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Review: Holistic pest management against early blight disease towards sustainable agriculture

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Abstract

Alternaria species are well-known aggressive pathogens that are widespread globally and warmer temperatures caused by climate change might increase their abundance more drastically. Early blight (EB) disease, caused mainly by *Alternaria solani*, and brown spot, caused by *Alternaria alternata*, are major concerns in potato, tomato and eggplant production. The development of EB is strongly linked to varieties, crop development stages, environmental factors, cultivation and field management. Several forecasting models for pesticide application to control EB were created in the last century and more recent scientific advances have included modern breeding technology to detect resistant genes and precision agriculture with hyperspectral sensors to pinpoint damage locations on plants. This paper presents an overview of the EB disease and provides an evaluation of recent scientific advances to control the disease. First of all, we describe the outline of this disease, encompassing biological cycles of the *Alternaria* genus, favorite climate and soil conditions as well as resistant plant species. Second, versatile management practices to minimize the effect of this pathogen at field level are discussed, covering their limitations and pitfalls. A better understanding of the underlying factors of this disease and the potential of novel research can contribute to implementing integrated pest management systems for an ecofriendly farming system.

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1 INTRODUCTION

Early blight (EB), caused by Alternaria species, is one of the major diseases in the production of tomato (Solanum lycopersicum), potato (Solanum tuberosum) and other plants, and is most prevalent on unfertilized or otherwise stressed plants. Infection by this polycyclic disease led to production losses of 35-78% in tomato and 5–40% in potato, respectively.¹ In North America, the annual cost for fungicide application is estimated to be \$21.4 to \$44.8 million.² Alternaria species are among the few pathogens that can sporulate when exposed to several short-wet periods alternating with dry periods.³ Phytotoxic metabolites are produced such as alternariol, altersolano, altertoix, macrosporin and solanpyrone.⁴⁻⁶ 6 Dark brown to black lesions with concentric rings in the senescing leaves of potato and tomato are common symptoms, and others are stem lesions and fruit rots. Alternaria species are abundant in agricultural soils globally⁷ and it is considered to be one of the most aggressive soil-borne pathogens in the world.⁸ Furthermore, increasing attention has been paid to these species nowadays since warmer temperatures due to climate change can favour an increase in their hotspots over the world.⁸ Alternaria species cause not only plant disease but also exhibit harmful effects on human and animal health. More than 70 toxins produced by the mycotoxin of *Alternaria* are found in a wide range of food and animal feed products in many countries.

The genus Alternaria is divided into 24 sections based on molecular and morphological traits.⁹ While A. solani is the most recognized causative agent of EB, other species, including A. alternata, A. arborescens and, A. porri, are also found on leaflets with symptoms of early blight in potato¹⁰ as well as A. linariae and A. grandis in tomato.^{11–13} A. solani is equally aggressive on both crops, while A. tomatophila is highly aggressive to tomato but

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2 HOST-PATHOGEN-ENVIRONMENT INTERACTION

The disease triangle is a bedrock illustrating the factors involved in the emergences and severity of plant disease. The triangle consists of (i) a susceptible host, (ii) a favourable environment for the development of the disease and (iii) a virulent pathogen (Fig. 1). A better understanding of each component allows us to set up more practical strategies for pest management. What environmental factors favour spore germination and dispersion of EB? What kind of underlying factors in the plant can induce resistance? How can the population of pathogens be decreased? Breaking down the complexity of the plant pathogen in nature by using the triangle method enables us to answer these questions.

