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Review Article

Tomato early blight (*alternaria solani*), pathogen, disease development and defense response phytohormone signaling

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Abstract

Alternaria solani, the necrotrophic fungal pathogen of Solanaceae family belonging to Dothideomycetes, causing early blight received significant interest among all the fungal pathogens of tomato. The pathogen is widely distributed and is an economically important member of the class Ascomycota. The genus comprises of opportunistic necrotrophic or parasitic pathogens of tomato and relevant species. The carnage by this necrotrophic pathogen accounts for huge and drastic losses to the agriculture production worldwide. It has also been linked to the cosmopolitan decline in wild and cultivated tomato species of the world. In order to overcome the burden of the disease, there is a critical need to develop effective strategies for early blight management. However, in order to handle the disease trouble, there is a fundamental need to be aware of the phylogeny, taxonomy, transmission mechanism of early blight and phytohormone defense signalling implicated in response to disease by plants. So, the collective information regarding early blight disease development must be readily available to the researchers. In this context, this review shall provide an imperative information resource on the whole biological aspect of the fungal pathogen and a way forward to deal with this pathogen efficiently.

Keywords: *Lycopersicon esculentum*, Pathogenesis, *Alternaria solani*, Signalling, Salicylic acid, Jasmonic acid.

INTRODUCTION

Kingdom fungi are considered among the important and abundant eukaryotic community on this planet and constitutes about 2.5 million species. However different fungi acquire various characteristics of pathogenicity and infect wide range of plants and animals (Hawksworth & Lucking, 2017; Agrios, 2005). Pathogenicity behavior shown by the fungal pathogens poses biggest threat to the agriculture. Among the fungal groups, Alterneria species are the common parasitic fungi belonging to phylum Ascomycota of class Dothideomycetes and genus Alternaria. The predisposing factors for the development and the progression of infection structures of the Alterneria pathogen on the *Lycopersicon esculentum* depend primarily on temperature for incubation and relative humidity of air and the germination of *Alternaria solani* spores that occurs at wide temperatures (Chaerani et al., 2006). The yield loss from early blight has been estimated to a range of 71.66 % and 78.51% under severe outbreak (Adhikari et al., 2017; Datar & Mayee, 1981). The older leaves are attacked severely and the lesions enlarge days after infection till they cover the whole leaf. The concentric rings are encircled by chlorotic areas on the leaves, stem resulting in reduction of the photosynthetic zones, defoliation and early senescence induction. In response to infection attack, plants develop preformed and constitutive mechanisms that involves the regulation of SAR and various genes operated by SA and JA signaling pathways are involved in providing disease resistance response in plants (Backer et al., 2015; Yi et al., 2014). Due to the enormous profitable losses inflicted by early blight infections, it becomes essential to cover in detail study on the pathogenesis and transmission mechanisms in order to develop effective control strategies and prevention of early blight. So, this review is an attempt to provide broad knowledge about the biology, variety, distribution and pathogenesis of *A. solani* on *L. esculentum* and defense signaling methods mediated by the host plants to develop immune response against biotrophic and necrotrophic fungal pathogens.

Origin and cultivation of *Lycopersicon esculentum*

The genus Lycopersicon belongs to Solanaceae family in the major Angiosperms (Flowering plants) plant group and is an economically important genus, containing approximately about 2,700 species and about 98 genera worldwide (Bohs, 2007). The *L. esculentum* originated from Mexico and Peru and forms centre of diversity for wild type relatives (Gould, 1992; Larry & Joanne, 2007). However, the centre of origin of *L. esculentum* has been localized between the mountain ranges of Andes and the Pacific coast of western South America (WWF & IUCN, 1997). However, on the basis of research carried out from the Tomato Genome Consortium 2012, there are the three wild tomato species viz. *S. galapagense, S. pimpinellifolium* and *S. cheesmaniae*, that are closely linked to the varieties of already grown tomato species that were found on the Galapagos Islands, (Menda et al., 2013). L. esculentum is diploid with a chromosome number of 12 (2n=24, AABB) that was identified by (Barton, 1950). *L. esculentum* is having the relatively small genome size of 950Mb per haploid nucleus (Arumuganathan & Earle, 1991) and it is acquiescent to genetic analysis by possessing characteristics such as diploidy, self-pollination, and a relatively short period of generation and is also used for research perspectives that have been reviewed by (Ji & Scott, 2006).

