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Genes/Quantitative Trait Loci and Associated Molecular Mechanisms Identified in *Capsicum* Genome for Tolerance to Abiotic and Biotic Stresses

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Abstract

Capsicum is one of the most important vegetable crops of the family Solanaceae and is widely used as spice due to its pungent nature. Besides, *Capsicum* fruit rich in metabolites and vitamins; and also has anticancerous property, which further increases the importance of this crop. However, *Capsicum* crop is highly affected by abiotic/biotic stresses such as drought, heat, cold, salinity, and pathogens. To overcome these stresses, plants adapted several mechanisms such as the production of osmoprotectant, proline, galactinol and raffinose, and the reduction of reactive oxygen species. Autophagy also plays an important role to provide tolerance against stresses through degradation of toxins. Among the others, transcription factors and plasma membrane intrinsic proteins, and plant endophytes are found to be involved in regulating stress tolerance mechanism. Furthermore, in *Capsicum* genome, a number of genes and quantitative trait loci (QTLs) involved in stress tolerance mechanism have been identified. In this chapter, a detail compilation of important molecular mechanisms and associated genes/QTLs involved toward imparting abiotic and biotic stress tolerance in *Capsicum* genome is made.

7.1 Introduction

Environmental stresses including both abiotic and biotic stresses have major effects on different developmental processes in plants. To overcome these stresses, plants adopted different mechanisms including production/accumulation of osmoprotectants, chaperones, and increasing superoxide radical scavengers. Among the major abiotic stresses, drought, cold, heat, salinity, and cold stresses are the most common in *Capsicum* crop. Beside abiotic stresses, several pathogens also damage *Capsicum* crop by causing several diseases. For example, *Phytophthora capsici* causes rot disease on various plant parts such as root, shoot, leaf, and fruits. Several other diseases including leaf spot (caused by *Xanthomonas campestris*), viral disease (caused by tobacco mosaic virus TMV, cucumber mosaic virus CMV, tomato spotted wilt virus TSWV, and potyvirus) also damage *Capsicum* plants severely. These diseases cause retorted growth and development and ultimately reduced yield and quality of fruits.

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N. Ramchiary and C. Kole (eds.), *The Capsicum Genome*, Compendium of Plant Genomes,
https://doi.org/10.1007/978-3-319-97217-6_7

In winter crops including *Capsicum*, low temperature in root zone is most deleterious and cause turgor loss due to osmotic stress (Islam et al. 2014). At molecular level, low temperature in root zone may lead to several other imbalances like protein denaturation, membrane disorganization and damage, increased production of reactive oxygen species (ROS), change in cytoplasm viscosity, and enzyme activity (Janska et al. 2010; Krasensky and Jonak 2012). These abnormalities further affect different plant growth and developmental processes and may cause premature senescence, reduced fertility, wilting, chlorosis, reduced leaf expansion, necrosis, and ultimately plant death (Mahajan and Tuteja 2005). In *Capsicum*, significant economic loss may occur due to poor fruit set and quality due to biotic/abiotic stresses (Sanghera et al. 2011). To acclimate under stress, plant produces increased level of compatible solutes, such as proline, raffinose, and glycine betaine which stabilizes different cellular structures, and removes excess ROS and maintain redox balance.

Similarly, abscisic acid pathway is widely known to provide tolerance against abiotic stresses mainly in drought and osmotic stress. Upon availability of endogenous ABA, ABA-responsive element (ABRE) and MYC/MYB systems become functional which is required for expression of *rd22* gene (Abe et al. 1997). Sequences encoding MYC and MYB genes are essential for the ABA- and drought-responsive expression of *rd22*. Furthermore, NAC transcription factors (containing *AP2* domain to increase tolerance) are also induced under drought stress and in the presence of endogenous ABA.

Different parameters are used to measure stress tolerance in *Capsicum* including gas exchange, plant height, shoot dry mass, root morphology (like length, projected area, root tips' number, and dry mass), pattern of central as well as secondary metabolites in different tissues like leave, root shoot, and carbon remobilization. For example, a cold stress tolerant variety exhibits more carbon/nitrogen ratio in leaves than roots and shows a higher level of γ-aminobutyric acid (GABA), proline, galactinol, and raffinose (stress related) in roots (Aidoo et al. 2017).

In the present chapter, an attempt has been made to compile several reported research findings in identification and characterization of functional role of important genes involved in abiotic and biotic stress tolerance in *Capsicum*, and subsequently, the crosstalk between abiotic and biotic stress signaling pathways is also discussed.

7.2 Genes and Associated Molecular Mechanism Identified for Abiotic Stress Tolerance in *Capsicum* Genome

Abiotic stress tolerance involves a complex mechanism. Sometimes, more than one stresses act in combination and affect the plant growth. In *Capsicum*, several genes involved in important pathway of tolerance against abiotic stresses have been characterized (Table 7.1). For example, Sheong and Wang (2008) identified a protein encoded by *CaAbsi1* gene which has a putative zinc finger protein in its C-terminus and is upregulated in early stage of salt stress (high concentrations of NaCl or mannitol), and after six hours under cold stress. Besides, up-regulation in response to oxidative stress, methyl viologen, hydrogen peroxide, and abscisic acid suggested that *CaAbsi1* plays an important role in multiple abiotic stresses tolerance mechanism.

