Buckeye Rot of Tomato in India: Present Status, Challenges, and Future Research Perspectives

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Abstract

Tomato in India is commonly exposed to various diseases of fungal, bacterial, and viral origin, resulting in substantial yield losses ($\geq 50\%$). Buckeye rot (caused by *Phytophthora nicotianae* var. *parasitica*) is among the major constraints in the successful cultivation of tomato crops in various parts of the world, including the Solan district of Himachal Pradesh state, India. The fruit rot becomes more devastating under high humidity and wet soils. Symptoms generally appear on green fruit as alternate dark- and light-brown concentric rings. The genome size of *P. nicotianae* var. *parasitica* is 82 Mb with $>23,000$ predicted genes. High humidity ($>60\%$) and optimal temperatures (20 to 25°C), along with rainfall (≥ 10 mm), help to disperse the pathogen because the inoculum reaches the fruit through splashing rain. Sporangia germinate indirectly by producing zoospores at 20 to 25°C or directly via germ tubes

at $>25^{\circ}\text{C}$. In the absence of suitable resistant varieties, no single management practice is sufficient to keep the disease below the economic threshold level; therefore, integration of cultural and chemical methods is preferable. This article aims to focus on the etiology and management challenges of buckeye rot. We recommend innovative disease management strategies such as identification and deployment of resistant cultivars as well as spraying of synthetic chemical fungicides, biocontrol agents, and use of abiotic chemicals that induce resistance for developing sustainable crop production practices.

Keywords: abiotic resistance, buckeye rot, genome, *P. nicotianae* var. *parasitica*, tomato

Tomato (*Solanum lycopersicum* L.), a member of the family Solanaceae, is among the most important commercial vegetables worldwide because of its nutritive value and wide adaptability. It is one of the world's most consumed vegetable crops after potato (FAO 2021). It is grown in tropical, temperate, and subtropical agro-climatic regions. The global area under tomato cultivation is estimated at around 4.76 million ha with 182 million metric tons of production (FAO 2021). China (31%) and India (13%) are the major producers (Añibarro-Ortega et al. 2020). In India, tomato is grown on 8.09 million ha with an annual production of 19.7 million tons (Ashwathappa et al. 2020). The northwestern Himalayan region of India produces 0.50 million tons annually on 0.014 million ha in Himachal Pradesh state, where tomato is grown from April to October and fruiting coincides with the monsoon season (Fig. 1) (Idris et al. 2015).

Buckeye rot is caused by *Phytophthora nicotianae* var. *parasitica* (Dastur) G. M. Waterh. 1963 (van Breda de Haan 1896; Waterhouse 1963) and is regarded as one of the most devastating tomato diseases in certain regions (Sharma and Dohroo 2004). The disease results in up to 40% loss of fruit growing under open field cultivation. Under a tropical rainy climate, disease outbreaks reduce annual production by more than 30 to 50% (Ashwathappa et al. 2020; Sharma et al. 2009).

Brief history, current scenario, approaches, limitations, and conclusions of past reviews. Buckeye rot was first reported in 1915 from Florida (United States) from fields where crop loss was approximately 15% (Sherbakoff 1917). Bancroft (1910) previously reported the occurrence of a brown rot of tomato from England but, later, Sherbakoff (1917) clarified differences between buckeye and brown rot based on disease epidemiology and symptomatology. Wager (1935) reported buckeye rot from Eastern Transvaal (now Mpumalanga province of South Africa), where it caused heavy losses to green fruit (Sharma and Dohroo 2004). Since then, the disease has caused losses of $\geq 40\%$ in Denmark, Germany, China, Indiana, Sardinia, and Sweden.

In India, the occurrence of buckeye rot was first documented from the Chambaghat area of Solan district (1,200 to 1,550 m above sea level) (Jain et al. 1961), where $\geq 35\%$ loss of tomato had been observed. Since then, it has been reported in northern, northwestern, southern, and central parts of India at elevations of 500 to 1,700 m (Chowdappa et al. 2016; Dar et al. 2004; Shah 2009; Sohi 1978; Sokhi and Sohi 1982) (Fig. 2), resulting in yield losses between 30 and 70% (Chowdappa et al. 2016). Under favorable conditions for disease development, incidence in Indian tomato fields may climb to 90% (Bharat and Gupta 2011), and the annual economic loss of the country was estimated to be U.S.\$1,34,417.60 with the introduction of hybrid cultivation in 1995, where fruiting starts from the first internode and remains in proximity to the soil (Gupta et al. 2006; Kaur et al. 2019).