Tomato (*Lycopersicon esculentum* Mill.) is one of the important and widely grown vegetable crop of the globe. In tropical countries, it forms the major food and cash crop. Among vegetables, tomato ranks first among processing crops. It forms the richest source of various vitamins, minerals and phenolic antioxidants (Rick, 1980; Vinson et al., 1998). India forms the second largest tomato producing country after china (FAO 2012) and produce 11% of tomato according to Indian Institute of Vegetable Research (Indian Council of Agricultural Research) Varanasi-221305, Uttar Pradesh (India). The original site of domestication of tomato is probably in Mexico (Picken et al., 1985; Taylor, 1986). Although cultivated as an annual crop, tomato grows as a perennial in its original habitat in the Andean region.

Tomato (*L. esculentum*) forms one of the best studied cultivated dicotyledonous plant, it is one of the excellent model organism involved in both basic and applied plant research (Rick and Yoder 1988). Tomato belongs to the genus Lycopersicon that contains eight wild species (Taylor, 1986). Binomial classification proposed Solanum lycopersicum as the botanical name of tomato. After that, the genus name Lycopersicon (Latin-Wolf Peach) and afterward the name as *Lycopersicon esculentum* for cultivated tomato and *Lycopersicon pimpinellifolium* for wild tomato by (Miller, 1754). The plant typically grows up to a height of 1-3 meters and has a weak stem. It is perennial in habitat and grows in temperate climates as an annual crop. The global production of *L. esculentum* is about 3.782 thousand metric tons. *L. esculentum* production reached up to 16.82 thousand metric tons occupying about 8.65 thousand hectors (Indian Horticulture Database, 2011). These are some important tomato cultivars grown in India viz. Pusa Red Plum, Pusa Early Dwarf, Pusa-120, PKM-1, Pusa Ruby Red, DK-1 Selection -21, Tomato-308, K-21, Rajshri, Dhanashri, Vaishali, Arka Saurabh, Arka Vikash ARTH 3, ARTH 4, Shalimar-1, Shalimar-2, Hisar Anmol, Hisar Arun, Hisar Lalima, Hisar Lalit, Krishna, KS 2, Matri, MTH 6, NA 601, etc.

Alternaria early blight disease of *L. esculentum*

Among the biotic stress, early blight disease caused by the necrotrophic pathogen *A. solani* (Ellis and Martin) has been reported from many countries viz., Canada, India, the United States and Nigeria to cause yield loss up to 79% (Basu, 1974b; Datar & Mayee, 1981). It is one of the important diseases that causes complete defoliation in extreme cases and is most damaging to tomato (*Lycopersicon esculentum* MILL) (Peralta et al., 2005). Apart from *L. esculentum*, various Alternaria species influences most crops, including Brassicae, cauliflower and broccoli (*Brassica juncea, Brassica oleracea* L.) turnip and field mustard (*B. rapa* L., *B. campestris* L.), radish (*Raphanus sativus*) and cabbage (*B. oleracea*). In hierarchy, Alternaria fungi is classified in Kingdom Fungi belonging to Phylum Ascomycota; Subdivision Pezizomycotina; Class Dothideomycetes; Order Pleosporales; Family Pleosporaceae; Subfamily mitosporic Pleosporaceae; Genus *Alternaria* (http://www.eol.org/pages/188343/names). Most of the Alternaria species are saprophytes that are commonly by soil or on decomposing host tissues (Bart & Thomma, 2003). There are about 299 species that are scheduled in the genus Alternaria (Kirk et al., 2008). *Alternaria* propagation is vegetative in nature, conidial spores are airborne and are found on objects, water and on soil. There are very rare cases of Sexual recombination (teleomorphy) in Alternaria species. On artificial media, Alternaria spp. can be grown on PDA (potato-dextrose agar) and radish dextrose agar (RDA) (Thakur & Kolte, 1985).

Biology of Alternaria pathogen

Various plant species involving wide range of cruciferous plants and plants belonging to Solanaceae family are affected by Alterneria species viz., *A. alternata* (Fr.), *A. brassicae* (Berk.), *A. solani* and *A. brassicicola* (Schw.) (Ellis & Martin). Oleiferous and vegetable Brassicas are affected by *A. brassicicola* and *A. brassicae* species. The vegetable Brassicae are greatly infected by the former species while the oleiferous are inhabited by the later species (Humpherson-Jones, 1989). *A. solani* causes early blight of Solanaceae family including potato and tomato species (Datar & Mayee, 1981). *A. Alterneria* cause Alterneria blight and other diseases to over 380 host plant species. The genus Alterneria was first recognized by (Nees, 1817). These are cosmopolitan in distribution and the pathogens are strongly influenced by climatic conditions, with the highest record of disease incidence in wet seasons and in areas receiving

comparatively high precipitation (Vloutoglou, 1994; Hong & Fitt, 1995; Humpherson-Jones & Phelps, 1989).