2.1 Biological cycle and climate factors

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The optimum temperature for EB epidemics is in the range of 20–30 °C.¹⁸ As few as 3 hours of continuous leaf wetness between 21 and 25 °C is sufficient for EB lesion formation¹⁹ and at 24 \pm 2 ° C, the infection appears within 4–6 h of leaf wetness.²⁰ There is variability with different geographic regions, with an optimal temperature in temperate regions of 22–28 °C, while the most conidia production under tropical conditions occurs at 29–35 °C.²¹ Radiation affects the germination of the spores. The light range

between 300 and 500 nm appeared to be responsible for inhibition in germination meanwhile wavelengths above 750 nm do not postpone germination.²² The conidiophores are formed under high humidity and light, whereas conidial formation is favoured by alternate high and low humidity in the dark. Conidia disperse from the soil surface and fall on leaves and infect them. The primary factors for disseminating conidia are rain, wind and insects.^{19,21} Relative humidity (RH) is also a crucial parameter for the biological cycle of *Alternaria* species. At high humidity on leaf surfaces, especially after dew, conidial initiation occurs. A duration of 4–6 hours of leaf wetness after inoculation with conidia is sufficient to ensure the onset of EB.²⁰ The link between lower temperature and higher RH during the night is favourable for the development of sporulation¹⁸; the new spores are released during the day when the temperature increases.

An interrupted wet period (IWP) plays an essential role in the biological cycle of *A. solani* and *A. alternata*. Unlike other fungi, germinating spores of these fungi can survive dry conditions and after rewetting of the leaf the germination process recommences. *A. solani* can produce seven times more conidia under IWP than during a continuous wetting period of the same duration.²³ This unique characteristic enables it to adapt to different regions such as the northwest of Spain, where alteration in air humidity occurs frequently.

2.2 Dispersal pattern

Compared to *P. infestans*, the dispersal range of *Alternaria solani* is limited to within the proximity of the field, whilst dispersal distances of hundreds of metres or kilometres is the case for *P. infestans*.²⁴ The reduction in the spore density of *A. solani* starts at a distance of 400 m and from 600 m further away the initial population of EB at crop emergence is negligible.²⁵ *A. alternata* achieves longer dispersal distances than *A. solani*, showing seven times higher aerial conidial concentration than *A. solani*, probably due to the smaller spores.²⁶ New infections of *A. alternata* in a field probably come from locations surrounding the field, whereas the localized canopy of host plants within a field is the primary source of *A. solani* conidia.

The unique characteristic of this pathogen is that when RH and wet leaf surface are high, along with prolonged leaf wetness (>12 h) and lower wind speed, the spore dispersion is diminished.²⁷ By contrast, when wind speed is high, together with less wet leaf surface, spore catches increase.²¹ In another report,²⁸ a

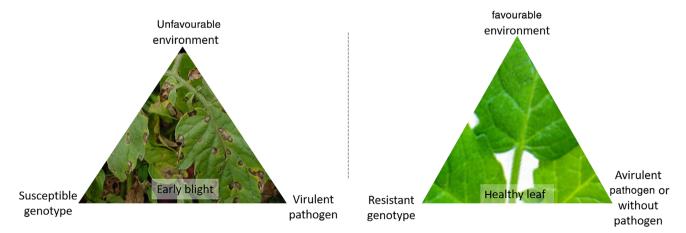


Figure 1. Two contrasting cases of disease triangles illustrating host genotypes, pests and environments for pest management against early blight.

strong correlation was found between dispersal and conditions favourable for sporulation in *Alternaria* spp. The spores of *Alternaria* spp. belong to aeroallergens and a daily average of the spore concentration (100 m⁻³) has been widely accepted in aerobiological research as a relevant threshold for respiratory allergy risk.²⁹

Pathogen-induced foliar damage at the early bulking stages of potato results in more significant yield loss than during potato tuber maturation and late bulking. The importance of fungicide disease management at early bulking growth stage is highlighted in the meta-analysis work after gathering data from 23 trials.³⁰ The impact of EB severity at early bulking on relative yield loss was 32% in comparison with that at tuber maturation-late bulking, which was 19% of relative yield loss. There is another report on a crop loss model by this disease using yield loss as a function of disease severity.³¹