The infected fruit initially develop small, brown, water-soaked spots, which eventually increase in size. Sokhi and Sohi (1982) reported that the disease was most serious during the tropical monsoon period (July to August) in nonsprayed plots (34% fruit rot) compared with plots where fungicides (copper-oxychloride, mancozeb, and propineb) were sprayed (approximately 1.5%).

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Sherbakoff (1917) coined the name ‘buckeye rot’ because the disease resembled an eye of a buck (male deer). Lesions exhibit broad zonation on green fruit. However, some researchers have observed fruit spots without zonation. Immature green fruit are more susceptible to the disease than mature yellow, pink, and red fruit (Gadekallu et al. 2020; Gupta et al. 2017).

Bridging the research gap. The cultivation period (April to October) of tomato in Himachal Pradesh is usually accompanied by intense disease and pest-insect pressure. Though the average annual productivity of this off-season solanaceous crop in this region is reported to be <0.60 million tons, off-season production usually brings profits to the hill farmers. Although buckeye rot is one of the devastating diseases of tomato fruit production, only a handful of studies have been reported thus far from the Indian perspective. Therefore, the present article describes a detailed overview of buckeye rot to highlight the occurrence, epidemiology, symptomatology, and genetic and pathogenic diversity of this disease. This article is designed to provide an insight into host–pathogen molecular and biochemical interaction dynamics at local and global scales. The present review aims to bridge the critical research gaps of the previous and contemporary documented literature on etiology, socioecological perspectives, and management strategies. We build up a conceptual framework that demonstrates polygenic gene reactions (along with dominant genes) that may contribute to defense response mechanisms when pathogens attack.

Disease Symptoms and Pathogenesis

Although symptoms of the disease appear in a range of crop growth stages, the most striking symptoms develop on immature green fruit. Fruit that are in contact with soil or near to soil level are the most vulnerable to the disease due to the soilborne nature of the pathogen. Immature fruit of all ages were susceptible to the disease

and had an incubation period of 48 h (Dodan 1991; Liu and Wang 2020; Sharma et al. 2009). Symptoms appeared as water-soaked, light-brown spots (Fig. 3) which increased in size as they formed concentric rings of alternating dark and light brown. The lesions enlarged rapidly and, within 3 to 4 days, covered the entire fruit surface. The infected fruit turned dark brown and the fruit skin became soft. Sporangia and sporangiophores developed as white superficial growth on the surface of infected fruit under warm and humid weather conditions. With the invasion of saprophytic microorganisms, infected fruit may decompose rapidly (Foysal et al. 2020).

The pathogen may cause postemergence damping-off of seedlings in the nursery (Gupta and Paul 2001). Tomato stems and roots are also affected by *P. parasitica*, resulting in stem girdling, foliage blight, blossom blight, and collar rot under controlled conditions (Kanja and Hammond-Kosack 2020). Water-soaked lesions develop on roots, which gradually dry and turn dark brown (Gupta and Paul 2001; Jones et al. 1997). From the root, the infection spreads upward on seedlings through the xylem and pith tissues in vascular bundles. Infected seedlings remain stunted and the foliage becomes dull, dark green. Xylem tissues are either lignified or become hollow cylinders, resulting in tissue desiccation. This leads to shriveling of the stem base, after which the plant dies quickly (Dar et al. 2004; Sharma 1992). Also, leaves in direct contact with the ground become infected by the soilborne inoculum. Dissemination of the pathogen is also favored by splashing water. Leaf blight symptoms are of less significance (Jones et al. 1997; Singh 1999). On infected petioles and stems, blackish green lesions appear which lead to the collapse of the petiole and stem. In general, petiole infections originate from infected leaf blades and spread to the stem and fruit stalks (Shridhar 2017).

Pathogen description. Sherbakoff (1917) identified the causal organism of buckeye rot as *P. terrestria* but, later, Tucker (1931) identified it as *P. parasitica* (Chowdappa et al. 2016). On the other

Fig. 1. Tomato cultivation practices in **A** and **B**, the open field and **C** and **D**, polyhouse conditions (variety: Hybrid Himsona; climate: subtropical to subtemperate; altitude: 1,200 to 1,550 m; growth stage: fruiting).

hand, Bewley (1922) and Richardson (1941) described earlier that *P. cryptogea* and *P. parasitica* might be responsible for tomato stem, fruit, and root rot diseases (Koka et al. 2020). However, after Waterhouse (1963), it was widely accepted that the causal organism responsible for buckeye rot was *P. nicotianae* var. *parasitica* (Dastur) G. M. Waterh. 1963. The mycelium of the pathogen is hyaline and coenocytic with finely granular protoplasm, and typically branches at right

angles with a slight constriction at the point of branching. In very old mycelium, septa may form at an irregular interval. The sporangio-phores usually arise from hyphal threads and produce sporangia, generally at their tips in nature; whereas, in culture, sporangia are terminal as well as intercalary. Sporangio-phores vary from 100 to 230 μm in length (Sharma and Dohroo 2004); they proliferate and produce new sporangia by pushing aside older sporangia. Sporangia

Fig. 2. Distribution of buckeye rot of tomato across the different states of India. Shading in the map indicates the buckeye-rot-infected regions. The inset map shows the Solan district, the place of the first occurrence of buckeye rot in India.

