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Pathogenesis mechanisms employed by *Alternaria* species

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Abstract

Alternaria species are mainly saprophytic fungi, but some have acquired pathogenic capacities causing plant diseases over a broad host range. More than 70 phytotoxins are produced by them from which only a small proportion have been chemically characterized and reported to act as mycotoxins. Host-selective toxins (HSTs) produced by *Alternaria* plant pathogens are generally low-molecular-weight secondary metabolites with a diverse range of structures that function as effectors controlling pathogenicity or virulence in certain plant–pathogen interactions. This review summarizes all the diseases caused by *Alternaria* spp., mycotoxins produced by *Alternaria* spp. and the recent advances in elucidating mode of action of host specific *Alternaria* toxins at physiological, biochemical and molecular levels.

Keywords: *Alternaria spp., mechanism, mode of action, phytopathogenesis, toxin*

Introduction

The genus *Alternaria* includes many saprophytic and endophytic species. It was first described by Nees in 1816 with *Alternaria tenuis* as the only species, which was later renamed as *Alternaria alternata* (Fr.) Keissl. (Meena *et al.*, 2010). All *Alternaria* species lack sexuality, and are thus classified into (kingdom fungi, sub-kingdom Eumycotera, phylum fungi Imperfecti, form class Hypomycetes, form order Moniliales, form family Dematiaceae, genus *Alternaria*). Many pathogenic *Alternaria* species produce toxins which facilitate their necrotrophic life style. Prior to colonization, necrotrophs kill their host cells at a distance by producing both toxins, and lytic enzymes. They often trigger genetically- programmed apoptotic pathways, or directly cause cell damage resulting in necrosis. Many species of *Alternaria* produce toxins with broad host ranges, but some agronomically important species produce host-specific toxins with a narrow range often to the cultivar level. *Alternaria* species are important pathogen of many crucifers which also produces carcinogenic, teratogenic and mutagenic mycotoxins. Researchers around the globe are using this necrotrophic pathogen to study molecular mechanisms of plant defense (Oliver & Ipcho, 2004, Thaler *et al.*, 2004, Rowe & Kliebenstein, 2010).

Lawrence *et al.* (2008) used *Alternaria brassicicola* (Schwein.) Wiltshire as a model representative for their basic research on virulence and generalized the role of toxins in the pathogenesis mechanism employed by *Alternaria* genus. Chung (2012) also studied the stress response and pathogenecity of the necrotrophic fungal pathogen *Alternaria alternata.* This review summarizes the recent advances in pathogenesis of *Alternaria* spp. at physiological, biochemical and molecular levels, and also discusses the present understanding of the mode of *Alternaria* host specific toxins.

Plant diseases caused by *Alternaria* species

The genus *Alternaria* includes both non-pathogenic and pathogenic species causing diseases on agronomically important plants including cereals, ornamentals, oilcrops, vegetables and fruits in table 1 (Rahman *et al.*, 2002, Thomma, 2003, Agrios, 2005, Raja *et al.*, 2006, Meena *et al.*, 2010).

Table 1. *Alternaria* species causes various diseases on different hosts

Species	Host	Symptoms	Location	Reference
A. acalyphae	Kucing Galak (*Acalypha indica*)	Leaf spot	Seychelles Islands	Kingsland, 1984
A. alternata	Aloe (*Aloe vera*)	Leaf spot	Pakistan	Bajwa *et al.*, 2010
	Aloe (*Aloe vera*)	Leaf spot	Louisiana	da silva & Singh, 2012
	Almond (*Prunus dulcis*)	Leaf spot	California	Teviotdale *et al*., 2001
	Apple (*Malus Communis*)	Postharvest Decay during Cold Storage	Pennsylvania	Jurick *et al.*, 2014
	Barbados nut (*Jatropha curcas*)	Inflorescence blight	Sinaloa (Mexico)	Angeles *et al*., 2012
	Baby's breath (*Gypsophila paniculata*)	Leaf spot	Bulgaria	Margina *et al*., 1999
	Banana (*Musa)*	Leaf spot	United States	Parkunan *et al*., 2013
	Big leaf hydrangea (*Hydrangea macrophylla*)	Leaf spot	Italy	Garibaldi *et al*., 2007
	Big bend bluebonnet (*Lupinus havardii*)	Stem blight	Texas	Colbaugh *et al*., 2001
	Desert zinnia (*Zinnia acerosa*)	Flower blight	Texas	Colbaugh *et al*., 2001
	Bladder dock (*Rumex vesicarius*)	Leaf spot	India	Sankar *et al*., 2012
	Black mangrove (*Bruguiera gymnorrhiza*)	Leaf spot	China	Lin *et al*., 2014
	Cherry (*Prunus avium)*	Leaf spot	Greece	Thomidis & Tsipouridis, 2006
	Cherry fruits (*Prunus avium*)	Black spot	China	Zhao & Liu, 2012
	Compass plant (*Silphium laciniatum*)	Blight	Poland	Wagner & Jamiolkowska, 2004
	Cotton (*Gossypium hirsutum*)	Stem canker	-	Laidou *et al*., 2000
	Chinese dwarf Banana (*Musa*)	Leaf spot	China	Fu *et al.*, 2014
	Crown flower (*Calotropis gigantean*)	Leaf spot	Rajasthan	Sain *et al*., 2009
	Cucumber (*Cucumis sativus*)	Leaf spot	-	Vakalounakis, 1990
	Desert Zinnia (*Zinnia acerosa*)	Flower blight	Texas	Colbaugh *et al*., 2001
	Date Palm (*Phoenix dactylifera*)	Postharvest Black Spot	Spain	Palou *et al*., 2013
	English walnut (*Juglans regia*)	Leaf spot	-	Belisario *et al.*, 1999
	Fig (*Ficus carica*)	Fruit Rot	Montenegro	Latinovic *et al*., 2014
	Gopher plant (*Euphorbia lathyris*)	Blight	China	Yu *et al.*, 2011
	Heart-leaved houttuynia (*Houttuynia cordata*)	Leaf spot	China	Zheng *et al*., 2011
	Hop cones (*Humulus lupulus*)	Infection	Australia	Pethybridge *et al.*, 2001
	Kiwifruit (*Actinidia deliciosa*)	Dieback	-	Tsahouridou & Thanassoulopoulos, 2000