2.3 Susceptibility to EB infection and protection mechanism of wild genotypes

The epidemic development of EB varies mostly depending on the type of plant cultivar.^{5,6} Ideally, the later the maturity time, the less susceptible the cultivar is to Alternaria infection.³² This is related to the fact that early maturity cultivars have a trait of determinate growth and have no ability to sprout new foliage continuously, consequently retaining older and senesced foliage on the plant, which is where lesions of EB start to appear. By contrast, the delayed fruit initiation occurs in late-maturing varieties, and relatively young leaves grow continuously during the cropping season.⁵ The older or senesced foliage is a hotspot of EB. Incidence of EB is closely related to the nutrient contents in plant tissue and sugar; alkaloid contents and phenols are the primary chemical compounds that trigger the infection.⁵ A plant enriched with glucose could inhibit the production of cell-wall-degrading enzymes by A. solani.^{33–35} By contrast, alkaloids, which play an essential role as antimicrobial and antifeedant compounds,³⁶ have been found in laboratory assays to prevent the growth of A. solani in potato leaves. Phenols are involved as secondary metabolite compounds for the plant protection system. Plants resistant against EB have reportedly contained a high content of phenols along with the activities of defence-related enzymes including phenylalanine ammonia-lyase (PAL) peroxidase, chitinase and polyphenoxidase, which increase strength to the host cell wall, resulting in the inhibition of pathogen invasion.^{37–39}

Wild genotypes of potato and tomato in the *Solanum* genus, originally from South America, are a beneficial resource of germplasm resistance to EB disease.^{40–42} The genotypes that belong to *S. habrochaites* and *S. arcanum* were found to be moderately or highly resistant to EB.^{5,43} The resistant wild-type cultivars strongly activate several pathways of plant response, including glycol-alkaloid, flavonoid and lignin biosynthesis by up-regulating gene expressions.⁴⁴ However, some others have a wide range of variations in the magnitude of resistance, including *S. arcanum*, *S. peruvianum*, *S. neorickii*, *S. chilense* and *S. habrochaites*. This heterogeneity within the same genotype could be related to local adaptations to EB.⁴⁵

2.4 Molecular research

The species *S. lycopersicum* is susceptible to numerous diseases. However, many resistance genes have already been identified in genotypes of wild or domesticated species and crossed into commercial genotypes. It is estimated that most cultivars have resistance to a minimum of six diseases in the case of pure lines and up to 10 diseases in hybrids.⁴⁶ A classic example of durable resistance is to the fungus *Verticillium* (Ve). The approach of using a Veresistant locus was introduced more than 60 years ago in commercial cultivars and is present in many tomato cultivars on the market.⁴⁷ Using this technique, research has been developed for more stable and efficient resistance to EB in tomatoes and potatoes.⁶

Susceptibility genes can also affect the degree of resistance against EB disease in addition to resistance genes.⁴⁸ The resistance to EB can be achieved by regulating the expression of susceptibility genes in plants using the method of silencing genes.⁴⁹ The sequencing and resequencing associated with transcriptomics and metabolomics may enable the identification of genes responsible for the most efficient and long-lasting resistance to EB. In addition, the method of DNA editing techniques (CRISPR/CAS9) is a clear-cut approach to create commercial and highly resistant genetic material, and the use of CRISPR/CAS9 for resistance to *A. alternata* has recently been published.^{50–52}

Quantitative trait loci (QTLs) and marker-assisted selection can facilitate the identification and characterization of resistant/susceptible genes, and this technique enables the transfer of the resistant genes to commercial varieties more quickly and efficiently. Some wild species that can be crossed with S. lycopersicon have QTLs associated with resistance to EB.^{53,54} By contrast, the classical breeding method requires more time and has some constraints, such as dependency on the donor parent of the resistance gene, that may require the use of a third genotype for transferring the gene of interest. Some species have fruit characteristics that are very different from commercial tomatoes and potatoes. Some wild species are self-incompatible as S. arcanum,⁵⁵ which remains with green color at maturity stage, not producing lycopene or being highly pubescent like S. habrochaites.^{56,57} Thus, methods such as marker-assisted selection can accelerate the development of new cultivars resistant to Alternaria spp. Using QTL technologies, more than 30 resistance cultivars with EB resistance genes in tomatoes were found.⁶ Other approaches for Alternaria species such as next-generation sequencing technologies⁵⁸ and the semi-nested PCR-based method⁵⁹ are also attractive tools.