Fig. 3. Symptoms of buckeye rot of tomato on green fruit.

vary in shape and size under natural epiphytotic conditions. Generally, they are broadly ovoid to globose in shape but elongated to barrel-shaped sporangia are also found occasionally (Fig. 4). The sporangia usually have one hemispherical papilla at the tip but, occasionally, sporangia with two papillae are also found. Sporangia size varies from 25.5 to 58.0 by 20.0 to 52.0 μm on the host while, in culture, they are 24.0 to 52.5 by 19.5 to 48.5 μm (Fig. 4) (Kaur et al. 2020). The sporangia usually germinate by releasing 8 to 16 zoospores through the papilla opening but occasionally germinate by producing germ tubes (at $>25^{\circ}\text{C}$). After release, zoospores become kidney shaped with two lateral flagella and move actively in water for about 30 min, then become encysted (6.8 by 10.2 μm in size) (Kaur et al. 2020; Koka et al. 2020).

Chlamydospores are smooth, globose, and slightly yellowish with thick brown walls (20 to 60 μm in diameter), produced abundantly in culture, and germinate by producing zoospores or germ tubes. Antheridia are amphigynous, spherical, or oval and 10 by 12 to 16 μm in size (Kaur et al. 2020). Oogonia usually measure <28 μm in diameter. Although they are usually produced readily in culture, they are often produced very sparsely and slowly (Kaur et al. 2020; Shridhar 2017). At maturity, the wall of the oogonium becomes rough, thick, and yellowish-brown in color. Oospores are aplerotic and 18 to 20 μm in diameter, with a thick wall (2 μm) (Fig. 4). Molecular identification of the pathogen causing buckeye rot in India was carried out through analysis of DNA sequence coding for the internal transcribed spacer (ITS) region with primer pair ITS1 (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-CTCC GCTTATTGATATGCT-3') (Fig. 5) (Sharma et al. 2021). The sequence analysis identified the pathogen as *P. nicotianae* and the sequence was deposited with the accession number MF398189 (Fig. 6). Also, phylogenetic analysis of sequences coding for the ITS region of *P. nicotianae* var. *parasitica* isolates (Sharma et al. 2021; Shilpa et al. 2017) revealed that significant differences were present at the genome level, and large diversity existed within the pathogen population.

Host range of pathogen. *P. nicotianae* var. *parasitica* has an extensive host range. It can cause damping-off, root rot, crown rot, leaf blight, stem canker, tip blight, and fruit rot in 72 host genera of over 58 families (Bose et al. 2002; Jones et al. 1997). Various researchers have listed hosts of *P. nicotianae* var. *nicotianae* among fruit, vegetable, plantation, and flowering crops (such as pineapple, parsley, carnation, chili, chrysanthemum, citrus, coconut, grape, guava, hibiscus, and sesame) (Gupta and Paul 2001; Singh 1999). The pathogen can also infect cucurbitaceous, solanaceous, and legume crops such as bitter melon, cowpea, bean, okra, brinjal, chili pepper, cucumber, pointed gourd, ridge gourd, and snake gourd (Roy 1997). A list of the global distribution of different (selected) species of *Phytophthora* for various agri-horticultural and forest crops is provided in Table 1.

Isolates of *P. parasitica* from tomato plants were found to be more pathogenic to tomato fruit than isolates from other hosts such as pineapple, parsley, hibiscus, carnation, and brinjal and soil (Bose et al. 2002), whereas an isolate of papaya was found to be nonpathogenic on tomato. Isolates of *P. parasitica* collected from different host plants showed cultural and pathogenic variation (Shilpa and Kaur 2018). Twenty isolates of *P. parasitica* were collected from buckeye rot-affected tomato fruit which showed significant differences for mycelial growth and pathogenic characteristics such as incubation period and disease incidence; however, no correlation could be established between mycelial growth and virulence (Sharma 1992). Cultivar Money Maker possessed good horticultural traits and resistance to buckeye rot and was found to be susceptible to fruit rot (Dodan et al. 1995), which was attributed to the appearance of more aggressive strains of the pathogen. Considerable variation in cultural and pathogenic behavior was observed among 26 different isolates of *P. nicotianae* var. *parasitica* collected from different agro-climatic zones of Himachal Pradesh, India (Dodan and Shyam 1994). However, there was no correlation between mycelial growth, zoospores, size of sporangia, chlamydospores, and pathogenic behavior among these isolates. Furthermore, the existence of assemblages of virulence and