During abiotic stresses, highly toxic ROS (single oxygen, superoxides, peroxide, and hydroxyl radicles) are produced in mitochondria, chloroplast, and peroxisomes and may damage to cellular components including DNA, RNA, protein, lipid, therefore, need immediate detoxification by certain enzymatic or non-enzymatic scavenging systems (Apel and Hirt 2004). One of the important scavenging systems involves methionine sulfoxide reductases (MSR) which convert methionine sulfoxide back to methionine. Capsicum MSR-B2 (CaMSRB2) has been shown to provide tolerance against drought stress in rice. Transgenic rice (CaMSRB2) showed less

Table 7.1 List of genes reported to be involved in abiotic stresses in *Capsicum*

Gene/family	Description	Stress	Reference/s
BI1	BAX inhibitor 1 involved in program cell death	Cold, salinity, drought, flood, and heavy metal	Isbat et al. (2009)
CaAbsi1	Putative zinc finger protein in its C-terminus	Salt and cold	Seong and Wang (2008)
F-box genes	Sub-unit of E3, involved in ubiquitination activity	Cold, salt, and osmotic	Chen et al. (2014)
CaMSRs	Methionine sulfoxide reductases, reduces level of ROS	Drought	Kim et al. (2014a, b)
CaDHNs	Dehydrin and lysine-rich hydrophilic protein	Drought and cold	Szabala et al. (2014), Jing et al. (2016)
CaPAL1	Phenylalanine ammonia-lyase; major gene of phenylpropanoid metabolism	Pathogen defence	Kim and Hwang (2014)
CaATGs	Autophagy-related gene	Heat	Zhai et al. (2016)
CaPUB1	Pepper U-box E3 Ubiquitin Ligase	Drought	Min et al. (2016)
CaWRKYs	Contain WRKY domain	Heat, salinity, and drought	Oh et al. (2006), Cheng et al. (2016)
CaZFP1	Cys2/His2-type zinc finger transcription factor	Drought tolerance	Kim et al. (2004)
CaNACs	NAM, ATAF, and CUC transcription factors	Cold, salt, and drought	Guo et al. (2015), Diao et al. (2018)
CaKR1	Ankyrin-repeat domain C(3)H(1) zinc finger protein	Cold	Seong et al. (2007)
CaBiPs	Binding protein	Heat, drought, osmotic, and salinity	Wang et al. (2017)
CaChis	Chitin-binding proteins	Pathogen defence, cold, and salinity	Ali et al. (2018)
CaPIPs	Plasma membrane intrinsic proteins, aquaporins	Chilling, salt	Yin et al. (2015)
CaPGIPs	Polygalacturonase-inhibiting proteins	Cold treatment	Wang et al. (2013)
CaXTHs	Xyloglucan endotransglucosylase/hydrolase	Drought, high salinity, and cold	Cho et al. (2006b), Choi et al. (2011)
CaRma1H1	RING E3 Ub ligase	Drought and salt	Lee et al. (2009), Seo et al. (2012)
CabZIPs	Basic leucine zipper	Drought	Lee et al. (2006), Moon et al. (2015)
CaRAVs	Related to ABI3/VP1, transcription factor	Drought, salt, and pathogen	Sohn et al. (2006)
CaGLIP1	GDSL-type lipase	Salicylic acid, ethylene, and methyl jasmonate	Hong et al. (2008)
CaMLO2	Mildew resistance locus O	Abscisic acid and drought	Kim and Hwang (2012), Lim and Lee (2014)
CaRING1	Ring-type protein	Drought	Lim et al. (2015a, b)
AGO/DCL/RDR	Argonaut protein, Dicer-like protein, and RNA-dependent RNA polymerase	Cold, drought, and salinity	Qin et al. (2018)

(continued)

Table 7.1 (continued)

Gene/family	Description	Stress	Reference/s
CaARFs	Auxin-responsive factors	Salinity, cold, and heat stresses	Yu et al. (2017)
CaDRT1	*Capsicum annuum* DRought Tolerance 1	Drought	Baek et al. (2016)
CaWDP1	WPP Domain protein, involved in ABA signaling	Drought and NaCl treatments	Park et al. (2017)

oxidative stress, increased level of yield, and survival rate (Kim et al. 2014a, b). Further, it has also been suggested that *CaMSRB2* may target porphobilinogen deaminase (*PBGD*), which is involved in chlorophyll synthesis.

Dehydrins are hydrophilic proteins produced in response to abiotic stress to provide tolerance to plant. Dehydrin contains highly conserved lysine-rich amino acid sequence (EKKGIMDKIKEKLPG, also called K segment) at C-terminus, and serine residues (S-segment), and a consensus sequence (Y-segment) at N-terminus. SKn are acidic dehydrins which are mostly accumulated in plant cell in response to freezing stress (Rorat 2006). *DHN24* (a SK_3 dehydrin) found upregulated in phloem cells under drought and cold stresses (Szabala et al. 2014) suggested that it might play a role in drought tolerance. Similarly, *DHN3* was found to be associated with cold and salt stresses (Jing et al. 2016).