Metabolomics technology is an emerging tool used extensively in the pathogenic research field to identify toxic compounds in host plant cells induced by microorganisms. Metabolomic research related to *A. alternata* showed that chlorogenic acid is a metabolic acid with higher quantity in the resistant genotype compared to the susceptible. Chlorogenic acid was inoculated into *in vitro* cultures of *A. alternata* and the contents of alternariol, alternariol monomethyl ether and tenuazonic acid were analyzed. At 4 days after inoculation, chlorogenic acid almost wholly inhibited the synthesis of mycotoxins due to the presence of alternariol. A direct effect of chlorogenic acid on these mycotoxins could help to explain the mechanism of fungus infection.⁶⁰

As the disease is greatly influenced by environmental conditions, it is believed that more comprehensive research associating resistance to EB with concomitant resistance to abiotic factors is desirable.

2.5 Soil

Soil is an essential biosphere for the development of EB in the biological cycle. In general, infected plant debris on the soil surface carries over the disease to the following season, mainly when the soil is dry. Hence, soil moisture and temperature are crucial components of survival. *A. solani* can overwinter with/without a host in the range of -3.3 to 21.2 °C. This fungus can survive in soil from the previous cropping season over 8 months, but not 16 months. Under these circumstances, crop rotation is recommended. An optimal interval for the rotation is 2 years for potato,^{61,62} while 3- to 5-year crop rotation is recommended for tomato.⁵ The underlying reasons for the difference in the duration was not found in the literature.

Plants exposed to nutrient starvation are more susceptible to infection. Nitrogen is vital for EB resistance, and several previous works highlight the importance of nitrogen supply. It is reported⁶³ that nitrogen content and the area under the disease progress curve (AUDPC) have a significant correlation with potato starch yield. By contrast, a potato plant with lower nitrogen has more chance of becoming infected by A. solani. High nitrogen content in plant tissues may prolong vegetative growth and delay ripening, which results in less vulnerability to EB infection. Nitrogen input directly affects healthy leaf area duration and absorption of the radiation, but does not affect the resistance against EB once it appears, implying that adequate application at the right time needs to be implemented.⁶⁴ It is also recommended to apply the nitrogen fertilizer at two or three different timings rather than make a one-time application as this allows an increase in potato yield.63-65 However, the yield would be reduced if application was split more than four times because the limited nitrogen supply at each application is the defining factor rather than the appropriate timings.66

Unlike nitrogen, phosphorous and potassium are not considered as essential factors for EB infection. By contrast, several micronutrients such as boron and zinc are important for plant resilience against *Alternaria* species given that deficiencies of these nutrients create leaky and unstable cell membranes in plants, releasing a massive number of organic compounds from cells, which could be a suitable food source for *Alternaria* species.⁶⁷ In particular, the importance of zinc for plant protection against EB is highlighted in several scientific reports: zinc intervenes with the synthesis of activating metabolic reactions, production of chlorophyll and carbohydrate, and the synthesis of tryptophan, which converts later to auxin. The content of organic carbon in the soil does not affect EB infection.⁶⁸

Soil texture is essential for control of fungi infection. After heavy rainy days, necrotic EB lesions appear, especially in sandy soils,³¹ and this tendency is also confirmed in the case of Belgium potato regions after 2-year trials.⁶⁹ An underlying factor of this result could be nutrient deficiency. The interlink between rotation duration and soil texture should be highlighted as shorter rotation occurs in a sandy region, in contrast to clay soil, which gives potatoes more chance to become infected by EB. There is a report on increased susceptibility of crops grown in sandy soils under plantparasitic nematode attack of about 200 infective juveniles of a root-knot nematode, Meloidogyne incognita, per plant, which eventually caused severe damage in plant growth and chlorophyll content.⁷⁰ In general, except for the stem nematode Ditylenchus dipsaci, the nematode population is higher in coarse-textured soil such as sandy soil compared with clay soil, and this might partly affect EB depending on the crop host suitability and nematode densities at planting.^{64,71}