Fig. 4. Morphological identification (microscopic view) of papillate sporangia of *Phytophthora nicotianae* var. *parasitica*. **A**, Pure culture. **B**, Coenocytic mycelium under light microscope. **C** and **D**, Sporangium stained with lactophenol aniline blue under light microscope.

Fig. 5. Schematic representation of PCR amplification of internal transcribed spacer region (ITS) of *Phytophthora nicotianae* var. *parasitica* with primers ITS1 and ITS4. Amplification of a single band of approximately 900 bp was observed (Shilpa et al. 2017).

avirulence was not exhibited by any isolate but, based on their aggressiveness pattern and nondifferential host–isolate interaction, 18 were grouped as pathogenic strains (Jones et al. 1997).

Diversity and genomics of *P. nicotianae* var. *parasitica*. Molecular characterization of different isolates of *Phytophthora* isolated from different hosts was grouped into four subgroups and isolates of tomato were grouped in one subgroup (Chowdappa 2007). Kaur et al. (2019) examined significant differences in cultural, morphological, and molecular diversity among *P. nicotianae* var. *parasitica* isolates collected from different parts of Himachal Pradesh, India, and divided 17 isolates into four cultural groups and three categories based on morphological characteristics. Genetic diversity analysis using inter-simple sequence repeat (ISSR) primers and molecular phylogenetic methods (unweighted pair group method with arithmetic means cluster analysis and maximum likelihood) grouped 17 isolates into two major clusters with a similarity coefficient of 0.44, where cluster I was composed of 6 isolates and cluster II contained 11 isolates (Kaur et al. 2019; Yusoff et al. 2020). Shilpa and Kaur (2018) documented that, among various tomato lines used for the genetic diversity study or analysis, Solan Vajr was susceptible and some other lines were tolerant to buckeye rot. Clear polymorphism was found in amplification of expressed sequence tag simple sequence repeat (EST-SSR) primers (SSR markers) among the parental lines (Fig. 7). The genome of *P. nicotianae* was completely sequenced. The genome size was 95.32 Mb with about 23,275 predicted genes (Yuan et al. 2021). In *P. parasitica*, the number of predicted genes was higher than those in *P. infestans* or *P. sojae* (the broader host range of *P. parasitica* could be explained based on its larger number of predicted genes compared with *P. infestans* and *P. sojae*) (Kaur et al. 2019).

To study gene function and improve disease management, genetic manipulation is required. Genetic transformation is usually difficult for most oomycete fungi. Genetic manipulation in *Phytophthora* could be achieved through the following four methods: (i) polyethylene glycol (PEG)-mediated transformation, (ii) particle bombardment, (iii) *Agrobacterium tumefaciens*-mediated transformation, and (iv) electroporation of zoospores. Out of these four methods, the PEG-mediated transformation method was found to be the most efficient in *P. parasitica* to study various cytological and pathogenesis processes (Ah-Fong et al. 2008; Bottin et al. 1999; Kebdani et al. 2010).

Fig. 6. Statistical model analysis of phylogenetic inference of isolated *Phytophthora nicotianae* (accession number MF398189) causing buckeye rot of tomato (maximum likelihood and Tamura-Nei model). Percentage of trees in which the associated taxa clustered together is shown next to the branches (modified after Shilpa et al. [2017]).

Disease Cycle and Epidemiology

In areas where tomato crops are grown without rotation in the same field, the oomycete pathogen overwinters in the soil as either oospores or chlamydospores and remains viable in the soil for at least 1 year. The pathogen has also been reported to be internally seedborne and remains viable in seed for more than 1.5 years

(Sohi 1978). With the advent of monsoon rains (the second fortnight of June), along with the presence of high soil moisture and moderate temperatures (20 to 25°C), oospores and chlamydospores start germinating by producing mycelium and sporangia. The sporangia, in turn, produce biflagellate zoospores which, after swimming for some time in the film of water, lose flagella and become encysted (Hanson