	Kiwifruit (*Actinidia deliciosa*)	Leaf spot	Turkey	Karakaya & Celik, 2012
	Kiwifruit (*Actinidia deliciosa*)	Leaf spot	Italy	Corazza *et al*., 1999
	Lemon (*Citrus*)	Brown spot	Yunnan Province China	Wang *et al*., 2010
	Lime (*Citrus*)	Brown spot	Peru	Marin *et al*., 2006
	Lemon (*Citrus*)	Black rot	-	Peever & Carpenter Boggs, 2005
	Lemon (*Citrus*)	Brown Spot	Spain	Vicent *et al*., 2000
	Marigold (*Tagetes erecta*)	Leaf Spot	Beijing, China	Li *et al*., 2014
	Melon	Leaf spot	Mid-Atlantic Region of the United States	Zhou & Everts, 2008
	Pomegranate (*Punica Granatum*)	Black spot	Spain	Berbegal *et al*., 2014
	Peace lily (*Spathiphyllum*)	Leaf spot	Argentina	Cheheid *et al*., 2000
	Paneer dodi (*Withania coagulans*)	Leaf Spot	India	Sharma *et al*., 2013
	Philodendron (*Philodendron*)	Leaf Spot	China	Zhou *et al*., 2014
	Potatoe (*Solanum tuberosum*)	Leaf Blight	South Africa	van der Waals *et al*. 2011
	Prickly-ash (*Zanthoxylum piperitum*)	Blight	China	Yang *et al*., 2013
	Switchgrass (*Panicum virgatum*)	Leaf Spot	Tennessee	Vu *et al*., 2012
	Tobacco (*Nicotiana tabacum*)	Brown spot	Connecticut and Massachusetts	LaMondia, 2001
	Tomato (*Solanum lycopersicum*)	Leaf blight	Pakistan	Akhtar *et al*., 2004
	Toothed Dock (*Rumex dentatus*)	Leaf Spot	Pakistan	Siddiqui *et al*., 2009
	Thorowax (*Bupleurum chinense*)	Leaf blight	China	Zhang *et al*., 2010
	Tea (*Camellia sinensis*)	Leaf spot	China	Zhou & Xu, 2014
	Vine spinach (*Basella alba)*	Leaf blight	India	Sankar *et al*., 2011
	Wonder tree (*Idesia polycarpa*)	Leaf spot	China	Sun *et al*., 2014
A. arborescens	Tomato (*Solanum lycopersicum*)	Stem canker	-	Kirk *et al*., 2008
A. arbusti	Asian pear (*Pyrus pyrifolia*)	Leaf lesions	-	Kirk *et al*., 2008
A. arotiincultae	Carrot (*Daucus carota*)	-	New Zealand	Trivedi *et al*., 2010
A. bataticola	Sweet potato (*Ipomoea batatas*)	Leaf spot and stem blight	South America	Lopes & Boiteux, 1994
A. blumeae	Hunchback's mother (*Blumea aurita*)	Lesions	-	Kirk *et al*., 2008
A. brassicae	Daikon (*Raphanus sativus cv. longipinnatus*)	Leaf spot	California	Koike & Molinar, 1997
	Whitetop (*Lepidium draba)*	Leaf Spot	North America	Caesar & Lartey, 2009
	Canola	Gray leaf spot	Argentina	Gaetan & Madia, 2005
	Abyssinian Kale (*Crambe abyssinicia*)	Leaf spot	Australia	You *et al*., 2005
A. brassicicola	Cauliflower (*Brassica oleracea*)	Leaf blight	Rajasthan	Porwal & Kothari, 1970
	Field Pannycress (*Thlaspi arvense*)	Leaf spot	Geneva, NY	Cobb & Dillard, 1998
	Dyer's Woad Leaf (*Isatis indigotica*)	Leaf spot	China	Gao *et al*., 2014

A. brunsii	Cumin (Cuminum cyminum)	Blossom blight	-	Kirk *et al*., 2008
A. cassiae	Cowpea (*Vigna unguiculata*)	-	-	Grange & Aveling, 1998
A. cichorii	Radicchio (*Cichorium intybus*)	Leaf spot	California	Koike & Butler, 1998
A. carthami	Snow lotus (*Saussurea laniceps*)	Leaf spot	China	Zhao *et al*., 2008
	Safflower (*Carthamus tinctorius*)	-	-	Kirk *et al*., 2008
	Snow Lotus (*Saussurea laniceps*)	Leaf Spot	China	Zhao *et al*., 2008
A. carotiincultae	Carrot (*Daucus carota*)	Leaf blight	-	Kirk *et al*., 2008
A. conjuncta	Parsnip (*Pastinaca sativa*)	-	-	Kirk *et al*., 2008
A. cucumerina	Cucurbit (*Cucurbita argyrosperma*)	-	-	Kirk *et al*., 2008
	Pumpkin (*Cucurbita pepo*)	Leaf spot	North Caucasus (Russia)	Gannibal, 2011; Sikora, 1994
A. cinerariae	Leopard plant (*Farfugiu japonicum*)	Leaf spot	Japan	Sakoda *et al*., 2010
A. compacta	Climbing hydrangea *(Hydrangea anomala* subsp. *Petiolaris)*	Leaf spot	Italy	Garibaldi *et al*., 2008
A. chlamydospora	Ashwagandha (*Withania somnifera*)	Leaf blight	-	Vanitha, 2008
A. cheiranthi	Wallflower (*Erysimum cheiri*)	-	-	Bambridge *et al*., 1985
A. dauci	Carrot (*Daucus carota*)	Leaf blight	Israel	Ben-Noon *et al*., 2001
	Carrot (*Daucus carota*)	-	-	Kirk *et al*., 2008
A. dianthicola	Ashwagandha (*Withania somnifera*)	Leaf blight	India	Maiti *et al*., 2007
A. dichondrae	Kidney grass (*Dichondra repens)*	Leaf blight	Australia	Sivapalan & Pascoe, 1994
A. euphorbiicola	Cole	-	-	Kirk *et al*., 2008
A. gaisen	Pear (*Pyrus communis*)	Ring spot	-	Kirk *et al*., 2008
	Rice (*Oryza sativa*)	Leaf spot	Pakistan	Akhtar *et al*., 2014
A. grandis	Potato (*Solanum tuberosum*)	Early blight	Brazil	Rodrigues *et al*., 2010
A. gossypina	Cotton (*Gossypium hirsutum*)	Leaf spot and boll rot	-	Hopkins, 1932
A. helianthi	Sunflower (*Helianthus annuus*)	Stem and foliar blight	Louisiana	Singh & Ferrin, 2012
A. helianthinficiens	Sunflower (*Helianthus annuus*)	Leaf spot	Korea	Cho and Yu, 2000
	Sunflower (*Helianthus annuus*)	Foliar and Stem Blight	Croatia	Vrandecic *et al*., 2012
A. heveae	Rubber Tree (*Hevea brasiliensis*)	Black Leaf Spot	China	Cai *et al*., 2014
A. infectoria	Wheat (*Triticum aestivum*)	-	-	Kirk *et al*., 2008
A. interrupta	Potato (*Solanum tuberosum*)	Early blight	Iran	Taheri *et al*., 2009
A. iridicola	Blackberry-lily (*Belamcanda chinensis*)	Leaf blight	Korea	Yu *et al*., 2000
A. jacinthicola	Water hyacinth (*Eichhornia crassipes*)	Leaf blight	-	Dagno *et al*., 2011
A. japonica	Cole crops	-	-	Kirk *et al*., 2008
	Arugula (*Diplotaxis tenuifolia*) and garden rocket (*Eruca vesicaria*)	Leaf spot	Italy	Garibaldi *et al*., 2011
	Chinese cabbage (*Brassica rapa*)	Damping-off	China	Ren and Zhang, 2012
	Arugula (*Diplotaxis tenuifolia*)	Leaf spot	California	Tidwell *et al*., 2014
A.	Largehead atractylodes rhizome	Leaf spot	China	Tan *et al*., 2012