Diagnostic symptoms and damage by *A. solani* on *L. esculentum*

A. solani affects various portions of host species including fruits, leaves and whole plant at all stages of development. *A. solani* disease symptoms are characterized by the development of spots on stem, leaf and fruit on the host plant (Sherf & Macnab, 1986). Symptoms include small brown spots that are surrounded by yellow discolorations (Barsdale & Stoner, 1977). The spots enlarge and become brown to black dark lesions with concentric rings that can result in severe defoliation and damping-off. Symptoms are initially observable on lower leaves forming circular and light brown to greyish or dark brown spots from less than 0.5-12mm diameter and move upwards towards the younger leaves as the plant matures, resulting in the reduction of photosynthetic potential of the plant (Rotem, 1994). Sometimes the spots are oblong or linear and sunken due to coalescing of them on the mid ribs of the leaves. Later on, prominent round black spots emerge on leaves and stem. These spots may band together leading to the blackening of entire leaves or weakening of the whole stem with the development of extended lesions and disease appears initially on older leaves. Generally, water and nutrient uptake by the plant is not affected by the Alternaria species as the pathogen do not exclusively target host roots or vessels. Alternaria species survive as mycelium or spore on decomposing plant remains, as the pathogen is not having any sexual stage (Rotem 1994). Normally, the plant tissue that is weakened due to stress, wounding or any other factor are more susceptible to the Alterneria infection than healthy host tissues. Alterneria becomes highly parasitic once it came in close proximity to the weakened host tissue, illustrating that the difference between saprophytic and parasitic behavior of pathogen is not always obvious. This pathogen is responsible for the major yield loss in Solanaceae family and forms the major factor for economic impact. This disease cause decline and crop loss in both fresh and stored products. *A. solani* often occurs in Conjugation with *A. Alternata*. This confounds the precise estimate loss in the field by this pathogen Figure 1.

Morphology of *Alternaria solani*

A. solani develop as fast-growing and thick colonies in the *in vitro* cultures and are usually circular to irregular, brown to dark brown in color. Mycelium of the fungi is immersed with branched, septate, hyaline and thick hyphae (4-8µ) (Ellis, 1971). Conidiophores grow individually or in petite groups or more from the hyphae, more often simple, erect or ascending, straight or flexuous, bent at sharp angle, more or less cylindrical at the base but sometimes slightly swollen, septate, pale brown to olive-brown in color and up to 110 µm in length, 6–10 µm thick, 0-2 µ longitudinal thick, having solitary to numerous small, but distinct conidial scars.

Conidia usually exist as single or occasionally in short chains, They are usually smooth, straight or slightly curved and are highly septate, club shaped divided in both horizontal and vertical directions, 9–11 oblique septa, 0–2(–3) longitudinal or transverse septa, conidia arise through small pores from the conidiophore wall and are acropleurogenous in nature. Conidia are having an overall length of 150–300 µm, 15–19 µm width, pale golden or olivaceous brown, smooth, beak pale colored, 75-350µ long and regularly 20-30µ (occasionally up to 40µ) thick and the beak is about 1/3 to ½ the length of the conidium and having thickness of 5-9µ (Ellis, 1971) Figure 2.

Figure 1. Symptom development and damage by *A. solani*.

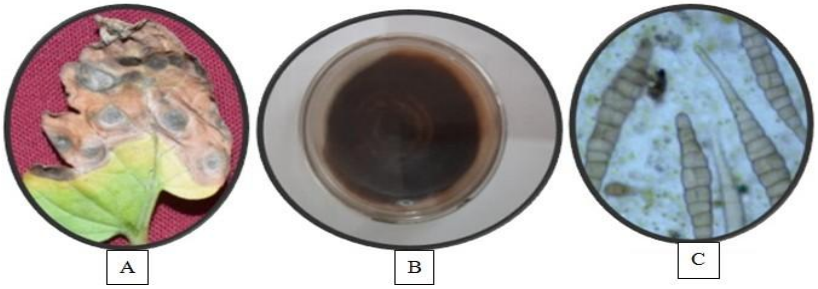

Figure 2. *A. solani* on PDA media and conidia of *A. solan*i (x200).