Table 1. Summary of geographical distribution, occurrence, and pathogen diversity of different (selected) *Phytophthora* spp. for various agricultural and forest crops and trees^a

Pathogen	Host	Disease	Location, region
<i>Phytophthora capsici</i>	Pepper, watermelon, squash, cucurbits	Leaf blight, root/stem rot, fruit rot, soft rot	Africa, Asia, Europe, North, and South America
<i>P. infestans</i>	Tomato, potato	Late blight, downy mildew	Africa, Asia, Europe, Australia
<i>P. pseudocryptogea</i>	Banksia, potato, grass tree, brinjal	Root rot	South America, Australia, Asia
<i>P. cinnamomi</i>	Walnut, avocado, chestnut, peach, pineapple	Dieback, crown/root rot, ink disease, heart rot	Africa, Asia, North and South America, Europe
<i>P. nicotianae</i>	Tomato, onion, cotton, bell pepper, tobacco, ornamentals	Fruit rot, stem blight, black shank, crown rot	Africa, Asia, North, and South America
<i>P. cactorum</i>	Apple, strawberries, orchids, rhododendron	Root rot, crown rot, cankers, collar rot, black rot	Africa, Europe, North, and South America
<i>P. megakarya</i>	Cocoa tree, taro, African oil palm, avocado	Black pod rot	West and Central Africa
<i>P. cryptogea</i>	Tomato, sugar beet, sunflower, oat, chestnut, tulip, ornamentals	Foot rot, stem/leaf rot, root/shoot rot and shanking, ink disease	Asia, Africa, Europe, South America, Oceania
<i>P. andina</i>	Tree tomato, pear melon	Leaf blight, stem rot	South America
<i>P. drechsleri</i>	Tomato, turnip, apple, cabbage, chili pepper, bean	Stem/root rot, fruit rot, collar rot, soft rot, canker	Asia, Africa, North America, Oceania
<i>P. terrestris</i>	Tomato, peach, walnut, avocado, peach	Ink disease, fruit/root rot	Africa, Europe, Asia, Oceania
<i>P. betacei</i>	Tree tomato	Late blight	South America
<i>P. pamivora</i>	Coconut, areca nut, rubber, black pepper, citrus	Fruit rot, bud rot, root rot, cankers	Africa, Asia, Oceania, South America
<i>P. citricola</i>	Orange or other citrus fruit	Root rot, brown rot	Africa, Asia, Europe
<i>P. porri</i>	Tulip, carrot, onion, leek	Blight, collar/root rot, crown rot	Asia, North America
<i>P. erythroseptica</i>	Potato, tomato	Rhizome rot, root rot, pink rot, shanking	Africa, Asia, North America
<i>P. syringae</i>	Apple, pear, almond	Root/collar/fruit rot, Canker	Asia, Europe, South America

^aSources of information: Koka et al. (2020), Liu and Wang (2020), Sharma and Dohroo (2004), and Shridhar et al. (2019).

S. No.	Name/ Accession No.	Susceptible/ Tolerant
1.	Solan Vajr	Susceptible
2.	Hawai 7998	Tolerant
3.	EC-520075	Tolerant
4.	EC-251649	Tolerant
5.	EC-528373	Tolerant
6.	EC-126902	Tolerant

M denotes 100 bp Molecular Size Marker

Fig. 7. Molecular parental polymorphism survey using expressed sequence tag simple sequence repeat (EST-SSR), inter-simple sequence repeat (ISSR), and genomic SSR primers (SSR markers based on assisted genetic diversity evaluation) (Shilpa et al. 2017). Lane M: 100-bp molecular marker; lane 1: susceptible variety Solana Vajr; and lanes 2 to 6: tolerant lines Hawai 7998, EC-520075, EC-251649, EC-528373, and EC-126902, respectively.

et al. 2016). These encysted zoospores, which are the source of primary infection, are splashed by rain to immature green fruit. After establishment of contact between zoospores and the fruit surface, the zoospores start germinating within 3 h by the germ tube and give rise to appressoria on the fruit surface (Dodan 1991). Infection hyphae that usually develop from the appressoria penetrate the cuticle directly.