longipes	(*Atractylodes macrocephala*)			
	Tobacco (*Nicotiana tabacum*)	-	-	Kirk *et al*., 2008
	Carrot (*Daucus carota*)	Leaf Blight	Israel	Vintal *et al*., 2002
	Potato (*Solanum tuberosum*)	Leaf spot	Pakistan	Shoaib *et al*., 2014
	China Root (*Smilax china*)	Leaf spot	China	Long *et al*., 2009
A. molesta	Porpoises (*Phocoena phocoena*)	Skin lesions	-	Kirk *et al*., 2008
A. multirostrata	Rough Mexican clover (*Richardia scabra*)	Blight	-	Jackson and Simmons, 1968
A. mali	Apple (*Malus communis*)	Necrotic leaf spot	Turkey	Ozgonen and Karaca, 2005
A. palandui	Onion (*Allium cepa*)	leaf blight	-	Karthikeyan *et al*., 2005
A. panax	Sun King (*Aralia cordata*)	Leaf spot	Japan	Zhang *et al*., 2009
	Japanese *aralia* (*Fatsia japonica*)	Leaf blight	Europe	Garibaldi *et al*., 2004
	Ginseng (*Panax ginseng*)	Blight	Australia, Canada, China, Italy, Japan, Korea, Netherlands, New Zealand, Spain, United Kingdom, United States and Venezuela	Woodhall and Sansford, 2006
	Octopus tree (*Schefflera actinophylla*)	Leaf spot and blight	Hawaii	Alfieri *et al*., 1994
	Ginseng (*Panax quinquefolius*)	Leaf spot and blight	Hawaii	Alfieri *et al*., 1994
A. passiflorae	Passion-Vine (*Passiflora*)	Brown- spot	New Zealand	Brien, 1940
A. petroselini	Fennel (*Foeniculum vulgare*)	Seedling damping-off	Netherlands	Pryor & Asma, 2007
	Parsley (*Petroselinum crispum*)	Leaf blight	-	Kirk *et al*., 2008
	Chinese Hickory (*Carya cathayensis*)	Leaf Blight	China	Liu *et al*., 2013
	Fennel (*Foeniculum vulgare*)	Leaf Blight	Spain	Bassimba *et al*., 2012
A. porri	Leek (*Allium*)	Purple blotch	California	Koike & Henderson, 1998
	Chicory (*Cichorium endivia* L.)	Leaf Spot	Argentina	Sarasola, 1970
	Velvet Bean (*Mucuna pruriens*)	Leaf Spot	China	Ye *et al*., 2013
A. radicina	Carrot (*Daucus carota*)	Black Rot	Michigan	Saude & Hausbeck, 2006
A. raphani	Chinese radish (*Raphanus sativus*)	Black patches	Canada	Su *et al*., 2005
A. saponariae	Soapwort (*Saponaria*)	Leaf spot	California	Koike *et al*., 1999
A. selini	Parsley (*Petroselinum crispum*)	Crown decay	-	Kirk *et al*., 2008
A. sesami	Sesame (*Sesamum*)	Leaf spot	-	Kirk *et al*., 2008
A. sesamicola	Sesame (*Sesamum indicum*)	Blight	-	Singh *et al*., 1980
A. smyrnii	Alexander (*Smyrnium olusatrum*)	Leaf spot	-	Kirk *et al*., 2008
A. solani	Potato (*Solanum tuberosum*)	Early blight	Idaho	Wharton *et al*., 2012
	Potato (*Solanum tuberosum*) and tomato (*Solanum lycopersicum*)	Early blight	-	Kirk *et al*., 2008

	Potato (Solanum tuberosum)	Early Blight	Idaho	Miles *et al*., 2013
A. tenuissima	Pigeonpea (*Cajanus cajan*)	Blight	India	Sharma *et al*., 2012
	Siberian Ginseng (*Eleutherococcus senticosus*)	Leaf spot	China	Gao *et al*., 2011
	Strawberry (*Fragaria*)	Fruit rot	Korea	Lee *et al*., 2001
	Broad bean (*Vicia faba*)	Leaf spot	Japan	Honda *et al*., 2001
	Blueberry disease (*Vaccinium myrtillus*)	Leaf spot	China	Luan *et al*., 2007
	Candytuft (*Iberis sempervirens*)	Leaf spot	Italy	Garibaldi *et al*., 2005
	Leopard Plant (*Farfugium japonicum*)	Leaf spot	Korea	Lee *et al*., 2013
	Apple (Malus communis)	Postharvest Decay	United States	Kou *et al*., 2014
	Green Amaranth (*Amaranthus hybridus*)	Leaf Spot	-	Blodgett *et al*., 1999
	Potato (*Solanum tuberosum*)	blight	China	Zheng & Wu, 2013
	Blueberry (*Vaccinium corymbosum*)	Leaf spot	Western Australia	You *et al*., 2014
A. tomatophila	Tomato (*Solanum lycopersicum*)	Early blight	Brazil	Rodrigues *et al*., 2010
A. triticimaculans	Wheat (*Triticum aestivum*)	Leaf spot	Argentina	Kirk *et al*., 2008
	Wheat (Triticum aestivum)	Leaf spot	Argentina	Perello *et al*., 1996
A. yaliinficiens	Ya Li pear (*Pyrus*)	Leaf spot	U.S	Roberts, 2005
A. zinniae	Zinnia (*Zinnia elegans*)	Leaf spot	Germany	Pape, 1942
A. zinniae	Marigold (*Tagetes patula*)	Spot and flower blight	-	Chandel and Singh, 2010
A. sp.	Strawberry (*Fragaria*)	Fruit rot	Taiwan	Ko *et al*., 2008
	Barberry (*Berberis*)	Stem spot	Iran	Mairabadi *et al*., 2005
	Highbush Blueberry (*Vaccinium corymbosum*)	Leaf spot	South Korea	Kwon *et al*., 2014
	Apple (*Malus communis*)	Leaf blotch	Australia	Harteveld *et al*., 2014
	Tea plant (*Camellia*)	Leaf spot	Italy	Garibaldi *et al*., 2007
	Japanese Plum (*Prunus*)	Leaf spot	Korea	Kim *et al*., 2005
	Loquat (*Eribotraya japonica*)	Fruit Rot	Taiwan	Ko *et al*., 2010
	Hazelnut (*Corylus avellana*) and Walnut Fruit (*Juglans regi*)	Leaf spot	-	Belisario *et al*., 2004

Host selective toxins
Disease determinants of *Alternaria* spp.