There is an interaction between *Alternaria* species and other microorganisms. *Burkholderia* bacteria have a co-habitant relationship with *A. alternata* under nutrient-limited conditions, using multiple substrates provided by the fungi which attenuated the starvation response observed when these bacteria are grown alone.⁷² Concomitantly, this symbiotic mechanism can also limit

the phytopathogenic activity of *Alternaria* species,^{72,73} meaning that *Burkholderia* can play a role as a biological agent of *Alternaria* species.^{49,74} Rhizobacteria in the soil are known as a pathogen control. However, 59% of rhizobacteria failed to enhance resistance against EB.⁷⁵ Concerning the interaction of *A. solani* with other fungi groups, it is reported that *Arsenicum album*, *Nitricum acidum* and *Staphysagaria* can inhibit the mycelium growth of *A. solani* under *in vivo* conditions.⁷⁶ A reduction in soil extracellular and intracellular enzymes (e.g. dehydrogenase, phosphatase, β -glucosidase and urease) is observed in fungus-infected soil, implying that pathogens probably change the redox activity of plants by nutrient leaching, resulting in altered soil enzyme activity.⁷⁷

2.6 Functions of existing forecast models and the limitations of model usages

Decision support systems (DSS) for proper pest management with fungicides to minimize the damage from EB infection have been developed for over 40 years. Several simulation models were implemented in the 1970 and 1980s, and the most recognized ones are FAST (Forecasting *Alternaria Solani* on Tomatoes), TOM-CAST (Tomato Disease Forecast) and EPIDEM (*Alternaria solani* on tomatoes and potatoes). To modify and update, other derivate models have been created as decision support^{78–80} (e.g. CU-FAST, PA-FAST, NJ-TOM-CAST, WISDOM and Plant-Plus).

2.6.1 FAST model

The FAST DSS, known as a long-run product, was created for forecasting EB in tomato and then adjusted to potato field conditions.⁸¹ It comprises two empirical submodels to determine periods when environmental conditions are favourable for EB disease development.^{82,83} One submodel includes leaf wetting time and mean air temperature, and the second submodel contains the daily severity-rating (R), estimated by three environmental parameters: (i) mean air temperature for the past 5 days, (ii) hours of RH higher than 90% for the past 5 days and (iii) total rainfall for the past 7 days. This model enables the following three indicators to be forecast: (i) total of all severity disease values (TS) since the initial stage of the growing season, (ii) 7-day cumulative severity value (CS) and (iii) 5-day cumulative rating value (CR), calculated by totalling R values for the past 5 days. Based on the two threshold options of CS and CR values, this support model has successfully reduced the application frequency while the blight severity remained at the same magnitude with the commercial schedule.^{19,84}

2.6.2 TOM-CAST model

TOM-CAST is another long-run DSS which has a much simpler approach to facilitate implementation than the FAST model. Using a small component of the FAST model (hourly leaf wetness and temperature), disease severity values (DSVs) are determined.⁸² The value range of the DSVs^{15–20} defines the pest control schedule. Subsequent treatment is conducted with a pesticide, originally arranged with *chlorothalonil*. Other work⁸¹ demonstrated the performance of TOM-CAST for six other fungicides comparing with a weekly schedule, highlighting the marketable yield with this model. The limitation of TOM-CAST is the fact that it is not a maturity-based model; no variable related to plant growth is included. Tuning DSVs to adjust to local conditions and varieties is challenging, requiring data from trials done over several years to find the optimal DSV values.⁸⁵ To improve this model, a new model, the modified-TOMCAST model, was created by complementing the DSS with a crop maturity module.^{86,87} This updated model is useful to adjust the variability of different varieties in crop growth until maturation by changing the thresholds of the model at different crop stages. However, it should be highlighted that there exist some limitations of using these models. For instance, the IWP is not taken into consideration as a component of the model.^{23,27} Also, rigorous calibration and validation of temperature intervals are required for different cropping conditions, such as semi-arid and irrigated systems.