The oomycete pathogen invades intracellularly, inward as well as radially. The invading hyphae are smooth in exterior texture with granular protoplasm, branching profusely in the host parenchyma. These hyphae penetrate deep into fruit and invade seeds. Symptoms develop on fruit 3 to 4 days after infection begins (Sajad and Jamaluddin Abid 2017). When most of the area of the fruit is covered with the lesions, it becomes mummified and falls on the ground. Mycelium pushes through the fruit epidermis and cuticle by rupturing it and grows on the fruit surface under humid conditions, producing sporangia on simple branched sporangiophores. Sporangia are further splashed by rain and cause secondary infection. When the conditions become unfavorable, the oomycete either produces chlamydospores or goes into sexual reproduction and produces oospores (Fig. 8) (Kaur et al. 2019). *P. parasitica* is a predominantly heterothallic organism and requires two mating types, A1 and A2, for oospore formation (Kaur et al. 2019; Ko 1981). Genetic variation among pathogens generally occurs through sexual reproduction, which produces different genotypes and pathotypes that help pathogens to adapt under unfavorable conditions, particularly on resistant host genotypes (Hanson et al. 2016). However, it is still unclear how much of a role sexual reproduction plays in the *P. parasitica* life cycle.

The pathogen survives in the form of chlamydospores and oospores in both soil and infected seeds (Koka et al. 2020). The pathogen remains viable for more than 2 years in the soil (at a depth of 10 cm) and survives longer under wet conditions than dry conditions (Sharma 1992; Shridhar et al. 2019). Sherbakoff (1917) observed that fruit growing on or near the ground were most susceptible to buckeye rot. Inoculum surviving in the soil is splashed from the soil with spattering rains and, after infection, sporangia are produced on fruit and are carried by moist wind and water to adjoining fruit (Kaur et al. 2019).

The oomycete usually shows optimum growth at 25 to 30°C. However, Hooda et al. (2011) reported that temperatures of <20°C or >25°C did not support sporangia germination by means of zoospore release. Maximum fruit infection under field conditions occurs at a temperature range of 20 to 25°C, with relative humidity >60% and rainfall ≥10 mm (Hooda et al. 2011). Fruit in direct contact or near the soil were readily attacked by the pathogen (Singh et al. 2020). However, infection of fruit as high as 45 cm above the ground was also noted. Sharma and Sohi (1983) hypothesized that high doses of nitrogen, along with irrigation at 5- to 6-day intervals, increased yield but also the incidence infected fruit, due to enhanced production of zoospores.

Dodan (1991) concluded that incidence of buckeye rot was positively correlated with total rainfall, mean relative humidity, and mean minimum temperature. Multiple linear regression fitted to disease incidence identified, in order of importance, total rainfall, mean relative humidity, mean maximum temperature, and mean minimum temperature (Koka et al. 2020; Singh et al. 2020). Mean maximum temperature had an inverse relationship with buckeye rot incidence (Liu and Wang 2020). Though temperature tended to be favorable for disease development throughout the crop season, epiphytotic conditions occurred only with the advent of monsoon showers (June to July). Frequent rains during fruiting maintain high humidity levels for the sporangia to germinate and cause infection and aid dispersal of inoculum through splashing.

Management

Cultural and chemical practices. The use of cultural practices is of immense importance due to degradation of natural resources resulting from the nonjudicious application of agrochemicals. Sherbakoff

(1917) advocated staking of plants in the field, which was also found effective by Wager (1935) and Sharma (1992). Also, wider spacing was adopted to control this disease (Hooda et al. 2011), because disease spread was slower with 90-cm than with 40- to 50-cm spacing between plants in a row (Kumar and Sugha 2000). Foliage and fruit up to a height of 30 cm can be removed to avoid providing inoculum for severe disease outbreaks (Kaur et al. 2019; Sharma and Sohi 1975). Mulching with Himalayan pine needle (*Pinus roxburgii*), combined with subsequent application of copper oxychloride (0.3%), controlled the disease without creating visible residue deposits on fruit and reduced dispersal of inoculum by rainwater. Similarly, intercropping of double rows of tomato with double rows of maize suppressed buckeye rot incidence compared with intercropping tomato with bean, rapeseed, or mustard (Kumar and Sugha 2000). Application of furrow or surface irrigation (a common practice) and ensuring optimum crop water use usually created unfavorable microclimatic conditions for buckeye rot while maximizing crop growth (Bhardwaj and Masand 1995; Gupta et al. 2006).