Alternaria species being most ubiquitous and saprophytic fungi produces toxins (Rotem, 1994). Determination of the exact mode of action of phytotoxic compounds in pathogenesis or virulence is critical and it can be determined by studying virulence and sensitivity of toxins produces by different isolates on host genotypes (Strange, 2007, Meena *et al.,* 2012). Recently, Rotondo *et al.* (2012) compared the *Alternaria* spp. collected in Italy with *A. mali* (Roberts) and other AM-toxin producing strains and suggested that the production of the AM-toxin might be involved in pathogenesis by some of the Italian isolates of *A. alternata*.

Host-selective toxins (HSTs) are mycotoxins which are often essential for both host specificity and pathogenicity, whereas the non-selective toxins (NSTs) are mycotoxins which are important only for virulence. HSTs are produced during germination of spores on plant surfaces (Mausunaka *et al.,* 2005). HSTs are generally low-molecular-weight secondary metabolites but many HSTs like Ptr ToxA and Ptr ToxB by *Pyrenophora tritici-repentis* (Died.) Drechsler, Sn Tox1 and Sn ToxA by *Stagonospora nodorum* (E. Mull.) Hedjar and AB toxin by *A. brassicicola* (Schw.) Wiltsh, are proteinaceous in nature (Wolpert *et al.,* 2002, Friesen *et al.,* 2007, Manning *et al.,* 2009).

Other HSTs are AP- toxin by *Alternaria panax* (Whetzel) (Quayyum *et al.,* 2003), destruxin B & ABR toxin by *A. brassicae* (Berk.) Sacc. Maculosin & AS toxin by *A. alternata* (Fr.) Kressler . Tomato pathotype of *Alternaria alternata* produce two forms of AAL-toxins which are mono-esters of propane-1,2,3 tricarboxylic acid (TA) and 2,4,5,13,14- pentahydroxyheptadecane (TB) (Wang *et al.,* 1996). *Alternaria alternata* pathotypes Japanese pear, Strawberry, tangerine, rough lemon, and apple, respectively, produce AK toxin I and II, AF- toxin I, II and III, ACT- toxin Ib and IIb, ACR toxin , and AM-toxin. Host- specific toxins responsible in causing plant diseases are listed in table 2.

In a study on pathogenic- HST- producing and non-pathogenic- NST- producing *A. alternata* pathotypes, it was revealed that only the pathogenic pathotypes carried small extra chromosomes (Akamatsu *et al.,* 1999, Thomma, 2003). All the toxins produced by *A. alternata* pathotypes are similar in structure. Genes associated with the synthesis of AK, AF and AM toxins are clustered together on small chromosomes (Tanaka & Tsuge, 2000, Johanson *et al.,* 2000; 2001, Hatta *et al.,* 2002). Many mutants have been included in studies determining involvement of toxin in disease development. Johanson *et al.* (2000) cloned and sequenced the cyclic peptide synthetase gene responsible in the synthesis of AM-toxin; this gene has no introns and is 13.1 Kb in length. Mutants obtained by transformation of a wild type toxigenic isolate with disruption vectors were toxin-minus which were unable to cause disease symptoms on susceptible apple cultivars. Recovery of genomic DNA flanking the integration site revealed two genes ak1 & ak2. ak1 encodes a carboxyl activating enzyme, while ak2 encodes a protein of unknown function. Targeted gene disruption showed that both ak1 and ak2 genes were necessary for pathogenicity and toxin production. Homologues of both genes were detected in both tangerine and pear pathotypes, but not in other pathotypes or non-pathogenic isolates.

Several other mycotoxins and phytotoxic metabolites produced by *Alternaria* species include:, Alternaric acid, alternariol, solanapyrone and zinnolide by *A. solani* (Ellis & G. Martin) (Anderson *et al.,* 2008), Alternariol monomethyl ether by *A. dauci* (J.G. Kuhn) (Ostry, 2008), erythroglaucin and anthraquinones by *A. porri* (Ellis). Ciferri (Ostry, 2008), ATC-toxin by *A. tenuissima* (Kunze) Wiltshire (Ostry, 2008), and zinnolide and znnimidine by both *A. solani* (Sorauer) and *A. cichorii* (Natrass) (Ostry, 2008). Zinnolide and Znnimidine are structurally similar to Zinnole which is the only common metabolite produced by *A. porri, A. dauci* and *A. solani* (Horiuchi *et al.,* 2003). Alternaric acid, produced by *A. solani,* although not phytotoxic when sprayed alone on tomato leaves, but it is the major metabolite responsible for the development of necrotic and chlorotic symptoms. Alterporriols, altersolanols, macrosporin and tentoxin are produced

Table 2. A list of Host-specific toxins and their diseases

Disease	Pathogen species	Toxin	Target site	Chemical structure	References
Alternaria stem cancker of tomato	*Alternaria alternata* f.sp. lycopersci (tomato pathotype)	AAL-Toxin	Sphingolipid & ethanolamine metabolism	Ester of propanetricarboxylic acid and aminodimethylheptad ecapentol	Bottini and Gilchrist, 1981
Brown spot of tangerine	*Alternaria alternata* f.sp. citri tangerine	ACT toxin	Plasma membrane	Ester of amino acid epoxydecatrienoic acid	Kohmoto *et al.*, 1993
Black leaf spot of strawberry	*Alternaria alternata* f.sp. fragariae (strawberry pathotype)	AF toxin	Plasma membrane	Ester of amino acid epoxydecatrienoic acid	Nakatsuka *et al.*, 1986
Black leaf spot of Japanese pear	*Alternaria alternata* f.sp. kikuchiana (Japanese pear pathotype)	AK toxin	Plasma membrane	Ester of amino acid epoxydecatrienoic acid	Nakashima *et al.*, 1985
Brown spot of rough lemon	*Alternaria alternata* f.sp. citri jambhiri (rough lemon pathotype)	ACR toxin	Mitochondria	Polyhydroxyalkenyl I dehydropyrone	Gardner *et al.*, 1985
Alternaria blotch of apple	*Alternaria alternata* f.sp. mali (apple pathotype)	AM toxin	Chloroplast and plasma membrane	Cyclic depsipeptide	Okuno *et al.*, 1974
-	*Alternaria alternata* (spotted knapweed pathogen)	Maculosin	-	-	Stierle *et al.*, 1988
-	*Alternaria alternata* (sunflower pathogen)	AS-toxin	-	-	Liakopoulou-kyriakides *et al.*, 1997
Black spot of rapeseed	*Alternaria brassicae*	Destruxin B	-	cyclidepsipeptide	Bains & Tiwari, 1987
Black leaf spot of *Brassica* spp	*Alternaria brassicicola*	AB-toxin	-	Protein	Chaube & Pundhir, 2005
Brown spot of Tobacco	*Alternaria alternata* Tobacco pathotype (*A. longipes*)	AT -toxin	-	-	Chaube & Pundhir, 2005
-	*Alternaria brassicae*	ABR-toxin	-	-	Parada *et al.*, 2008
	Alternaria panax	AP-toxin	-	-	Quayyum *et al.*, 2003