2.6.3 Pitfalls of forecast model application

The pitfall of using these models with fungicides is the ability of microorganisms to avoid sensitivity to the chemicals. Indeed, many different types of fungicides are used for EB, including (i) maneb, mancozeb, difenoconazole, boscalid, fluopyram, boscalid, fluopyram and chlorothalonil in the EU,¹⁵ (ii) boscalid and fluopyram in North America,^{88,89} and (iii) difenoconazole and ethylhydrogen-phosphate in Asia.⁹⁰ However, the high genetic diversity of A. solani enables it to adapt to fungicides and shift the population towards more resistant isolates.^{15,91-94} Fungicide resistance against quinone outside inhibitor (QoI) was described first in the USA^{92,93} and a decade later in Germany,⁹⁵ while resistance against succinate dehydrogenase inhibitors (SDHIs) was found in Idaho. Among 39 strains of A. solani collected in 2009, only three strains were resistant to SDHIs and all to azoxystrobin. A year later, 57% of the isolates were resistant to boscalid.⁹⁶ In a survey in the USA in 2010 and 2011, approximately, 80% of all A. solani assayed were found to have some level of resistance to boscalid, with about 5% and 75% of the population moderately resistant (to concentrations of 5–20 μ g mL⁻¹) and highly resistant $(>20 \ \mu g \ mL^{-1})$ to the fungicide. Nearly 99% of all boscalidresistant isolates possessed the F129L mutation in the cytrochrome b gene, responsible for QoI resistance, indicating that an

A. solani population with dual fungicide resistance predominates in the states surveyed.⁹⁴ In Belgium, 83 *A. solani* and 53 *A. alternata* isolates were collected during 2014 and 2015 to assess the prevalence of SDHI mutants. The isolates were screened for the presence of amino acid substitutions in the different subunits of the succinate dehydrogenase gene (*SdhB, SdhC* and *SdhD*). The isolate screening revealed that mutations causing a reduced sensitivity towards SDHIs were widespread in the Belgian *Alternaria* population: 70% of the *A. solani* and 41% of the *A. alternata* isolates possessed one or more mutations.⁹⁷

3 PRACTICAL STRATEGIES

The durability of host resistance is affected by the evolutionary potential of the pathogen and the inoculum pressure. The resistance genes in the plant coevolve with those of the pathogen's virulence, implying that consecutive cultivation of the same cultivars is not appropriate. The importance of proper pest management has to be considered for (i) minimization of the disease on crop leaves, (ii) decrease of potential inoculum in the field and its product, including mycotoxins, and (iii) avoiding the fate of breaking genetic resistance. Elimination of weeds as such as S. nigrum and S. carolinense, considered potential inoculum sources of Alternaria spp., can reduce the risk of sporulation.⁴⁶ In addition, elimination of senescent leaves, apical pruning and vertical support favour radiation in the canopy and increase ventilation, which reduces water film on the leaf blade and eliminates contaminated debris and senescent leaves with greater susceptibility to the pathogen.

IPM is a holistic approach for sustainable agriculture. It relies on the type of cropping system, geography and development stage of plants, which are discussed in subsequent sections. It is reported⁶ that EB can be controlled by three measures: fungicide treatment, use of resistant cultivars and cultural practices. The first

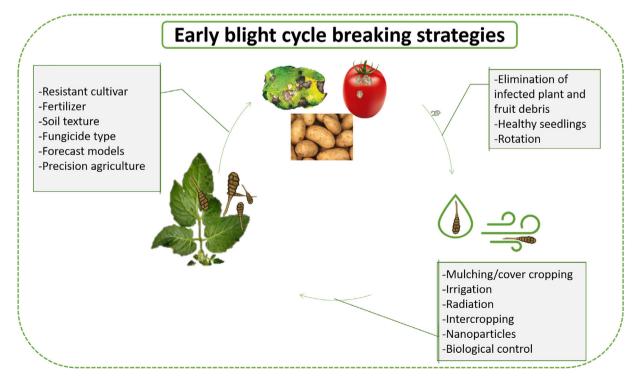


Figure 2. Different practices of pest management against early blight disease.



two measures are described above; in this section, the feasible practices for IPM are addressed (Fig. 2). The following agronomic practices can minimize or prevent possible damage caused by EB.