Autophagy also plays a vital role in stress tolerance through the degradation of damaged and denatured protein and thus reduces toxic level. In *Capsicum*, 15 autophagy-related genes (ATG) called *CaATGs* have been identified which got upregulated during abiotic stresses like salt, drought, heat, and cold. During heat stress, *CaATG* genes have higher expression in heat-tolerant genotype than heat-sensitive genotype. It has also been found that *CaATGs* interact with heat shock proteins of HSP90 family (Zhai et al. 2016).

7.2.1 Role of Ubiquitin Genes During Abiotic Stress Tolerance

Ubiquitin is one of the key regulators of several cellular functions such as protein sorting, endocytosis, and hormone signaling and mostly function through protein degradation. It is a peptide having highly conserved 76 amino acids. Three main enzymes named E1, E2, and E3 are involved in protein degradation through ubiquitin. E1 activates ubiquitin, E2 forms complex with activated ubiquitin and attached to the target site, and E3 catalyzes the isopeptide bonds. On the basis of sub-units, E3 can be RING-type/U-box E3 class and SKP-type cullin/CDC53-F-box. Both the types of E3 subunits have been well characterized and found to be involved in abiotic stress tolerance in *Capsicum* in separate studies. Cho et al. (2006a, b) isolated a peptide called putative U-box protein 1 (*CaPUB1*) with U-box motif (essential for E3 activity) from water-stressed hot pepper. *CaPUB1* is found to be induced under different abiotic stress conditions like drought, salinity, and cold stress. Overexpression of *CaPUB1* in transgenic *Arabidopsis* showed longer hypocotyls and root, higher plant growth rate, and early bolting than wild-type. However, under abiotic stress conditions such as drought and low temperature, transgenic *Arabidopsis* plants showed increased sensitivity than wild-type plants suggesting *CaPUB1* gene to be a negative regulator of abiotic stress tolerance. Similarly, in another study conducted in rice, overexpression of *CaPUB1* showed hypersensitivity under drought stress (Min et al. 2016); however, under cold stress, overexpression of *CaPUB1* provided tolerance in transgenic rice. Moreover, cold inducer marker genes including *DREBs* and cytochrome *P450* also showed higher expression in overexpressing *CaPUB1* rice lines compared to the wild-type plants suggesting *CaPUB1* to be a positive regulator of cold stress. On the other hand, F-box protein, a member of SCF (Skp–Cullin–F-box) protein complex (another subunit type of E3) was also found to play an important role in gene regulation during stress response (Chen et al. 2014). In *Capsicum*, *CaF-box* gene has been found to be differentially expressed predominantly during salt stress along with cold stress, and also in response to abscisic acid (ABA) and salicylic acid (SA).

7.2.2 Role of Plant Aquaporin Genes During Abiotic Stresses

Plasma membrane intrinsic proteins (PIPs) are membrane-bound proteins that allow transmembrane transfer of water (Chaumont et al. 2001). It has been suggested that besides water transmission, PIPs also play important role in the transportation of solutes and CO_2, and other physiological processes like stomatal opening, cell elongation, seed germination, and ripening (Forrest and Bhave 2007). Moreover, plant aquaporin also takes part in providing tolerance against biotic/abiotic stresses. In *Capsicum*, upregulation of *PIP-1* (isolated from P70) under cold and salt stresses suggested that it may be involved in providing tolerance to these stresses and increased susceptibility against salt of silent *PIP1* further confirmed its involvement in stress tolerance (Yin et al. 2015).

7.3 Role of Transcription Factors in Abiotic Stress Tolerance

Transcription factors are key regulators of cell signaling both internally and externally. In plants, several transcription factors have been characterized to play important role in abiotic stress tolerance (Gahlaut et al. 2016). In *Capsicum* also, several transcription factors including BAX inhibitor 1, WRKY, NAC, CAZFP1, bZIP like, RAV, GRAS, Dof, ARF, and PF1 have been found to be involved in abiotic stress tolerance.

7.3.1 BAX Inhibitor 1

In response to environmental stresses, plants follow programmed cell death (PCD) to eliminate damaged cells. BCL2-associated x protein (BAX) is found to be important regulator of PCD and balanced by the activity of *BAX inhibitor-1* (*BI-1*). In *Capsicum*, *CaBI-1* has been cloned and found to be upregulated in response to different abiotic stresses like cold, salinity, drought, flood, and heavy metal stresses and provides tolerance to plants against these stresses (Isbat et al. 2009). Loss of function of *CaBI-1* enhances cell death and shows more susceptibility toward cold stress.

7.3.2 WRKY and NAC Transcription Factor Genes

WRKY is one of the largest transcription factor families in higher plants, which contains WRKY domain (WRKYGQK peptide and Cx4–5Cx22–23HxH or Cx7Cx23HxC zing-finger structure). *WRKY* transcription factors have been found to be involved in several biological and physiological processes including stress tolerance. Totally 61 *WRKY*s genes (called *CaWRKY*s) have been identified in *Capsicum* (Cheng et al. 2016). Constitutive expression of 16 *CaWRKY*s suggested an involvement of WRKYs in fundamental developmental processes in *Capsicum*. Most of the WRKY genes (60%) are expressed in fruit tissues. Differential expression of 26, 27, and 14 WRKY genes under heat, salinity, and drought stresses, respectively, suggested active involvement of these WRKY genes in fruit development under abiotic stresses (Cheng et al. 2016).