in cultures of *A. porri* and *A. solani* (Suemitsu *et al.*, 1992). *Alternaria alternata* produces a number of mycotoxins, including alternariol, alternariol monomethyl ether, altenuene, altertoxins I, II, III, and tenuazonic acid (Ostry, 2008, Zhou & Qiang, 2008). Nine novel compounds closely related to ACTG-toxin, termed as tricycloalter-narenes, were isolated from a strain of *A. alternata*, from *B. sinensis* (L.) which was earlier used for the production of the non-specific phytotoxin tentoxin (Nussbaum *et al.*, 1999). Liebermann *et al.* (2000) also reported isolation of 11 new bicycloalternarenes as well as ACTG-toxins A and B. *Alternaria brassicae* (Berk.) Sacc. produces cyclic depsipeptide phytotoxin including Homodestuxin B, Destruxin B2 & desmethyldes-truxin B (Ayer & Pena-Rodriguez, 1987, Buchwaldt & Green, 1992, Montemurro & Visconti, 1992, Agarwal *et al.*, 1994, Parada *et al.*, 2008). *Alternaria brassicicola* produces despeptides and fucicoccin-like toxic compounds and also proteinaceous Brassicillin A (Pedras *et al.*, 2009, Cooke *et al.*, 1997, MacKinnon *et al.*, 1999).

Mode of action of HST's

Understanding the mechanism of action of HSTs provide a better picture of host pathogen interactions and resistance mechanisms. Of the two approaches used to study the mode of action of pathogen, one is the study of host selectivity at the molecular level, and the other at the cellular level. Hypersensitive response (HR) is one of the most effective defense mechanisms developed by plants against their pathogens where several pathogenesis-related proteins (PR) participate and necrosis of the tissue at the site of infection and formation of phytoalexins occur (Agrios, 2005).

At Physiological level

The effect of phytotoxins on plants at the physiological level is characterized by the malfunctioning of many physiological processes including respiration, transpiration, photosynthesis, translocation, growth and development. It is also characterized by the appearance of specific symptoms including wilting, growth suppression, chlorosis, necrosis, and spotting of aerial portions.