Alternaria brassicicola

A. brassicicola colonies are amphigenous, effuse, dark blackish brown in color and smooth in morphology. Vegetative structure forms mycelium is immersed, hyphae is branched and septate. At initial is hyaline and later is brown to olivaceous brown in color and are smooth both inter and intracellular and having thickness of 1.5-7.5µ. Conidiophores rising through stomata are solitary, or in groups of 2-15 or more and (Ellis, 1971). Conidia arise through small pores of the conidiophores wall, arise frequently in chains. Conidia are sometimes branched, acropleurogenous, straight, nearly cylindrical and slightly tapering towards the tip. The basal cell is often curved and the cell at the apex resembles more or less to a truncated clone is always small and broad, septate having frequently less than 5 transverse septa but usually few and up to 6 longitudinal septa.

Alternaria alternate

In vitro colonies of *A. Alternata* are usually black and sometimes gray. It is a common saprophyte that is mostly present on various kinds of host plants and other substrates as food stuff and soil. Straight or flexuous, simple or branched conidiophore are present and occur singly or in petite groups, condiophores are sometimes geniculate pale to mid olivaceous or golden brown, smooth and up to 50 µ long with single or multiple conidia scars (Ellis, 1971). Conidia arise in chains and are long, the conidial chains are branched, obclavate, ovoid, with small conical beak. Conidia are smooth and having 8 transverse and many longitudinal septa and having pale to mid golden brown color.

Alternaria disease development (Epidemiology of pathogen)

Disease development and the progression of infection structures of the pathogen on the *L. esculentum* depend primarily on temperature for incubation and relative humidity of air. While, the effective germination of spores of *Alternaria* species occurs at broad temperatures and wide temperature ranges are associated with effective germination (Peralta et al., 2005). Hypheal growth of *A. solani* occurs at optimum temperature range of 25-27 ºC. *In vitro* studies revealed that *A. solani* sporulation is temperature-dependent and temperature spectrum of sporulation of *A. solani* is broader (24-27 ºC) and spores got completely developed and noticeable after 13 or 14 h, at 27ºC. During plant infection, air humidity of 95-100% lasting at least for 9-18 h is a significant requirement for successful infection development and progression by *A. solani* pathogen species Figure 3.

Alternaria toxin

A. solani produce and exude various types of phytotoxins as alternariol, altersolanol A, altertoxin, macrosporin and solanapyrone that are involved in the development of destructive diseases during infection to the plants. Diverse ranged phytochemicals are produced by the Alterneria species belonging to the HST clade (host-specific toxins). By deciding the spectrum of host plant, such compounds (HST) plays main role in the pathogenesis as well as elevating the degree of virulence and pathogenecity as well as the isolates, virulence and pathogenicity levels (Parada et al., 2008). Additional toxins have been reported to be