NAC is also a well-characterized transcription factor family involved in stress tolerance in plants; however, a limited study is available in *Capsicum* (Guo et al. 2015; Diao et al. 2018). Recently, *CaNAC2* has been isolated in *Capsicum* (Guo et al. 2015). *CaNAC2* has conserved NAC domain at N-terminus which encodes 410 amino acids' long polypeptide. Induced expression of *CaNAC2* after cold and salt stresses suggested that *NAC2* may be involved in stress mechanism. Loss of function mutants showed enhanced susceptibility against chilling stress and delayed the salt-induced leaf chlorophyll degradation. Recently, *104 CaNAC* genes have been identified and found to be distributed on all the 12 chromosomes of *Capsicum* (Diao et al. 2018). Under abiotic stress condition, several NAC genes showed differential expression. For example, *CaNAC72* showed >600-fold increased expression upon salt stress treatment along with 10 other *CaNAC* genes showing average 10-fold higher expression. Similarly, upon heat stress, total 10 NAC genes (*CaNAC13, CaNAC20, CaNAC27, CaNAC29, CaNAC35, CaNAC37, NAC53, CaNAC61, CaNAC72, and CaNAC102*) are found to be significantly upregulated; however, *CaNAC41* and *CaNAC86* get downregulated under stress condition. Further, under drought stress, more than 70-fold increased expression of two NAC genes (*CaNAC72,* and *CaNAC79*) suggested the involvement of these NAC genes in drought stress (Diao et al. 2018).

7.3.3 bZIP Transcription Factor Genes

Basic leucine zipper (bZIP), a large TFs family, consists of a 40–80 amino acid containing DNA-binding domain and a leucine zipper dimerization domain. In *Arabidopsis* and rice, a total of 75 and 89 bZIP TFs, respectively, are known to be involved in multiple mechanisms of biotic and abiotic stresses, plant development, seed maturation, etc (Muszynski et al. 2006). Group A bZIP genes (ABFs/AREBs) are found to be involved mainly in drought and salinity stresses (Yoshida et al. 2010). In *Capsicum*, *CaBZ1* has been characterized to be involved in salt and abiotic stresses (Moon et al. 2015). Ectopic expression of *CaBZ1* in potato provides tolerance against drought (Moon et al. 2015). Similarly, *CAbZIP1* provides tolerance against abiotic stresses in *Arabidopsis* (Lee et al. 2006).

7.3.4 ERF/AP2-Type and RAV Transcription Factor Genes

In *Capsicum*, Yi et al. (2004) characterized an ERF transcription factor gene (called *CaPF1*) for cold tolerance. Like other ERF/AP2-type TFs, *CaPF1* binds to GCC and CRT/DRE cis-elements. Higher expression of *CaPF1* has been observed under different treatments including chilling stress in transgenic *Arabidopsis*.

RAV (related to ABI3/VP1) is a new group of DNA-binding proteins transcription factors and contains two different plant-specific DNA-binding domains—(i) AP2/ERF DNA-binding domain at N-terminal and (ii) B3 DNA-binding domain of VP1/ABI3 at C-terminal (Kim et al. 2005; Sohn et al. 2006). A number of AP2/ERF-domain-containing proteins (such as DREBs, Tsi1, and CBFs) and VP1/B3 DNA-binding proteins (*VP1, ABI3*, and *ARF1*) are widely known to be involved in plant responses to biotic and abiotic stress (Gutterson and Reuber 2004; Kasuga et al. 1999; Park et al. 2001; Kirsten et al. 1998). In *Capsicum*, it has been found that *CaRAV1* interacts with oxidoreductase protein (*CaOXR1*) and provides extreme tolerance against osmotic and salinity stresses to the overexpressed (*CaOXR1/CaRAV1*) lines in *Arabidopsis* (Lee et al. 2010).

7.3.5 Auxin-Responsive Factors (ARFs) and DNA-Binding One Zinc Finger (DoF) Transcription Factor Genes

In *Capsicum*, 22 *CaARF* genes have been identified (Yu et al. 2017). These genes are grouped into six clusters and distributed on all the 12 *Capsicum* chromosomes. Most of the above-mentioned *CaARFs* showed different expression under abiotic stresses like salinity, cold, and heat stresses. Under salinity stress, nine and ten *CaARFs* got up- and downregulated, respectively. Under cold stress, expression of *CaARFs* differs in different tissues, for example, expression of *CaARF11* got upregulated in shoot, and however, its expression goes down in root at the same time. Similarly, differential expression of 11 *CaARFs* under heat stress condition suggested these *CaARFs* may be involved in heat stress tolerance (Yu et al. 2017).

Similarly, 33 *CaDoFs* have been identified in *Capsicum* (Wu et al. 2016) and found to be distributed across 11 *Capsicum* chromosomes (excluding Chromosome 7). Several *CaDoFs* showed significant differential expression under two stresses including heat and salinity (Wu et al. 2016).