3.1 Rotation

First and foremost, crop rotation is an essential practice to minimize the possibility of the onset of EB infection, given that continuous potato production in the same field over 2–3 years is risky.⁹⁸ Two years without potatoes is the minimum interval to delay the onset of EB in the potato field.⁹⁹ Rotation is an efficient practice not only for reducing pests and diseases but also for balancing soil nutrients, thus effectively improving the physical and chemical properties of soil and regulating soil fertility. However, there exist a couple of pitfalls in the practice: (i) the production schedule needs to be changed every year to increase land utilization and (ii) there is a possible reduction in economic return over several years due to less potato production, which is valuable as a cash crop for farmers.

3.2 Intercropping

The inhibition of the conidial movement of fungi results from the fact that the intercrop provides a physical barrier and microclimate modification to reduce conidial germination and development. Marigold is a recognized plant for the protection against *Pratylenchus penetrans* and a lower population of this nematode affects crop resistance to infection by pathogens such as *A. solani*.¹⁰⁰ Olfactory species [e.g. marigold (*Calendula officinalis*) and onion (*Allium cepa*)] are thought to be used for intercropping due to an antimicrobial allelopathy effect. However, intercropping will increase the difficulty of mechanical harvesting. In addition, the morphological characteristics and fertilizer requirements of intercropping crops and the cropping growth period needed to be taken into account.

3.3 Mulching and cover cropping

Mulching and cover cropping are also useful practices for reduction in EB infection.^{101,102} Disease incidence of foliar and fruit rot pathogens can be reduced by creating a physical barrier to keep fruit from coming into direct contact with soil and disrupting the rain splash distribution of inoculum of soil-borne fruit. Another hypothesis of reduction in splash dispersal is believed to be that (i) sensor wetness duration of the crop is reduced by mulch and (ii) soil particle dispersal is reduced. Moreover, mulching with plastic material is also effective for the prevention of soil evapotranspiration.¹⁹ Disadvantages of plastic mulching are cost and the need to use ecofriendly plastic.

3.4 Ultraviolet radiation

Blocking ultraviolet (UV) radiation by mesh or plant cover can retard the development of EB infection. Sporulation is affected by radiation exposure since the conidiophores are formed under high humidity and light.¹⁰³ It is worth mentioning that the UV blocking method can delay not only disease progression of EB but also other diseases caused by other pathogenic microorganisms.¹⁰⁴

3.5 Irrigation

The water regime is interlinked with EB germination. It is reported that sprinkler irrigation systems reduce disease incidence compared with furrow application, which creates excessive water condition in the field.^{105,106} The change in microclimate conditions by

irrigation reduces the incidence of this disease more in comparison with rainfed water systems. $^{98}\,$

3.6 Nanoparticles

Application of nanoparticles is an attractive tool to enhance plant protection against EB.^{107–110} Selenium, copper, silica and silver are the candidates for this method, which increases the antioxidant enzymes in plant tissues. Other work⁷⁷ has demonstrated the impact of biosynthesized silver nanoparticles in reducing EB and increasing plant growth as well as photosynthesis. Finding an optimal dose of a nanoparticle is a crucial point for implementation.

3.7 Plant growth promoting rhizobacteria, biological agents and mycorrhiza

An ecofriendly biological control is useful to minimize EB emergence. A versatile series of different antagonistic agents for control of *A. solani* and *A. alternata*, or plant growth promoting reagents (PGPRs), have been reported as biological agents of EB. *Streptomycetes* spp. are antagonists that reduce spore germination, mycelial growth and sporulation of EB.¹¹¹ Regarding the *Ascomycetes* group, *Trichoderma* species, such as *Trichoderma harzianum* and *Trichoderma viride*, are recognized PGPRs and biological agents against EB.^{112–115} Pretreatment of potato tubers with *Trichoderma* decreased the infection of new-crop tubers.¹¹⁵ It is presumed that *Trichoderma* has three strategies to enhance protection: (i) it is involved in the phytohormonal mechanisms of auxin and ethylene, (ii) it reduces gene expressions of some proteins involved in pyruvate kinase biosynthesis and (iii) it increases antioxidant enzymes in plant tissues.¹¹⁶