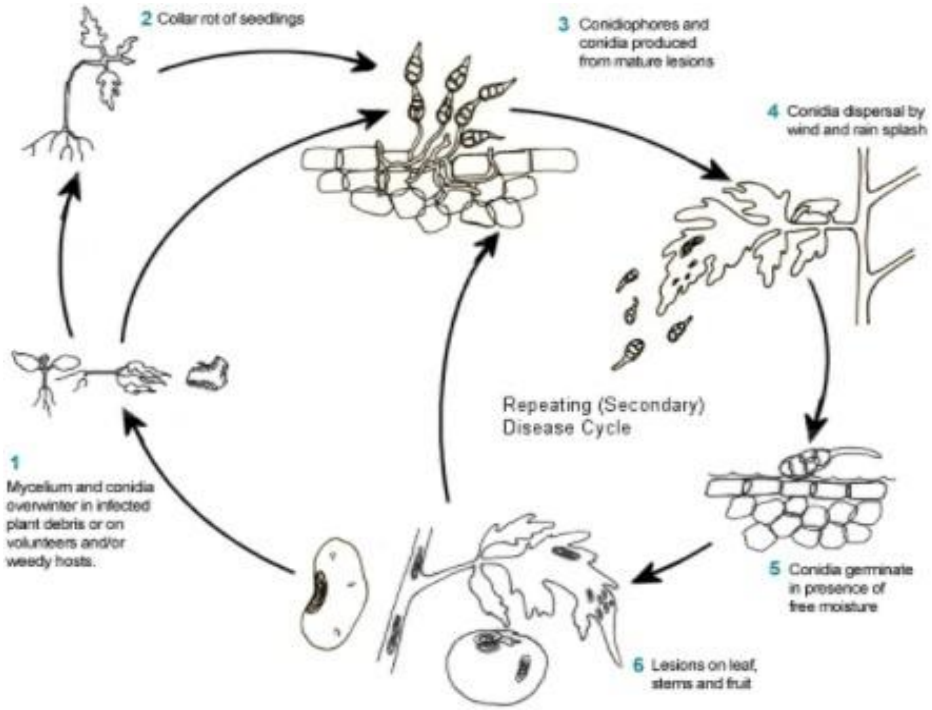

Figure 3. Schematic diagram of the life cycle of *Alternaria solani* (Kemmitt, 2002).

associated with species of Alterneria such as tentoxin, Brefeldin, AF-toxin, AK-toxin, AM-toxin, ACT toxin, AS-toxin maculosin and destruxin B (Meena & Samal, 2019). In addition to the above toxins, *A. brassicae* species develop four cyclic depsipeptide phytotoxins that belongs to the destruxins (Tewari & sBains, 1997). Under *in vitro* and *in vivo* conditions, this fungus produce a phytotoxin that belongs to the compounds named as Destruxin B (C30H51, N5O7, MW=593) and three additional phytotoxins are produced in minute quantity named as destruxin B2, homodestruxin B, and desmethyldestruxin B.

Developed of host resistance

For integrated disease organization, resistance to pathogens by host plants forms one of the imperative mechanisms. There is a need of instantaneous interest towards the control of this disease due to the regular appearance of disease symptoms among the various varieties of *L. esculentum*. Up to date, no elevated resistant source against *A. solani* has been recognized among the growing species of Lycopersicon. Multiple cultivars of *L. esculentum* are more susceptible to Alternaria early blight (Zhang et al., 2003), less information is available through literatures about the wide-ranging or non-host resistance mechanisms in host plants against such necrotrophic and toxigenic pathogens such as *A. solani.*

Development of defense mechanisms by plants in reaction to pathogen attack (preformed and constitutive)

Plants are being constantly subjected to various environmental challenges, as they are in close proximity to the environment. Various unfavorable environmental conditions as (overload or scarcity of water, nutrients, light and temperature profiles) and other biotrophic and necrotrophic pathogens eventually leads to damage to whole plant physically or bacterial and fungal disease development plants. Plant and pathogen combination may be very specific and this interaction between plants and particular fungi is very complex. Plants have developed diverse strategies against their pathogens that involves the use of antifungal chemicals. Multiple lines of defense mechanisms have been developed by the plants in order to defend themselves against biotic stress factors (Valcu et al., 2009). In order to protect themselves, pathogens have developed various mechanisms in order to evade the effects of various antifungal chemicals and smoothly cross these defense lines and successfully invade the host plants (Grayer & Kokubun, 2001).

The microclimate i.e. temperature, humidity, light conditions etc. has an initial right on the germination of fungal spores on the host plant surface after their attack. Before reaching the living protoplast, pathogen has to break several lines of defense in plants, including mechanical barriers as thick cuticle layer and other exudate compounds including chemicals that inhibit the germination of fungal spores and germ tube elongation in host plants. These pre-formed antifungal compounds produced by plants, also reffered as pre-infectional metabolites, prohibitins or phytoanticipins. Plants belonging to the family Solanaceae are known to produce phytoanticipins that includes a major steroidal glycoalkaloid α-tomatine (Arneson & Durbin, 1968). Resistance to fungal attack in tomato plants has been found to be linked with leaf enzymes as Polyphenol oxidases, Catalases, peroxidases and high deposits of leaf epicuticular wax that are involved to reduce the incidence of infection, germination of conidia and germ tube formation. If all these pre formed defense arms are not sufficient in restricting the pathogen infection (fungal spore germination and penetration of the hyphae) to the host plants. Then, plants set off various reactions and often generate reactive oxygen species (ROS) as alarming signals within the cell or to the neighboring cells (Glazebrook 2005). These warning signals led to incorporate the structural fortification of the cell wall, the hypersensitive response towards the pathogens by planned cell death, systemic acquired resistance (SAR) progress and the accreting of phytoalexins that is classified among the antifungal compounds.