7.4 Genes Involved in Biotic Stress Tolerance

In *Capsicum*, several genes have been characterized to play a vital role in providing tolerance against biotic stresses like bacteria, virus, and nematodes (Table 7.2). Bacteria called *X. campestris* causes leaf blight disease in *Capsicum*. Choi et al. (2007) identified a *CaPO2* gene to provide tolerance against this disease. A knockdown mutant of *CaPO2* showed increased susceptibility against *Xanthomonas*. Similarly, *CaMLO2* also reported to show resistance against *Xanthomonas* and silencing of this also show increased susceptibility toward disease represented by cell death and increased ROS (Kim and Hwang 2012; Zheng et al. 2013). *CaMLO2* interacts with a calmodulin-related gene, involved in cell death (*CaCaM1*), and

Table 7.2 List of genes reported to be involved in different biotic stress tolerance in *Capsicum*

Biotic stress	Genes	Description	Reference/s
Xanthomonas campestris resistance	*Bs Genes*	Bacterial spot	Romer et al. (2010), Vallejos et al. (2010)
	CaPO2	Peroxidase	Choi et al. (2012)
	CaMLO2	Mildew resistance locus O; associated with powdery mildew	Kim and Hwang (2012), Zheng et al. (2013)
	CaCaM1	Calmodulin 1; involved in hypersensitive cell death	Kim et al. (2014a, b)
Pseudomonas syringae resistance	*CaLOX1*	Lipoxigenase	Hwang and Hwang (2010), Lim et al. (2015a, b)
Phytophthora capsici resistance	*CaMsrB2*	Methionine sulfoxide reductase B2	Hong Truong et al. (2013), Oh et al. (2010)
	CaRGA2	Resistance gene analogs	Zhang et al. (2013)
	Ipcr	Inhibitor of *P. capsici* resistance	Reeves et al. (2013), Wang et al. (2015)
Ralstonia solanacearum resistance	*CaHDZ27* Related genes	Homeodomain–Leucine Zipper I	Mou et al. (2017)
Cucumber mosaic virus resistance	*cmv11.1*	Cucumber mosaic virus	Ben-Chaim et al. (2001), Yao et al. (2013)
ToMV resistance	*Cmr1*	The gene showed synteny with ToMV-resistance locus	Kang et al. (2010)
Potato virus resistance	*pvr's (4E (eIF4E))*	Potato virus Y (PVY) resistance	Ruffel et al. (2006), Hwang et al. (2009)
	PVY, PepMoV, and *PMMoV*	Potato virusY (PVY) resistance	Banerjee et al. (2014), Rubio et al. 2008)
	PVMV-HN	Potato virus Y (PVY) resistance	Gao et al. (2014)
Nematode resistant	*RKN*	Root-knot nematodes	Djian-Caporalino et al. (1999, 2001)
	Me4, *Mech1*, and *Mech2*	Meloidogyne species or its populations	Djian-Caporalino et al. (2001, 2007)
	CaMi	Nematode-resistant gene	Chen et al. (2007), Fazari et al. (2012)

regulated disease tolerance mechanism (Kim et al. 2014a, b). Likewise, a lipoxygenase-related gene (*CaLOX1*) was found to provide tolerance against *Pseudomonas syringae* (Hwang and Hwang 2010). *P. capsici* is one of the most harmful bacteria for *Capsicum* causing rot disease. In *Capsicum*, a gene related to reactive oxygen species (ROS) production called *CaMsrB2* has been characterized to provide resistance against rot disease (Oh et al. 2010). Similarly, *CaRGA2* and *Ipcr* (disease resistance inhibitor) also provide resistance against *P. capsici* (Zhang et al. 2013; Reeves et al. 2013).

Similarly, several genes are also reported to be involved in tolerance against viral disease like cucumber mosaic virus (cmv11.1), tobacco mosaic virus (TMV), potato virus Y (PVY), and potyviruses [including veinal mottle virus (PVMV), tobacco etch virus (TEV), chili veinal mottle virus (ChiVMV), PVY, and PepMoV], and has been reviewed recently by us (for details, see Chhapekar et al. 2018).

7.5 Crosstalk Between Abiotic and Biotic Stress Responses

Signaling pathways that are involved in plant defense against abiotic and biotic stresses share some common modules like involvement of transcriptional factors, ROS, signaling pathways (calcium signaling, ABA signaling, jasmonic acid signaling, and mitogen-activated protein cascades (Moller et al. 2007; Wong and Shimamoto 2009; Ton et al. 2009; Fonseca et al. 2009; Pitzschke et al. 2009; Walley and Dehesh 2010; Galon et al. 2010). These convergent nodes help plants to swiftly adapt to a changed environment involving abiotic/biotic stresses via these signaling crosstalks (Fujita et al. 2006; Atkinson and Urwin 2012, Fig. 7.1). Here, we describe a few examples of above-mentioned abiotic and biotic crosstalks in plants including *Capsicum*.