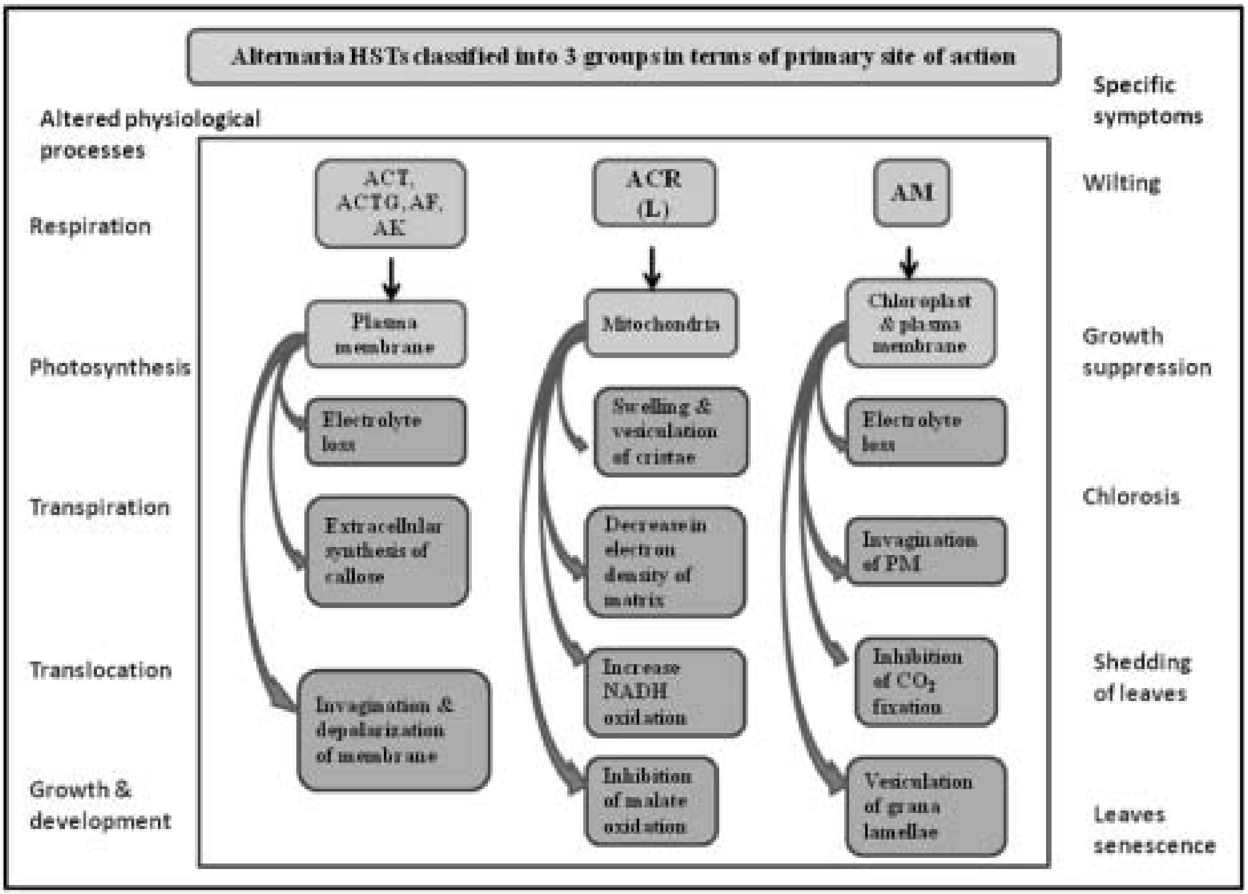
Physiological processes

Alternaria HSTs are classified into three groups in terms of primary site of action. AM toxin targets the chloroplast and plasma membrane, ACR (L) toxin targets mitochondria and ACT, ACTG, AK, AF toxins target the plasma membrane (Fig. 1). *A. solani* infection in potato decreases photosynthesis and increases respiration, in both necrotic and adjacent symptomless tissues (Livescu *et al.*, 1986). In general, respiration increases once parasitic relationships is established. *Alternaria* pathogens infect green aerial tissues and reduce photosynthetic activity, produce cytokinins which lead to the formation of Green Island below the germinating conidia on senescing tissues, and cause deformation in chloroplast and mitochondria (Chaturvedi, 1972, Agarwal *et al.*, 1994, Zheng *et al.*, 2006). In tobacco, treatment by *A. alternata* produced metabolites decrease chlorophyll content, soluble protein, photosynthetic O_2 production, catalase activity, and increase in H_2O_2 content in the senescence leaves (Jia *et al.*, 2010). Plasma membrane is a common active site for action of toxins in animal and plant cells. *Alternaria macrospora* (Zimm.) alters plasma membrane permeability in leaves, and increases leakage of electrolytes, mainly potassium ions (Park & Ikeda, 2008). In *Brassica juncea*, *A. brassicae* HST destruxin B inhibits almost all-macromolecular biosynthesis, promotes ion leaching, and causes aberrations in mitochondria and chloroplast. In tomato, *Alternaria solani* produced alternaric acid induces physiological and morphological modifications of the plasma membrane near plasmodesmata; modification includes localization of free ions in the vicinity of plasma membrane invaginations (Langsdorf *et al.*, 1991).

Specific symptoms

Toxins produced by *A. brassicae* cause brown necrotic spots on leaves and brown streaks on stem leading to yield losses (Aneja & Agnihotri, 2013). *Alternaria raphani* (Groves & Skolko) produces black stripes or dark brown, sharp-edged lesions on the hypocotyls of the seedling (Valkonen & Koponen, 1990) whereas, *A. brassicicola* produces black sooty velvety spots. *Alternaria* infection reduces size of leaves and number of flowers in

Fig.1. Schematic representation of changes at physiological level by *Alternaria* spp.



(Source : Park *et al.*, 1976; Akimitsu 1989; Otani *et al.*, 1995; Thomma 2003; Park and Ikeda 2008)

tomato (Coffey *et al.*, 1975), and stimulates shedding of infected leaves (Spross-blickle *et al.*, 1989).

At Biochemical level

Infection of Plants by pathogenic fungi may trigger several biochemical defense responses including enzyme synthesis, cell wall deposition of lignin and suberin, and accumulation of specific metabolites (Daayf & Platt, 2000, Abdel-Farid *et al.*, 2009). The mechanisms of host selective pathogenesis are not well understood at the biochemical level, even in cases where the toxin site of action is known.

Enzyme synthesis

The first physical barrier between plants and pathogen invasion is the cuticle (Schweizer *et al.*, 1996, Fan & Koller, 1998, Farah *et al.*, 2005) and cell wall, which inhibit both initiation and spread of infection. One characteristic feature of many phytopathogenic organisms is their ability to produce an array of extracellular and highly stable enzymes capable of degrading the complex polysaccharides of the plant cell wall and membrane constituents. Inoculation of *A. brassicae* on the leaves of *B. juncea* blight resistant cultivar RC-781 decreases the activities of cell wall degrading polygalcturonase and cellulose enzymes, but increases their activities in a sucepticible cultivar Varuna up to 3 days of infection (Garg *et al.*, 1999). Infection of *A. brassicicola* shows a differential and sequential induction of two classes of cutinolytic esterases. One class is expressed only in short duration contact (24hr) with intact cutin, but not induced by cutin monomer. The second class however, is induced by cutin monomers only in prolonged exposure with intact cutin. This differential behavior indicates a sequential recognition of cutin as a barrier to be penetrated and utilized as a carbon source in saprophytic stages. (Yao & Koller, 1995, Fan & Koller, 1998, Baker *et al.*, 2005). The small (7-10 KD), lipid transfer proteins (LTPs) are expected to be involved in wax transport because of their increased expression during drought condition (Beisson *et al.*, 2003, Cameron *et al.*, 2006, Jubert *et al.*, 2011). During *A. brassicicola* infection the *ltpg1* (GPI-anchored LTP) knockout mutant showed increased susceptibility (Lee *et al.*, 2009), but the genetically unidentified cutinase- deficient mutants were non pathogenic (Tanabe *et al.*, 1988). Suzuki *et al.* (2003) observed that during citrus-pathogen *A. alternata* infection, cutinase release from pegs functions as an aggressiveness factor for penetration into pear tissues (Perez *et al.*, 1991), and triggers a hypersensitive response (HR) in lemon seedlings characterized by phenylalanine ammonia–lyase induction (Roco *et al.*, 1993), scoparone synthesis (Perez *et al.*, 1994a), tissue maceration (Perez *et al.*, 1994b), participation in a signaling pathway including calmodulin, G protein and protein kinases (Ortega & Preze, 2001), and phosphoinositide metabolism (Ortega *et al.*, 2002). It was observed that the expression of hsr203j gene, a known marker for hypersensitive response is more in *A. brassicae* tolerant cultivar than in susceptible cultivar of *B. juncea* (Mishra *et al.*, 2011). Chitin is a component of fungal cell walls, which is absent in plants, yet plants produce chitin–degrading enzymes; chitinase produced in plants can directly affect the viability of fungal pathogens (Boller, 1995, Stacey & Shibuya, 1997, Shibuya & Minami, 2001). This is proved by overexpression of chitinase in transgenic plants which are generally more resistant to fungal pathogens. Further, it was observed that more chitinase is produced and accumulate at the site of fungal infection (Majeau *et al.*, 1990, Roby *et al.*, 1990, Wubben *et al.*, 1992). Chikkara *et al*. (2012) reported that co-expression of chitinase and ribosomal - inactive protein in *B. juncea* provides more protection against *A. brassicae*. AAL-toxin, structurally related to sphinganine, a member of sphinganine-analogue mycotoxin (SAMS), is an inhibitor of sphinganine-N-acyltransferase (Gilchrist *et al.*, 1994, Abbas *et al.*, 1994) enzyme important in sphingolipid biosynthesis leading to accumulation of free sphingoid bases (Brandwagt *et al.*, 2000, Spassieva *et al.*, 2002, Gechev & Hille, 2005). These long chain sphingoid bases (LCBs) are determinant in the occurrence of programmed cell death (PCD) in susceptible plants (Shi *et al.*, 2007, de Zélicourt *et al.*, 2009). SAMS inhibit ceramide biosynthesis. Biochemical and molecular data demonstrated that programmed cell death (PCD) triggered by AAL-toxin is also associated with H_2O_2 (Gechev *et al.*, 2004) as *atr* mutant of *Arabidopsis* show enhanced tolerance to H_2O_2 and reactive oxygen species (ROS) - induced cell death (Gechev & Hille, 2005, Gechev *et al.*, 2008). Brassinin hydrolases, a detoxifying enzyme (BHAb) of a crucifer phytoalexin brassinin, also plays an important role in development of disease caused by *A. brassicicola* in *Brassica* (Pedras *et al.*, 2009).