Systemic acquired resistance (SAR) is a diverse pathway of signal transduction by virtue of which plants protect themselves from pathogens. SAR forms the whole plant resistance response, following an early exposure to the pathogen. The initial exposure of the host plant to the pathogen results in the generation of endogenously translocated signal that leads to the activation of resistance mechanism in the non infected parts of the plant which are located remotely from the original site of infection (Pieterse & Van Loon, 1999). Hyper sensitive response resulting the cell death and restricts the spread of pathogen infection to other parts of host by inducing limited and complete resistance in host plant and induces the expression of number of defense genes, finally resulting to the advancement of a wide and long-term resistance to pathogens and recognized as systemic acquired resistance (SAR) (Kumar & Klessig, 2003) Therefore, SAR is a broad plant resistance mechanism induced through a local infection. There are separate set of reactions occurring at the site of infection during SAR than at the distant non infected site on the host plant. At the site of pathogen attack, host plants provide resistance response by processes including modifications of the cell wall, phytoalexins production and pathogenesis related (PR) proteins or establishment of hypersensitive reaction (HR) (Van Loon & Van Strien, 1999). HR is also associated with the host's unique identification of an avirulent pathogen during gene communication (Glazebrook 2001). Despite the approved the role of HR in induced defense mechanism in plants, it forms an important factor of attuned plant pathogen interactions. It has been commonly observed that there is the production of PRs before the pathogen infection challenge (Glazebrook, 2005).

One of the main regulators of SAR is salicylic acid (SA). However, the function of SA as a structural signal is not

yet apparent, however there is coordinated expression of a particular group of genes for defense in local and distal (uninoculated) tissues on the accretion of SA (Schenk et al., 2008). Apart from the genes that are expressed by SA mediated signaling pathway, jasmonic acid (JA)/ ethylene (ET)-mediated signaling pathway resulting in the accumulation of other defense signaling marker genes in plants against various pathogens and injury (Glazebrook, 2001). It has been found that in Arabidopsis (*Arabidopsis thaliana*), the upregulation of defense related genes on the activation SA signaling pathway provides resistance to biotrophic pathogens, while the activation of JA/ET signaling pathway and the upregulation of JA/ET signaling mediated defense related genes gets activated in response to necrotrophic pathogens,various infection to the plants by feeding and injuries (Glazebrook, 2005; Kessler & Baldwin, 2002), although, there are few exceptions (Thaler et al., 2004; Glazebrook, 2005).

Signaling during plant pathogen interface

Generally in plants, the identification of pathogen associated elicitor molecules or molecular patterns ($PAMP_s$) triggers baseline defense, that is not limited and provides the host plant a wide ranging resistance against pathogens (Boller & Felix, 2009). In order to protect themselves against the resistance response developed by host plant and cause successful disease development and progression in host, pathogens must escape or suppress the initial line of defense system laden by the host. Various plants express gene-for-gene resistance mechanism which is completely based on recognition of R receptor of the particular gene product centered on the pathogen. This recognition mechanism of avirulant gene products take out the biochemical reactions in a set which includes ROS generation, production of peroxides, superoxides, ion fluxes and phosphorylation of proteins, phytoalexin production (Grant & Mansfield, 1999). This response arrests the infection progression and ultimately results in the programmed cell death (Glazebrook, 2005).

In plants, various pathways exist in order to sense and respond to different environmental factors. Among them one of the important phenomenon known as cross-tolerance incidence, where the exposure of the plant part to any specific stress also contributes to the creation of resistance to other stress factors (Mullineaux et al., 2000), conferring that the fundamental responses against stress factors might share general and common process or in portions. Systematically acquired resistance (SAR) could be generated by local response that leads to the generation of signals systemically resulting in the enhanced resistance against secondary infections to the plant organs that were not yet colonized with pathogens (Sticher et al., 1997). In response to multiple stress challenges such as pathogen infection, wounding or excess damage by abiotic stress factors, there is subsequent change in the redox balance of plants that results in the ROS production among plants. Plants trigger a complex reprogramming system in order to respond particular pathogen and determine the redundant utilization of resources.