In plant, several hormones are involved in defense pathways including abiotic (ABA) and

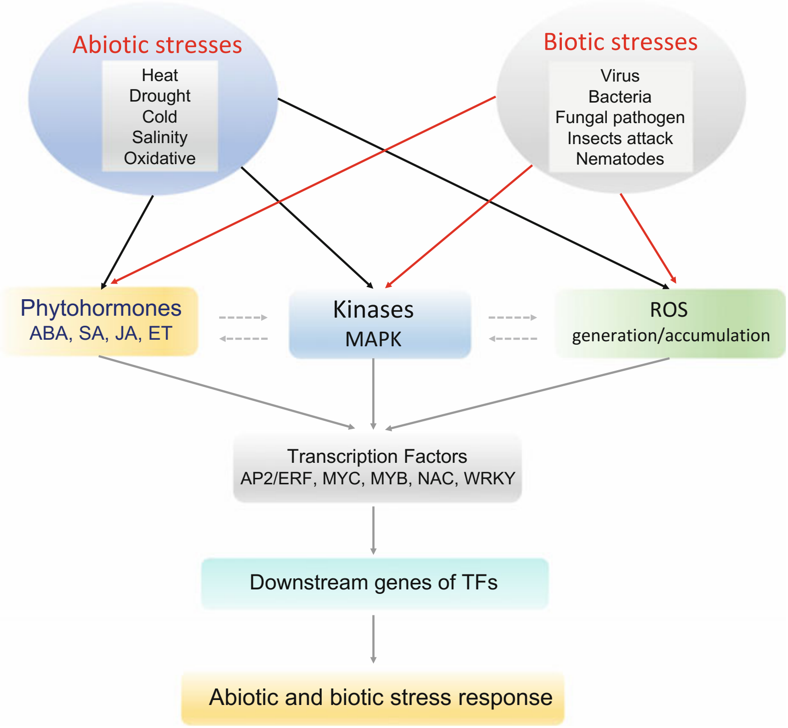

Fig. 7.1 Schematic diagram showing crosstalks between phytohormones, kinases (MPKK), reactive oxygen species (ROS), and transcription factor genes in plants during abiotic and biotic stresses

biotic (SA, JA, and ethylene) stresses. Further, ABA is also found to be involved in tolerance against biotic stresses, thus making this hormone enabled to create a crosstalk among different signaling pathways (Fujita et al. 2006; Yasuda et al. 2008; Lim and Lee 2014). In different crops like rice and tomato, as well as model plant *Arabidopsis*, ABA is found to be involved in resistance mechanism of different biotic stresses caused by *P. syringae*, *B. cinereal,* and *Magnaporthe grisea* (Audenaert et al. 2002; Mohr and Cahill 2003; Koga et al. 2004; Asselbergh et al. 2008; Jiang et al. 2010) through repression of the systemic acquired resistance (SAR) pathway and also through reduction of defense-related compounds like lignins and phenylpropanoids (Yasuda et al. 2008; Kusajima et al. 2010). On the other hand, examples are also available where ABA acts as positive regulator in biotic stress resistance (Asselbergh et al. 2008; Ton et al. 2009). In *Capsicum, CaMLO2* is transcriptionally induced under stress conditions (Kim and Hwang 2012) and is found to be upregulated under ABA treatment and drought. The overexpression of the *CaMLO2* gene in *Arabidopsis* reduces sensitivity toward ABA in germination and seedling growth stages. These results suggest that ABA signaling via *CaMLO2* may regulate drought stress (Lim and Lee 2014).

Mitogen-activated protein (MAP) kinase (MAPK/MPK) cascades are responsible for phosphorylation and dephosphorylation of proteins which significantly affect the regulation of physiological, morphological, and cellular processes and are also involved in defense mechanism involving hormone signaling and ROS (Jonak et al. 2002; Xiong and Yang 2003; Nakagami et al. 2005; Rodriguez et al. 2010; Atkinson and Urwin 2012). MEKK1/MKK2/MPK4/MPK6 cascades are found to be involved in signaling under biotic and abiotic stress conditions (Teige et al. 2004; Rodriguez et al. 2010) and play a crucial role of crosstalk signaling between abiotic and biotic stress mechanisms (Fujita et al. 2006; Zhang et al. 2006; Takahashi et al. 2011; Atkinson and Urwin 2012). MKK2–MPK4/MPK6 cascades are involved in cold and salt stress signaling (Ichimura et al. 2000; Teige et al. 2004); however, MEKK1–MKK4/MKK5–MPK3/MPK6 cascades are involved in pathogen defense response pathway via the regulation of expression of *WRKY 22*/*WRKY 29* genes (Nuhse et al. 2000). Recently in *Capsicum*, the involvement of MAPK cascade in response to abiotic (*CaMPK1* and *CaMPK3*; salinity and heat) and biotic stress (*CaMPK4; Ralstonia solanacearum* infection) has also been reported (Liu et al. 2015).

Another important player that is involved in crosstalk signaling during abiotic and biotic stresses is ROS (Fujita et al. 2006; Ton et al. 2009; Atkinson and Urwin 2012; Baxter et al. 2014). The ROS' signaling network is vastly conserved among plants and regulates various biological processes such as plant growth, development, and responses to biotic and/or abiotic stresses (Mittler et al. 2011; Baxter et al. 2014). During different types of stresses, ROS function differently. In general, ROS concentration induces during various abiotic stress conditions, i.e., drought, heat, and salinity stresses) and pathogen infection to minimize cell injury (Apel and Hirt 2004; Mittler and Blumwald 2010). Several, research findings in plants revealed that biotic and abiotic stress responses are mediated by a temporal–spatial synchronization between ROS and some other signals that rely on the production of several stress-specific compounds, chemicals, and hormones in plants (Baxter et al. 2014). Further, certain TFs integrate ROS-scavenging mechanisms in response to various types of stresses. *Arabidopsis* zinc-finger TF, ZAT12 regulates H_2O_2 levels in plants and its transcripts were induced by wounding, abiotic and biotic stresses. It also induces the expression of its downstream gene ascorbate peroxidase (*APX1*) and when overexpressed conferred tolerance to oxidative stress, freezing, and high light (Davletova et al. 2005; Vogel et al. 2005; Fujita et al. 2006). In *Capsicum*, a gene related to ROS production known as *CaMsrB2* has been characterized to provide resistance against rot disease (Oh et al. 2010). Another gene in *C. annuum,* i.e., receptor-like protein kinase 1 (*CaRLK1*), is also induced by pathogen infection and application of exogenous H_2O_2 (Yi et al. 2010). These findings suggest that the ROS signaling might mediate crosstalk between biotic and abiotic stress-responsive gene expression.

