007/s10658-005-2083-1>

Sun, H., Song, X., Guo, W., Guo, M., Mao, Y., Yang, G., Feng, H., Zhang, J., Feng, Z., Wang, J., Ma, Y., Zheng, C., Li, P., & Pan, D. (2023). Potato late blight severity monitoring based on the relief-mRmR algorithm with dual-drone cooperation. *Computers and Electronics in Agriculture*, 215, 108438.
<https://doi.org/10.1016/j.compag.2023.108438>

Sun, K., Wolters, A.-M. A., Vossen, J. H., Rouwet, M. E., Loonen, A. E. H. M., Jacobsen, E., Visser, R. G. F., & Bai, Y. (2016). Silencing of six susceptibility genes results in potato late blight resistance. *Transgenic Research*, 25(5), 731–742.
<https://doi.org/10.1007/s11248-016-9964-2>

Szajko, K., Plich, J., Przetakiewicz, J., Sołtys-Kalina, D., & Marczewski, W. (2020). Comparative proteomic analysis of resistant and susceptible potato cultivars during *Synchytrium endobioticum* infestation. *Planta*, 251(1).
<https://doi.org/10.1007/s00425-019-03306-z>

Takken, F. L., & Goverse, A. (2012). How to build a pathogen detector: structural basis of NB-LRR function. *Current Opinion in Plant Biology*, 15(4), 375–384. <https://doi.org/10.1016/j.pbi.2012.05.001>

The relation between the weather conditions and the occurrence of Potato blight (*Phytophthora infestans*). (1926). *Tijdschrift Over Plantenziekten*, 32(5), 139–140. <https://doi.org/10.1007/bf02812974>

Tiwari, J. K., Rawat, S., Luthra, S. K., Zinta, R., Sahu, S., Varshney, S., Kumar, V., Dalamu, D., Mandadi, N., Kumar, M., Chakrabarti, S. K., Rao, A. R., & Rai, A. (2021). Genome sequence analysis provides insights on genomic variation and late blight resistance genes in potato somatic hybrid (parents and progeny). *Molecular Biology Reports*, 48(1), 623–635. <https://doi.org/10.1007/s11033-020-06106-x>

Tsedaley, B. (2014). Late blight of potato (*Phytophthora infestans*) biology, economic importance and its management approaches. *Journal of Biology, Agriculture and Healthcare*, 4(25), 215–225.

Tuomenvirta, H. (2004). *Reliable estimation of climatic variations in Finland*.

Tuomenvirta, H., Alexandersson, H., Drebs, A., Frich, P., & Nordli, P. O. (2000). Trends in Nordic and Arctic Temperature Extremes and Ranges. *Journal of Climate*, 13(5), 977–990.
[https://doi.org/10.1175/1520-0442\(2000\)013<0977:tinaat>2.0.co;2](https://doi.org/10.1175/1520-0442(2000)013<0977:tinaat>2.0.co;2)

Van den Ackerveken, G. (2017). Seeing is believing: imaging the delivery of pathogen effectors during plant infection. *New Phytologist*, 216(1), 8–10. <https://doi.org/10.1111/nph.14755>

van der Hoorn, R. A. L., & Kamoun, S. (2008). From Guard to Decoy: A New Model for Perception of Plant Pathogen Effectors. *The Plant Cell*, 20(8), 2009–2017. <https://doi.org/10.1105/tpc.108.060194>

van der Lee, T., Robold, A., Testa, A., van't Klooster, J. W., & Govers, F. (2001). Mapping of Avirulence Genes in *Phytophthora infestans* With Amplified Fragment Length Polymorphism Markers Selected by Bulked Segregant Analysis. *Genetics*, 157(3), 949–956. <https://doi.org/10.1093/genetics/157.3.949>

van der Vossen, E. A. G., Gros, J., Sikkema, A., Muskens, M., Wouters, D., Wolters, P., Pereira, A., & Allefs, S. (2005). The *Rpi-blb2* gene from *Solanum bulbocastanum* is an *Mi-1* gene homolog conferring broad-spectrum late blight resistance in potato. *The Plant Journal*, 44(2), 208–222.
<https://doi.org/10.1111/j.1365-313x.2005.02527.x>

van Poppel, P. M. J. A., Guo, J., van de Vondervoort, P. J. I., Jung, M. W. M., Birch, P. R. J., Whisson, S. C., & Govers, F. (2008). The *Phytophthora infestans* Avirulence Gene *Avr4* Encodes an RXLR-dEER Effector. *Molecular Plant-Microbe Interactions*®, 21(11), 1460–1470.
<https://doi.org/10.1094/mpmi-21-11-1460>

Verzaux, E. (2010). *Resistance and susceptibility to late blight in Solanum: gene mapping, cloning and stacking*.