SA-dependent signaling pathway

Hyper sensitive response laden by pathogen attack regulates the SA defense signaling by triggering the activation of SA signaling pathway. During both compatible and incompatible interactions among pathogen and host, there is increase in the SA levels at the infection sites, thereby activating defense-related marker genes as PR1, PR2, PR5 (Ryals et al., 1996). It was demonstrated that SA is necessary for PR1 gene and SAR expression (Lawton et al., 1995). By studying the transgenic plants that encodes NahG gene, SA is having eminent role in local and systemic acquired resistance (SAR). EDS1 (enhanced disease susceptibility 1) and PAD4 (phytoalexin deficient 4) are required for SA biosynthesis. Whereas, for the regulation of SA biosynthesis both EDS5 and SID2 genes are involved (Shah, 2003). Interaction of EDS1 and PAD4 results in the SA accumulation and strengthening the defense response in the host (Feys et al., 2001). In Arabidopsis, a central regulator of SA signaling pathway is the non- expresser of PR gene (NPR1), also known as NIM1 and SAI1 and SAR signaling pathway is controlled by NPR1 (Glazebrook et al. 1996). Expression of PR genes is positively regulated by NPR1 that in turn is regulated by some SA induced WRKY proteins (Li et al., 2004). Various studies demonstrated that the levels of NPR1 gets elevated two to three folds on pathogen infection or SA treatment (Cao et al., 1997).

In Arabidopsis during SA signaling pathway, it was found that NPR1 interacts with TGAs that mediates the activation of PR1 expression (Zhang et al. 2003). On the other hand, during plant pathogen interaction, the transcription factor WRKY70 is required for the activation of PR17 expression. Although, induction of WRKY70 is NPR1 dependent and induced by SA. However, no known reports of direct interaction between WRKY70 and NPR1 have been found (Li et al., 2004). NPR3 and NPR4 that forms the paralogues of NPR1 and their binding affinity to SA is different (Fu et al., 2012). Although NPR1 plays a key role in signal transduction during SA signaling, resulting in the expression of PR genes and there is existence of NPR1 independent signaling also. A limitation to NPR1-independent but SA dependent signaling is that there is no any disease resistance and induction of PR genes in npr1 plants (Glazebrook et al., 1996). Thus, it was elucidated that there is a second unidentified signal that works in juxtaposition with SA to turn on the NPR1-independent defense signaling pathway in plants.

Jasmonic acid (JA) dependent signaling pathway

Jasmonic acid (JA) and ethylene (ET) mediated signaling have been found to provide defense response in plants in addition to SA signaling pathway (Balbi & Devoto, 2008). Jasmonates are comprised of both Jasmonic acid and methyl jasmonate (MeJA) and are derived from the α-linolenic acid. By the action of enzyme lipase, Jasmonates are released

from the chloroplast membranes and are later oxygenated by lipoxygenases (LOXs) (Wasternack, 2007). Jasmonates are involved in regulating the various physiological processes in plants including wound responses, defense against pathogen, insect attack and productiveness (Wasternack & Parthier, 1997). Jasmonates assist plants to deal with various stress factors of environment including drought, lower temperatures and salinity stress (Cheong & Choi, 2003). During the initiation of JA signaling pathway, Jasmonoyl-isoleucine that forms the active form of amino acid conjugate of jasmonic acid is perceived by SCFCOI1 complex that is ubiquitine ligase. On recognition of Jasmonoyl-isoleucine (JA-Ile) by CORONATINEINSENSITIVE1 (COI1), it results in the ubiquitination of JASMONATE ZIM DOMAIN (JAZ) proteins followed by subsequent proteosomal degradation. The degradation of JAZ proteins results in the activation of JA response and subsequently the expression of genes that were repressed by JAZ-mediated repression. Recent structural and pharmaceutical findings suggest that the Jasmonoyl-isoleucine JA-Ile is truly perceived by the complex of both COI1 and JAZ (Sheard et al., 2010). This is because JAZ domain is necessary and forms an important factor to trap the hormone in an open binding pocket of COI1 that recognizes the signal (JA-Ile) and the hormone is perfectly trapped to the binding site by the loop region in the JAZ protein; furthermore, these findings identified that inositol pentakisphosphate forms an important component of JA co receptor complex, showing interaction with both COI1 and JAZ during signaling pathway (Sheard et al., 2010). Various defense metabolites are produced by JA responsive genes. Apart from local defense, JA mediate the signaling flow by producing signaling molecules that circulate systematically to induce systemic responses (SAR) in the distant organs that were not initially infected by pathogen attack or herbivory and provide protection against upcoming infection (Howe & Jander, 2008; Koo et al., 2009).