Accumulation of specific metabolites

In Japanese pear, although infection by *A. alternata*, induces general resistance by increasing release of polysaccharides (Hayami *et al.*, 1982), its AK toxins increase susceptibility in cultivar Nijisseiki by suppressing production and release of polysaccharides (Otani *et al.*, 1991, Kodama *et al.*, 1998, Suzuki *et al.*, 2003). In Chinese cabbage, *A. brassicae* infection signiûcantly increases glucosinolates (aliphatic and indole) and anthocyanins, but decreases sucrose levels (Rosta´s *et al.*, 2002, Abdel-Farid *et al.*, 2009). Imazaki *et al.* (2010) reported that *A. alternata* pathotypes contain abundant peroxisomes which are very important in both tissue colonization and pathogenesis. Other functions of peroxisomes include fatty acid metabolism, acetyl-CoA generation, secondary metabolism, cell wall biogenesis, and peroxisome homeostasis.

At Molecular level

The interaction between plants and pathogens at molecular level are specific, complex and dynamic. Many responses are evoked in plants upon encountering pathogens, but relatively very few have been studied in detail. Key events in plant-pathogen interaction include perception of pathogen on the plant or cell surface by receptors/sensors, and transduction of these perceptions through various transcription factors and target genes which are involved in coordination of the appropriate responses (Hammond & Jones, 1996). Different types of both plant and pathogen genes have been shown to be involved in plant and necrotrophic fungal interaction. These responses range from genes that encode proteins like receptor/receptor kinase, cell wall degrading enzymes, toxins, and transporter proteins, to those involved in signal transduction cascades such as mitogen activated protein kinases (MAPKs), and various transcription factors like WRKY, NAC (Lawrence *et al.*, 2008, Wang *et al.*, 2009, Amselem *et al.,* 2011). Ghose *et al.* (2008) also studied the differential profiling of selected defense-related genes induced on challenge by *A. brassicicola* in resistant white mustard, and their comparative expression pattern in susceptible Indian mustard. These genes have similarity with receptor-like-protein-kinase genes, genes involved with calcium-mediated signaling, salicylic acid-dependent genes, and other functional genes in *Arabidopsis.* Various studies determining the role of receptor/receptor-like- protein in perception of fungal pathogens have been concluded. After the attack, the fungal cell wall is hydrolyzed by an enzyme chitinase, and fragment of cell wall chitin is perceived by a receptor known as chitin elicitor receptor kinase (CERK1) or Lys M receptor-like protein kinase (Lys M RLK1). A mutation in lys m gene blocks the induction of almost all chito-oligosaccharide-responsive genes and leads to increased susceptibility to fungal pathogens indicating that LysM RLK1 is essential for chitin signaling in plants (Wan *et al.,* 2008). Another receptor gene, Phytosulfokine Receptor (PSK-receptor) psk2 and pskr1, also got induced in *Arabidosis* leaves after *A. brassicicola* infection, which shows its role in pathogenesis (Loivamaki *et al.,* 2010).

Phytopathogenesis of *A. brassicae* on *B. juncea*

Molecular mechanism of Alternaria blight in *Brassica* shows involvement of chlorotic & necrotic toxins as well as of phytohormone. *Alternaria brassicae* produces a chlorotic toxin destruxin B that plays an important role in signal transduction leading to programmed cell death, and suppressing the defense system (Taj *et al.,* 2004). Differential expression of cell cycle proteins in toxin- treated leaves and calli, and overexpression of p53 suggest that the toxin-mediated perturbations in cell cycle eventually cause p53- induced - programmed cell death (PCD) (Khandelwal *et al.,* 2002). Interestingly, *A. brassicae* pathotoxin-induced-cell-death pathway was antagonized by a phytohormone zeatin, in cell culture of *B. juncea* (Pandey *et al.,* 2001). The antagonistic effect of these two structurally different entities strongly suggests the role of interactive- signaling -pathways in pathogenesis of Alternaria blight in *Brassica* species. Introgression of Osmotin, a known pathogenesis related PR-5 protein causes perturbation in resistance to biotic and abiotic stresses (Taj *et al.,* 2004). The effect of toxin and zeatin treatments on the *B. juncea* leaf proteome was investigated by using two-dimensional electrophoresis and liquid chromatography mass spectrometry (LCMS) techniques; results showed that 20 proteins were uniquely expressed in toxin treated leaf, while 27 proteins were expressed in together with toxin and zeatin. LCMS technique has also been used to identify a total of 15 proteins with differential expression in toxin treated leaves. The proteins identified in response to the toxin are glycosyl hydrolases, subtilisin like proteases, P-nitrophenyl phosphatase, malate dehydrogenase, heat shock, ribulose 1,5 bis phosphate carboxylase, Cucumisin-like serine proteases, Globulin like protein, and adenosine triphosphate (ATP) synthase (Singh et al. unpublished data). Shrama *et al.* (2007) also studied the proteome –level changes in *A. brassicae – B. napus* and suggested role of reactive oxygen species (ROS)- mediated- auxin- signaling in the pathosystem.

Mitogen-activated-protein-kinases (MAPK) cascades are also standard players in the signal transaction literature for diverse organisms (Madhani & Fink, 1998, Cobb, 1999). Activation of MAPK confers resistance to both bacterial and fungal pathogens (Sheen *et al*., 2002). Deciphering the MAP Kinase machinery components in *B. juncea,* reverse transcriptase polymerase chain reaction (RT-PCR) amplification of all 20 known MAPK has been done. Amongst the MAP Kinases 8, 12 and 18 showed no expression, expression of MAP Kinase 3, 10 and 14 were validated with the Northern Blot (Singh et al. unpublished data), MAPK 3 important gene directly correlated with the transcription factors, and expresses in compatible interaction of *A. brassicae* and *B. juncea* (Taj *et al.,* 2011). Expression of MAPKK4, MAPKK5, MAPKK9, MAPKKK1, Wrky 22 and Wrky 29 has also been validated by Real time PCR (Giri *et al.,* unpublished data). Expression analysis of MAP 2K 9 and MAP K 6 is also governed during pathogenesis of Alternaria blight in *A. thaliana*. where simultaneous increased levels up to middle stage of disease progression were observed (Kannan *et al.,* 2011).