A suite of systemic and nonsystemic fungicides has been evaluated in the last decades for control of this fruit rot disease. In India, however, rain-related delays in fungicide application often result in control failures. Proper timing of initial sprays is of prime importance to achieve a desirable level of disease control Bordeaux mixture, tribasic copper sulfate, captafol, copper oxychloride, zineb, mancozeb, and chlorothalonil have been used to control buckeye rot (Kumar et al. 2008). Application of captafol, mancozeb, and copper oxychloride at 40, 55, and 70 days after transplanting reduced incidence of buckeye rot and defoliation diseases and increased fruit yield (Bhardwaj 1991). The most effective approach was achieved by sequential application of metalaxyl/mancozeb and cymoxanil/mancozeb, which recorded satisfactory control of the disease (approximately 54.6%) with three fortnightly applications (Gupta and Bharat 2008; Shyam and Gupta 1996; Usha and Satheesh 2007). Amistar Top (azoxystrobin + difenconazole) was also found highly effective and limited the incidence of buckeye rot to 20.3%; a single application of azoxystrobin significantly limited the incidence to 21.41% (individual application), whereas one difenconazole spray was least effective (Bharat and Gupta 2011). Shridhar et al. (2019) evaluated various premixed fungicide products and found that fenamidone/mancozeb, famoxadone/cymoxanil, and metiram/pyraclostrobin were effective in controlling disease incidence under natural epiphytotic conditions.

Screening and identification of genetic or genomic resources. Wild cherry tomato plants (*S. lycopersicum* var. *cerasiforme*) do contain resistance genes but, under field conditions, they escape infection because fewer zoospores reach the small-sized fruit. Sources of resistance can then be used further for molecular-assisted breeding purposes. Several researchers have conducted molecular breeding for tolerance against this disease, though only a few cultivars and lines have been identified (Kaushal et al. 2020; Shilpa and Kaur 2018). Fruit of 11 tomato varieties were found highly resistant to natural or artificial infections by *Phytophthora parasitica* var. *terrestris* at Tennessee Agricultural Experiment Station; Sherbakoff's 57 × Oxheart was identified as having desirable fruit size and resistance to buckeye rot (Razdan and Sabitha 2009; Shilpa and Kaur 2018).

Resistance to buckeye rot had been reported in several lines and varieties, including hybrid N-64 (STEP 390 × HES 6578), Rossal, EC 129171/PI-2, EC 128-969, EC 129-166, EC 729-1, EC 122-62-1, EC 130035, and EC 129603 (Razdan and Sabitha 2009; Singh et al. 1997). Of 110 cultivars or germplasm lines evaluated under natural epiphytotic conditions, only one species—that is, *S. lycopersicum* var. *cerasiforme* (sensu lato *cerasiforme*)—was resistant. Line EC 129602 was categorized as moderately resistant (Joshi et al. 2009). The incidence of buckeye rot ranged from 8.5 to 11.0% in lines JTS-10-3, JTS10-2, BT-10, LE-79-5, JTS-10-1, and EC-191535-3 (Kumar et al. 2018).

Plant height, total acidity, ascorbic acid content, and total nitrogen content in green immature fruit affected resistance against buckeye rot (Sharma et al. 1974). Resistant cultivars usually contained high levels of phenolics (total and ortho di-hydroxy phenols), amino or ascorbic acids, and phenol oxidizing enzymes (polyphenol oxidase and peroxidase) compared with susceptible ones, which had high

sugar content (Razdan and Sabitha 2009; Singh et al. 1997). In mature tomato fruit, lycopene is the major coloring pigment that has antifungal properties, though the quantity of lycopene varies with the cultivar and size of the tomato fruit (Razdan and Sabitha 2009). Devi and Tiwari (2001) reported that the polygenic reactions (along with dominant genes) governed resistance in fruit rot whereas, for susceptible traits, multiple gene and allelic interactions were found in all crosses except Kt-15 × KT-10. Shilpa et al. (2017) evaluated the susceptible cultivar Solan Lalima and moderately resistant line EC-251649 through molecular markers and demonstrated a high level of polymorphism (71.1%) using ISSR, genomic SSR, and EST-SSR markers.

Induced systemic resistance. Induced resistance in plants, in general, can be activated by biotic and abiotic inducers of resistance. However, resistance induction in tomato plants against buckeye rot has been reported only by abiotic inducers. Acibenzolar-S-methyl and fosetyl-Al were evaluated for control of crown and root rot of tomato caused by *P. nicotianae* (Gilardi et al. 2014); acibenzolar-S-methyl provided the most effective disease control with three pre-plant leaf sprays at 7-day intervals. Of nine abiotic resistance inducers evaluated against buckeye rot under natural epiphytotic conditions, application of β -aminobutyric acid reduced disease incidence, provided 85.6% disease control, and increased fruit yield (Sharma et al. 2021; Shridhar 2017).

Integrated disease management. Considering the soilborne nature of the pathogen and infection caused by rain-splashed inoculum, a single management practice alone may not achieve the desired goal. Integrated management of buckeye rot may be achieved by reducing the initial pathogen inoculum and then slowing the rate of increase in these populations. The use of fungicides, resistant varieties, and

modified cultural practices may help in achieving these objectives. During the last two decades, a few resistance sources have been identified and resistance breeding efforts have been initiated, yet no variety or hybrid combining strong resistance with desirable fruit characteristics has been developed. However, efforts have been made to integrate cultural and chemical methods to obtain the best management practices.