Additionally, rhizobacteria are a practicable microorganism group for protection against *A. solani*.^{75,111,116–122} *Bacillus* sp. show antifungal activity by releasing Indole-3-acetic acid (IAA) and lytic enzymes and triggers for plant protection mechanisms.^{120,123} The combined application of PGPRs (e.g. *Bacillus subtilis* and *Trichoderma*) can strengthen the plant defence system by inducing these plant hormones as well as enhancing antioxidant enzymes including peroxidase and polyphenol oxidase.^{116,124,125}

Mycorrhiza reduces susceptibility to *A. solani*.¹¹⁶ Plant hormone signalling pathways (e.g. the jasmonic and salicylic acid pathways) and enzymatic activities related to phenol compounds⁶³ are activated by mycorrhiza. Supplying phosphorous by mycorrhiza interaction is not essential for the enhancement of the protection system against EB.¹²⁶ Interestingly, mycorrhiza can mediate plant–plant communication between healthy plants and pathogen-infected tomato plants⁶³ with the induction of defence signals such as peroxidase, polyphenol oxidase, chitinase, β -1,3-glucanase, phenylalanine ammonia-lyase and lipoxygenase. Inoculation of a local biological agent against EB is a recommended approach. As an example, the inoculation of *Macrolepiota* sp., belonging to the Basidiomycete family, is useful not only for biological control against *A. solani* but also for the enhancement of plant growth.

3.8 Treatment with organic products or biostimulants

Using organic materials and biostimulants for plant protection is also reported for pest management against EB. Biopolymers of sodium alginate,¹²⁷ extract of seaweed,¹²⁸ the neem tree¹²⁹ and the artemisia tree¹³⁰ were tested to protect plants from infection by EB. Other biostimulants such as humic acid, chitosan and thiamine have also been examined.^{131,132} The induction of antifungal enzymes and regulation of gene expression for defence systems

involved with plant hormones are the underpinning factors for the reduction in the infection.¹²⁷

3.9 Precision agriculture

Precision agriculture is an emerging approach that enables farmers to improve accuracy and reduce costs by a pinpoint application of crop protection agents using technologies such as hyperspectral imaging by drones and robotics. These technologies might also help to identify nutrient and water stress in the potato plant, which affects susceptibility to EB. DSS can be useful for forecasting the date of exceeding control thresholds and fungicide application. Using mathematical models, the time requirement for the processing of the data analysis can be minimized. The model FAST, for instance, is a forecast system for A. solani on tomato. BSPcast is a model derived from FAST by adapting it to the aetiology and epidemiology of S. vesicarium on pear. The model TOM-CAST was also derived from FAST as a weather-timed fungicide spray forecast, and its potential to reduce spray applications has been tested. Many papers on the detection of EB by hyperspectral images have been published.¹³³⁻¹³⁷ The wavelengths of 715¹³³ and 750 nm,¹³³ which belong to the range of near-infrared, are the most discriminative range of the spectrum for disease classification. Different algorithms based on deeplearning and machine-learning are applied for image processing techniques, and the accuracy of the models for disease detection of EB and LB in tomato leaves varies between 76% and 98%.¹²³ To increase the accuracy, the following points should be considered: (i) larger dataset size, (ii) higher spatial resolution or a broader spectral range and (iii) more advanced image-processing techniques. Overall, precision agriculture is a promising and conducive approach to protecting the environment and reducing production costs while reducing the use of fungicides and fertilizers.

FUTURE APPROACH 4

Novel technologies and agronomical practices can mitigate the damage of EB by making tomato and potato production more sustainable. Due to the intertwined complexity of EB disease, the idea of using one specific approach as the 'silver bullet' solution should be avoided (e.g. application of biological control without knowing soil fertility or fungi gene editing without considering field practices). By contrast, a multidisciplinary approach across different scientific domains from laboratory to field experiments can help us to understand more about underlying factors and allow us to co-design IPM with other stakeholders (e.g. farmers, seed distributors, fungicide companies). Further investigation should be conducted to determine an economic assessment of combined applications.

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