JA signaling induces the activation of transcription factor (JERF3), transcription for lipoxygenase (LOX2), allene oxide synthase and cyclase (AOS, AOC), oxophytodienoate reductase (OPR3), defective in anther dehiscence1 (DAD1) and jasmonic acid carboxyl methyltransferase (JMT) by JA signaling pathway (Pieterse et al., 2009; Pirrello et al., 2012). It was reported that A. thaliana mutants were highly susceptible to necrotrophic pathogens such as *A. brassicicola*, Pythium sp., *A. thaliana* as they were damaged in JA production or JA perception Figure 4.

Coupling between JA and SA signaling pathways

Plants are constantly subjected to various biotrophic, necrotrophic and hemi biotrophic fungal pathogens. To combat against these pathogens and on the basis of effectiveness of the attackers, plants use different mechanisms that efficiently regulate their defense repertoires. These defense mechanisms in plants against the attackers of sharp focusing are normally laden by hormonal crosstalk (Pieterse et al., 2009). After detailed characterization of signal crosstalk, SA and JA signaling pathways show antagonistic interaction to each other (Kunkel & Brooks, 2002). Biotrophic fungal pathogens induce SA- pathway that often suppresses the JA dependent defense signaling pathway (El oirdi et al., 2011) and the sensitivity and biosynthesis of JA can be depressed by the SA (Spoel et al., 2003). JA dependent defense response is apparently suppressed by the SA-inducing defense response against biotrophic pathogens by utilizing resources overJA-dependent defense responses. Similarly, JA defense signaling pathway can inhibit the SA dependent signaling pathway (Uppalapati et al., 2007).

CONCLUSION

By combining the available information on the identification and systematic of fungal pathogen, it is mostly based on the

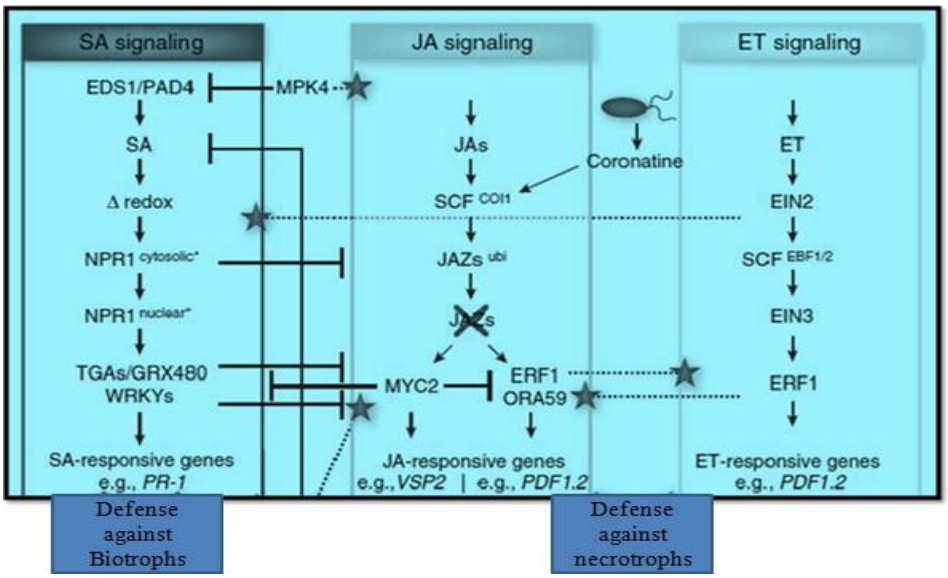

Figure 4. Phytohormone networking in plant immune response against pathogens (Pieterse et al., 2009).

morphological criteria of the dothideomycetic pathogenic fungi as they are mostly recognized based on their phenotypes. The physiology and disease development of fungi and defense signaling mediation by the host has been summarized in this review. This review fills up the present knowledge gap associated to the early blight disease caused by *Alternaria solani* and adds more information to the already available literature and provides sophisticated information regarding the distribution, disease development and defenses signaling strategy developed by the host. Understanding the physiology of pathogen, disease development and defenses signaling mediation by host plant forms the effective use of this literature to filter the phylogenetic category, pathogenicity-related genes and the control of disease development and progression of Alternaria spp. as the possible technologies have not yet been fully extended to the agriculture research in order to increase crop yield and enhance resistance to plant diseases. Therefore, modern techniques such as RNAi or CRISPR/Cas genome editing and gene silencing systems and detailed molecular studies of the host-pathogen interaction are urgently required to functionally distinguish the genes for pathogenicity in Alternaria group and afterward create the strategies for the control of early blight.

Conflict of Interest

The authors declare that there is no conflict of interest.

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