Deciphering the resistance mechanism in *Basella alba* (L.), against *A. brassicicola* shows the downstream signaling of MAPK-6 which was found to be activated after ethylene treatment (Taj *et al.,* 2010). This might be a significant step as up-regulation of ndr1/hin-1- like gene nhl25, and PR gene reported during *Basella alba* infection (Varet *et al.,* 2002); these genes were downstream targets of MAPK6 in *Arabidopsis* which are controlled by Salicylic acid (SA) (Desikan *et al.,* 1999, Ghose *et al.,* 2008). Activation of more than one member of MAPK by *Alternaria* suggests that MAPK cascades act as points of convergence and divergence in signaling, and might play a pivotal role in deciding whether disease should progress, or defense pathways defeat the pathogen. Transgenic potato plants carrying StMEK1 (MAPKK) also show resistance against *A. solani* by provoking oxidative burst-mediated plant defense (Yamamizo *et al.,* 2006).

Phytohormones in *Alternaria* pathogenesis

The involvement of phytohormone dependent pathway is well documented in plant pathogen interaction. Role of Jasmonic acid (JA)- dependent-signaling- pathway of necrotrophic pathogen, and Salicylic acid (SA) –dependent- signaling- pathway of biotrophic pathogen is also well documented. Mutants of JA, and/or Ethylene (ET)- signaling pathways, and JA-insensitive *coi-1* of *A. thaliana* respectively, show increased susceptibility, and resistance against *A. brassicicola* (Thomma *et al.,* 1999, Kachroo *et al.,* 2001, Nandi *et al.,* 2005, Mang *et al.,* 2009). Systemic expression of the JA-inducible pdf1.2 gene is also reduced after infection with *A. brassicicola*. This reflects the necessity of JA-mediated responses for expression of this trait (Glazebrook, 1999). In contrast, the SA-insensitive mutant *npr-1,* and SA-depleted *nahG* line has no effect on the resistance phenotype (Thomma *et al.,* 1998) indicating no direct involvement of SA as a signaling molecule. In another study, induction of SA signaling marker, PR1, and enhanced biosynthesis of the antifungal compound camalexin upon infection by *A. brassicicola* in *Arabidopsis* raises the possibility of cross-talk between these different signaling networks (Doares *et al.,* 1995, Kunkel & Brooks, 2002, Kachroo *et al.,* 2003a, 2003b). Over-expression of ngnpr3 gene in tobacco plant also shows the resistance against *A. brassicicola* (Zhang *et al.,* 2010). Jasmonic acid also helps in the modulation of MAP Kinase 4 and MAP Kinase 6 during phytopathogenesis of Alternaria blight in *A. thaliana*.

Furthermore, biosynthesis of antifungal compounds camalexin which plays a role against *Alternaria* pathogen has been found to be positively controlled by SA and ET. JA regulated lox gene is also known to play role during *A. brassicae* pathogenesis (Taj *et al.,* 2011). During incompatible interaction of *Arabidopsis* transgenic plant harboring CaLOX1-OX, lox1 mutant and *A. brassicicola*, it was discovered lox1 mutant plants are more susceptible than wild type, CaLOX1-OX transgenic, and CaLOX1 plants (Hwang & Hwang, 2010). Transcription of the plant defense genes pdf1.2 and Thi2.1 is enhanced in response to *Botrytis cinerea* (De Bary) Whetzel and *A. brassicicola* infection, and is dependent on ET, JA, and Oleic Acid (OA) signals (Epple *et al.,* 1995, Penninckx *et al.,* 1996, Kachroo *et al.,* 2003a, 2003b). Resurrection1 (rst1) mutant plants show more resistance to the necrotrophic fungi *Botrytis cinerea* and *A. brassicicola* by suppressing pathogen growth, sporulation, and disease symptoms, which might be due to altered cuticular waxes (Chen *et al.,* 2005), because the amount of cutin monomers, phytoalexin accumulation, and basal expression of the pdf1.2 gene were significantly enhanced in infected leaves (Mang *et al.,* 2009). Unlike rst 1 mutation, other mutations including mpk4, bik1 and wrky33, cause susceptibility to the necrotrophic pathogens *A. brassicicola* and *Botrytis cinerea* (Petersen *et al.,* 2000, Wiermer *et al.,* 2005, Veronese *et al.*, 2006, Zheng *et al.*, 2006, Mang *et al.,* 2009). Constitutive expression of VvWRKY2 in tobacco reduces susceptibility of *A. tenuis* to the seeds of transgenic tobacco (Mzid *et al.,* 2007). DEAD-box RNA helicase also plays role during *Arabidopsis- A. brassicicola* interaction. Transgenic *Arabidopsis* plant that over-expresses the osbirh1 gene (DEAD-box RNA helicase protein) also shows enhanced expression of PR-1, PR-2, PR-5, PDF1.2, and disease resistance against *A. brassicicola* (Li *et al.,* 2008).

At the cellular level, events during the infection by *A. solani* include general defense responses found also in other plant–pathogen interactions involving quantitative resistance. These responses are basically similar to hypersensitive responses in monogenic resistance, but they are expressed more slowly and at a lower level (Agrios, 2005, Chaerani & Voorrips, 2006).

Differential expression of genes in pathogen

During the course of infection, various genes of pathogen are also expressed and play role in fungal pathogenesis. Gene aafus3 which encodes for FUS3MAPK in *A. alternata* is required for conidial development and penetration of the fungus in plant (Lin *et al.*, 2010). Another study shows that deletion of abpro1 (transcription factor) and abnik1 (two component histidine kinase) gene of *A. brassicicola* results in 70 % and complete loss of virulence, respectively (Cho *et al.,* 2009). Cyanide hydralase, arsenic ATPase, formate dehydrogenase, are some other genes of *A. brassicicola* which are being expressed, and have a role in fungal pathogenesis (Cramer & Lawrance, 2004). Recently, one group shows that unfolded protein response (UPR) pathway also regulates the fungal pathogenesis, and abhac a gene encodes the major UPR transcriptional regulator; Loss of UPR in mutants of *A. brassicicola* resulted in complete loss of virulence (Joubrt *et al.,* 2011).

Future Aspects

The physiological, biochemical and molecular basis for resistance toward *Alternaria* pathogens is still mostly unknown despite recent advancements. There are still many uncovered distinct signaling pathways, enzymes and key regulatory factors involved in this process. Further studies on plant-*Alternaria* interaction require uncovering the different mechanisms employed by the pathogen to develop disease, and overpower the plant defense system. No doubt, these studies will promote our understanding of pathogenesis, and may provide clues to manipulate plant defense signaling pathways as resistance against this fungus, is controlled by multiple plant defense pathways, including both constitutive and inducible factors. Our objective in this review was to provide an overview of physiological, biochemical and molecular basis of phytopathogenesis of *Alternaria* species. Future work should focus on understanding the complete picture of *Alternaria* spp. complex affecting individual vegetable/ *Brassica* crops with very host-specific *Alternaria* species to elucidate the physiology of the early steps involved in signal recognition. There is also a need to study the relationship between pathogenic and molecular (sequence) variability among *Alternaria* isolates apart from relation with morphological and cultural data. Based on the sequence data of type culture, host differentials also need to be standardized.

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