TFs are another convergent node that play a crucial role in signal crosstalk under abiotic and biotic stress. For example, *MYC2* induced by ABA (key regulator of biotic/abiotic stress signaling pathway) suggested its involvement in crosstalks (Abe et al. 2003; Anderson et al. 2004; Asselbergh et al. 2008; Pieterse et al. 2009). Beside ABA, *MYC2* TF also acts as a positive regulator of JA-induced defense genes, however, negatively regulates combined JA/ethylene induced genes (Anderson et al. 2004; Pieterse et al. 2009). Another TF family MYB has also been found to be involved in the regulation of both biotic and abiotic stress regulation in plants (Dubos et al. 2010). For example, *MYB96* is upregulated under drought stress and also promotes ABA-dependent stress tolerance (Seo et al. 2011); and also, under biotic stress, *MYB96* regulates pathogenesis-related (PR) gene expression via ABA-dependent SA biosynthesis, thus acting as a node for crosstalk among stress responses (Seo and Park 2010). Other MYB TFs, i.e., *OsMYB4*, *AtBOS1,* and *TaPIMP1,* were involved in the regulation of broad-spectrum of different stresses including drought, salt, and pathogens (Mengiste et al. 2003; Vannini et al. 2006, 2007; Liu et al. 2011). In addition to MYB/MYC TFs, NAC and AP2/ERF TFs are also widely known to be involved in stress signaling (Xu et al. 2011). RD26, an NAC TF in *Arabidopsis*, is upregulated by JA, ABA, drought, salinity, and pathogen via regulation of ROS detoxification genes (Fujita et al. 2004; Atkinson and Urwin 2012). Similarly, in rice, *OsNAC6* was reported to be involved in tolerance against drought, salinity, and rice blast (Nakashima et al. 2007). Further, in wheat *TaNAC4* is upregulated in response to salinity, cold stress, and rust stripe fungus (Xia et al. 2010). Above-mentioned studies suggested that the NAC TFs also regulate cross-signaling between stress response pathways. Recently, in *Capsicum*, it is reported that the expression of NAC TFs (*CaNAC2, CaNAC72, CaNAC102*) was induced in response to cold, heat, and salt stress (Guo et al. 2015; Diao et al. 2018). AP2/ERF TF gene (*TSI1*) from tobacco is also involved in the regulation of both abiotic stress and pathogen response pathways. *TSI1* induces the expression of PR genes and can confer resistance to bacterial pathogen and salinity (Park et al. 2001). In *Capsicum*, a AP2/ERF TF gene *RFP1* was found to be involved in osmotic stress and pathogen defense (Hong et al. 2007; Asselbergh et al. 2008). Moreover, WRKY and DREB TFs also act as a key player in defense against biotic and abiotic stresses in many plant species including *Capsicum* (Qiu and Yu 2009; Tsutsui et al. 2009; Peng et al. 2011; Cheng et al. 2016). Altogether, these studies suggest that the TFs might mediate crosstalk between biotic and abiotic stress-responsive gene-expression networks. A list of TFs in *Capsicum* that may be crucial in controlling the response to biotic and abiotic stresses is given in Tables 7.1 and 7.2.

7.6 QTL Mapping for Abiotic/Biotic Stresses in *Capsicum* Genome

QTL mapping is a widely known approach to identify genomic loci associated with quantitative traits particularly complex traits. In agricultural crops, such as wheat, rice, maize, and tomato, a number of QTLs have been identified for abiotic stress tolerance including heat, drought, and cold. However, in *Capsicum*, no QTL mapping study is available for abiotic stress tolerance and majority of the QTL mapping studies are focused on pungency, fruit traits like color, shape, and other important agronomic traits (Chhapekar et al. 2018). Dozens of studies were also conducted to identify QTLs for biotic stress tolerance in *Capsicum* (Table 7.3). Using different marker systems starting from RAPD to SNPs, several QTLs have been reported for many biotic stresses caused by virus, fungus, bacteria, and nematodes. For *Phytophthora* resistance, a number of QTLs have been identified using different mapping populations including F_2, backcross, recombinant inbred lines, and doubled haploids. Interestingly, in most of the studies,

Table 7.3 List of QTLs identified to be associated with different biotic stress tolerance mechanism in *Capsicum*