Spraying of Dithane M-45, Bordeaux mixture, or captafol, along with staking and removal of foliage and fruit up to 30 cm above the soil surface, was the most effective and economical approach (Kumar et al. 2008; Sharma 1992). Integration of fungicide (Indofil M-45, 0.25%) sprays, cultural practices such as the clipping of lower leaves (15 to 20 cm), weeding, mulching with white polythene sheet, and regular removal of affected fruit not only reduced disease incidence drastically but also increased fruit yield appreciably (Dodan et al. 1995).

Gupta and Shyam (1998) conducted several experiments to determine the role of pine needle mulch alone and in combination with systemic (Ridomil MZ, 0.25%) and nonsystemic (Indofil M-45, Blitox-50, and Captaf at 0.25%) fungicides sprayed on mulch and foliage. They found that pine needle mulch and spray applications of Ridomil-MZ or Blitox-50 on mulch and foliage were the most efficacious techniques in managing this disease. Moreover, the application of Blitox-50 on pine needle mulch was found to be quite effective and avoided having any residue deposits on tomato fruit. However, this treatment had slightly less benefit/cost ratio (12.9) compared with its foliar application (16.7) (Razdan and Sabitha 2009; Shridhar 2017).

Krishan and Paul (2014) evaluated various botanicals as powder and crude extracts under in vitro conditions and recorded complete mycelial growth inhibition of *P. nicotianae* var. *parasitica* with

Fig. 8. Disease cycle of buckeye rot of tomato. Reproduced, by permission, from Gupta et al. (2017).

aqueous extract of marigold leaf powder. Also, crude extracts of *Eupatorium adenophorum* and *Melia azedarach* resulted in complete inhibition in mycelia growth of the pathogen (Shridhar et al. 2018, 2019). Among aqueous extracts, *Eucalyptus tereticornis* was found most effective and caused approximately 51.5% inhibition in mycelial growth of the pathogen, followed by *Artemisia vulgaris* (48.5%). Similarly, among cow-urine-based extracts, *E. tereticornis* was found to be most effective and caused approximately 72% inhibition of mycelial growth of the pathogen, followed by *A. vulgaris* (68.7%) (Shridhar et al. 2018). Biocontrol agents (*Trichoderma virens*, *T. hamatum*, *T. harzianum*, and *T. viride*) were also found to be effective and caused 77.6, 69.4, 68.5, and 67% mycelial growth inhibition, respectively (Sharma et al. 2018).

Future Research Directions and Conclusions

Buckeye rot has received more attention in India due to a massive shift in cultivation from open-pollinated varieties to hybrids, which initiate fruiting from the first node above the ground, making them highly vulnerable to rainsplash-deposited inoculum. Moreover, due to climate change, increasingly heavy rains can worsen spread of the pathogen. There is an urgent need to breed resistant varieties with desirable horticultural traits. Furthermore, due to growing concerns about residue-free produce, there is a need to develop innovative disease management strategies such as pesticides of plant origin, biological control agents (both fungal and bacterial), and induction of resistance through abiotic elicitors. The integration of innovative disease management strategies with suitable cultural practices may go a long way in controlling the severity of this disease.

Some of the actions that could be undertaken collectively throughout the world (particularly in the Indian scenario) may include (i) an integrated approach combining fungicides, weeding, mulching with pine needles or polythene sheets, and clipping of lower leaves; (ii) use of antagonistic microorganisms (such as *Penicillium patulum*, *Streptomyces griseus*, and *T. koningii*), as well as management of fungicide seasonal spray timing; (iii) taking up organic farming and use of biopesticides, including botanicals, for pest or disease management; (iv) creating and conserving wild habitats and maintaining them without harmful cultural operations; (v) inoculation of tomato cultivars with cultural filtrate or inoculum of *Glomus mosseae*, which can induce combined systemic and local resistance in tomato roots and enhance soluble phosphorus concentration in soil (El-Baky and Amara 2021; Pozo et al. 2002); (vi) planting of small-fruited cherry tomato or resistant parental lines; (vii) crop rotation and mixed cropping; and (viii) creating data-based education, awareness, and outreach programs among the farming community and stakeholders about the biophysical and biochemical aspects of host-pathogen interactions, to help them understand why certain management practices and combinations of practices are likely to be most effective and profitable.

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