Verzaux, E., van Arkel, G., Vleeshouwers, V. G. A. A., van der Vossen, E. A. G., Niks, R. E., Jacobsen, E., Vossen, J., & Visser, R. G. F. (2012). High-Resolution Mapping of Two Broad-Spectrum Late Blight Resistance Genes from Two Wild Species of the *Solanum circaeifolium* Group. *Potato Research*, 55(2), 109–123.
<https://doi.org/10.1007/s11540-012-9213-x>

Villamón, F. G., Spooner, D. M., Orrillo, M., Mihovilovich, E., Pérez, W., & Bonierbale, M. (2005). Late blight resistance linkages in a novel cross of the wild potato species *Solanum paucisectum* (series *Piurana*). *Theoretical and Applied Genetics*, 111(6), 1201–1214.
<https://doi.org/10.1007/s00122-005-0053-9>

Vossen, J. H., van Arkel, G., Bergervoet, M., Jo, K.-R., Jacobsen, E., & Visser, R. G. F. (2016). The *Solanum demissum* R8 late blight resistance gene is an *Sw-5* homologue that has been deployed worldwide in late blight resistant varieties. *Theoretical and Applied Genetics*, 129(9), 1785–1796.
<https://doi.org/10.1007/s00122-016-2740-0>

Wang, M., Allefs, S., van den Berg, R. G., Vleeshouwers, V. G. A. A., van der Vossen, E. A. G., & Vosman, B. (2008). Allele mining in *Solanum*: conserved homologues of *Rpi-blb1* are identified in *Solanum stoloniferum*. *Theoretical and Applied Genetics*, 116(7), 933–943.
<https://doi.org/10.1007/s00122-008-0725-3>

Wang, S., Boevink, P. C., Welsh, L., Zhang, R., Whisson, S. C., & Birch, P. R. J. (2017). Delivery of cytoplasmic and apoplastic effectors from *Phytophthora infestans* haustoria by distinct secretion pathways. *New Phytologist*, 216(1), 205–215. <https://doi.org/10.1111/nph.14696>

Wang, X., Zheng, K., Cheng, W., Li, J., Liang, X., Shen, J., Dou, D., Yin, M., & Yan, S. (2021). Field application of star polymer-delivered chitosan to amplify plant defense against potato late blight. *Chemical Engineering Journal*, 417, 129327.
<https://doi.org/10.1016/j.cej.2021.129327>

Wang, Z., Qiao, X., Wang, Y., Yu, H., & Mu, C. (2024). IoT-based system of prevention and control for crop diseases and insect pests. *Frontiers in Plant Science*, 15. <https://doi.org/10.3389/fpls.2024.1323074>

Witek, K., Lin, X., Karki, H. S., Jupe, F., Witek, A. I., Steuernagel, B., Stam, R., van Oosterhout, C., Fairhead, S., Heal, R., Cocker, J. M., Bhanvadia, S., Barrett, W., Wu, C.-H., Adachi, H., Song, T., Kamoun, S., Vleeshouwers, V. G. A. A., Tomlinson, L., ... Jones, J. D. G. (2021). A complex resistance locus in *Solanum americanum* recognizes a conserved *Phytophthora* effector. *Nature Plants*, 7(2), 198–208.
<https://doi.org/10.1038/s41477-021-00854-9>

Yoshida, K., Schuenemann, V. J., Cano, L. M., Pais, M., Mishra, B., Sharma, R., Lanz, C., Martin, F. N., Kamoun, S., Krause, J., Thines, M., Weigel, D., & Burbano, H. A. (2013). The rise and fall of the *Phytophthora infestans* lineage that triggered the Irish potato famine. *ELife*, 2.
<https://doi.org/10.7554/elife.00731>

Zaidi, S. S.-A., Mukhtar, M. S., & Mansoor, S. (2018). Genome Editing: Targeting Susceptibility Genes for Plant Disease Resistance. *Trends in Biotechnology*, 36(9), 898–906.
<https://doi.org/10.1016/j.tibtech.2018.04.005>

Zhang, X. J., Song, W. R., Chen, H., Qian, Z. H., Zeng, J., & Dong, S. M. (2021). Status and prospects of chemical prevention and control of potato late blight. *China Plant Prot*, 41, 33–39.

Zhao, J.-H., Zhang, T., Liu, Q.-Y., & Guo, H.-S. (2021). Trans-kingdom RNAs and their fates in recipient cells: advances, utilization, and perspectives. *Plant Communications*, 2(2), 100167. <https://doi.org/10.1016/j.xplc.2021.100167>

Zipfel, C. (2014). Plant pattern-recognition receptors. *Trends in Immunology*, 35(7), 345–351. <https://doi.org/10.1016/j.it.2014.05.004>