Trait	Population (parents)	Marker type	Method	Reference
Phytophthora resistance	$F_{2:3}$ (CM334/Chilsungcho)	RFLP, SSR, and gene based	CIM	Kim et al. (2008)
	RILs (YCM334/Tean)	SNP and SPP	BSA and CIM	Liu et al. (2014)
	DHs (H3/Van; Per/YW) and F_2 (YW/CM334)	RFLP, RAPD, and AFLP	IM and CIM	Thabuis et al. (2003)
	F_2 (CM334/JEP)	RAPD, SCAR, and AFPL	CIM	Quirin et al. (2005)
	BC (Yolo Wonder/CM334)	AFLP, SCAR, and CAPS	CIM	Thabuis et al. (2004)
	RILs (CM334/Early Jalapeno)	SPP	IM	Naegele et al. (2014)
Cucumber mosaic virus resistance	$F_{2:3}$ (BJ0747/XJ0630)	SLAF	IM and MQM	Li et al. (2018)
	F_2 and backcross (BJ0747/XJ0630)	SSR and ISSR	CIM	Yao et al. (2013)
	DH (H3/Vania)	RAPD, RFLP, and AFLP	IM and CIM	Caranta et al. (2002)
	DH (Yolo wonder/Perennial)	–	MQM	Tamisier et al. (2017)
	F_2, BC_1 and $F_{2:3}$ (PBC688/G29)	SLAF	MQM	Guo et al. (2017)
Root-knot nematodes	$F_{2:3}$ (Yolo Wonder/Doux Long des Landes)	SCAR, SSR, and SNP	regression, SIM, CIM, and nonparametric interval mapping	Barbary et al. (2016)
Anthracnose resistance	F_2 (Jatilaba/PRI95030)	AFLP, SSR, and gene based	MQM	Voorrips et al. (2004)
	Three way popu. (PBC932C/PBC80C)	SCAR-Indel and SSR-HpmsE032	Regression	Suwor et al. (2017)
	BC (17013/PBC932)	SSR, InDel, and CAPS	ICIM	Sun et al. (2015)
Thripe resistances	F_2 (AC 1979/4661)	AFLP, SSR, and SNP	IM and MQM	Maharijaya et al. (2015)
Powdery mildew resistance	DH (H3/Vania)	Gene based	IM and CIM	Lefebvre et al. (2003)
Potato Virus	DH (Yolo wonder/Perennial)	–	MQM	Tamisier et al. (2017)
PepMoVirus resistance	F_2 (CM334/Chilsungcho)	RAMP, RFLP, SSR, CAPS, AFLP, and BAC-end sequences	CIM	Kim et al. (2011)

RILs recombinant inbred lines; *DH* double haploid; *BC* backcross; *RFLP* restriction fragment length polymorphism; *SSR* simple sequence repeats; *SNP* single nucleotide; *RAPD* random amplified polymorphic DNA; *AFLP* amplified fragment length polymorphism; *SCAR* sequence characterized amplified region; *CAPS* cleaved amplified polymorphic sequence; *SPP* single position polymorphism; *SLAF* specific length amplified fragment; *ISSR* inter-simple sequence repeats

CIM composite interval mapping; *BSA* bulk segregant analysis; *IM* interval mapping; *MQM* multiple QTL mapping; *SIM* simple interval mapping

CM334 (potentially resistance against *Phytophthora*) was used as one of the parents along with a susceptible parent (like Chilsungcho, Tean, Yolo Wonder, and Early Jalapeno). Kim et al. (2008) identified four major QTLs (cumulative PVE ~66%) for rot resistance. Similarly, Liu et al. (2014) identified a major gene for *Phytophthora* resistance on chromosome 5. QTL mapping studies conducted for biotic stresses in *Capsicum* is summarized in Table 7.3.

7.7 Role of Plant Endophytes in Abiotic/Biotic Stress Tolerance

Plant endophytes mainly consist of bacteria present in plant tissues symptomatically and do not cause any visible infection. These endophytes are mainly present in intercellular spaces as well as vascular tissues. A number of bacterial species have been isolated from different plant organs like root, stem, leaves, and seed. Under stress conditions (abiotic/biotic), endophytes are found to provide tolerance to host against stresses. For example, some bacteria are found to provide better nutrition through nitrogen fixation under stress condition (Vessey 2003). Further, through the production of indoleacetic acid and cytokinin, endophytes provide better growth even under abiotic/biotic stress condition (Beyeler et al. 1999; Timmusk et al. 1999).

Ethylene is an important signaling molecule under abiotic/biotic stresses, and high level of ethylene may found harmful for plant growth except fruit ripening (Czarny et al. 2006). Basically, methionine acts as precursor for ethylene production and are converted via methionine–*S* adenosyl L methionine–1-aminocyclopropane 1–carboxylic acid (ACC)–ethylene. In *Capsicum*, some rhizosphere bacteria produce enzymes with deaminase activity which cleave ACC molecule and ultimately control product of ethylene under stress condition (Mayak et al. 2004). In another study (Sziderics et al. 2007), out of five bacterial strains isolated from *Capsicum*, four were found to produce indoleacetic acid and thus provide better growth under osmotic stress condition. Beside better growth, these strains were also found to be involved in the regulation of osmotic pressure and proline content. Two strains of azotobacter (EZB4 and EZB8) reduced the expression of two stress-inducible genes *CaACCO* and *CaLTPI* under abiotic stresses (Sziderics et al. 2007).

Acknowledgements This work was supported by UGC Resource Networking Grant, UGC-SAP, and DST FIST program to School of Life Sciences, Jawaharlal Nehru University, New Delhi, India.

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