1. Introduction

Crop yields are the major food resources for the population around the globe but due to increasing invasions from variety of pathogens including bacterial, viral, fungal, protozoan, nematodes and algal, there are substantial annual losses. Additionally, the extremities encountered by crops like extreme temperatures, heat, dry and arid conditions, toxins, weeds, chemical treatments, high salt concentrations and radiations further increase the crop damages (Sewelam et al.2016). Fungi is one of the major infection causing agent in plants that is responsible for destruction of around 125 million tons of major staple crops i.e. rice, maize, wheat, potatoes and soybean; in a year around the globe (Cas-tano-Miquel et al. 2017). Food serving sufficient to feed 600 million people goes in vain due to dearth of suppressing the potent fungal pathogens. The wide range of fungi impact plant hosts by cell wall degrading enzymes, releasing secondary metabolite toxins like mycotoxins that kills host cells and extracts host cell energy, calcium detoxification, guard cells and plant defense suppression, induction of programmed cell death, inter- kingdom silencing of specific plant immunity genes by fungal sRNA’s (Kim et al. 2008; Williams et al. 2011; Heller and Witt-Geiges 2013; Weiberg et al. 2015; Mbengue et al. 2016). The effects of such adverse situations can be circumvented by the plant intrinsic defensive mechanisms depending on the stretch and intensity of stress exposure, the prevailing growth conditions and ability to adapt the sudden shifts in environmental conditions (Miller et al. 2010). The plants respond by metabolic reprogramming and genetic expressions as a part of resistance mechanisms balancing the ongoing processes of growth & development and the pathogenic attacks (Yu et al. 2010; Bastas 2014). The advanced molecular studies have enabled the characterization of biochemical defense reactions occurring in plant cells (Hey et al. 2010). Plant defense mechanisms majorly detect microbe-associated molecular patterns (MAMP’s) or pathogen-associated molecular patterns (PAMP’s) or damage-associated molecular patterns (DAMP’s) through the pattern recognition receptors (PRR’s) such as PRR specifically detecting chitin during fungal attack and its kinase domain henceforth activates the downstream signaling cascade (Boller and Felix 2009; Torres 2010; Monaghan and Zipfel 2012). Signaling cascade is a highly evolved intricate network of signaling protection entities that a plant employs in detecting and fighting off the biotic and abiotic stresses (Petrov and Van Breusegem 2012; Xia et al. 2015). The highly complex signaling cascades need to be dealt from a centralized viewpoint as the pathways intertwine and overlap making the networking extremely diverse (Knight and Knight 2001). Reactive oxygen species (ROS) are a group of common molecules that have been lately found to play key centralized role in signaling in plants under multitudes of stressed conditions.

Oxygen in its ground state molecular form is a stable atmospheric component of Earth since around 2.7 billion years now (Halliwell 2006). It enables the long evolved, specialized and highly efficient aerobic mechanisms to take place in the cells that produce much more vital energy.
currencies than fermentation. Reactive oxygen species and their derivatives are a resultant of the proliferative oxygen excited states under normal metabolic activities but their homeostasis in plants alters subjected to the extreme changes in the surroundings whereby deciding the nature of functions played by ROS in cells (Karuppanapandian et al. 2011). These excited oxygen states result into radical and molecular non-radical forms including, superoxide radical (O$_2^•^−$), hydroperoxyl radical (HOH$^•$), hydroxyl radical (OH$^•$), peroxy radical (ROO$^•$), alkoxy radical (RO$^•$), excited carbonyl (RO$^•$), hydroperoxide (H$_2$O$_2$), singlet oxygen (O$_2^•$) and a close related nitrogen species, nitric oxide (Dismukes et al. 2001; Gill and Tuteja 2010; Vellosillo et al. 2010; Karuppanapandian et al. 2011). The foremost attention towards the production of reactive oxygen species during any pathogenic attack was reported during hypersensitive response in Solanum tuberosum on infection with Phytophthora infestans oomycetes (Doke 1983). In this article, reactive oxygen species mediated defense mechanisms specifically working during the fungal infections in plants are discussed followed by a case study on Verticillium wilts that affect major economically essential crops and ROS being involved in majorly all defenses makes them necessary for host protection along with other factors.

2. Contrasting roles of ROS in plants broadly

Reactive oxygen species are consistently produced at all times during aerobic metabolic reactions in every living cell including plants as well as animals. The homeostatic balance of its concentration is important in deciphering the beneficial roles played by ROS in the cells and their compartments.

2.1. ROS over-production and related severities

ROS exceeding the threshold limit in plant cells becomes a serious threat destroying essential cellular entities causing dysfunctions explaining the ubiquitous presence of antioxidants (Foyer and Noctor 2005; Fajic et al. 2015). ROS overproduction is somewhat undesirable for cellular environment causing oxidative damages to major macromolecules i.e. DNA, lipids and proteins (Apel and Hirt 2004; Das and Roychoudhury 2014). Antioxidants play the key role in defending plants from these harms through enzymatic components like catalase, superoxide dismutase, guaiacol peroxidase, ascorbate peroxidase, glutathione reductase, dehydroascorbate reductase, monodehydroascorbate reductase and molecules like flavonoids, ascorbate, glutathione, proline, phenolics, tocopherols and carotenoids (Noctor and Foyer 1998; Foyer and Noctor 2005). They maintain the balance of ROS molecules normally in the cells which otherwise leads to mutations, lesions in genetic material, disruption of building molecules, lipid peroxidation, that indirectly impact almost every cell activity ultimately leading to apoptosis or cell death (Rio et al. 1998; Mittler 2002; Mittler et al. 2004; Vellosillo et al. 2010).

2.2. Other side of the coin! ROS performing essential cellular roles

Reactive oxygen species have been a research focus lately and consequently it has been identified to play certain proliferative roles for plant cells when present in adequate concentrations. Under optimal concentrations it participates in signaling as signal molecules for crucial cellular processes of development and physiological importance, acts as scavengers against pathogenic attacks, modulates major signaling molecules like MAP kinases, G-proteins, transcription factors; combating abiotic stress tolerance, apoptosis and also shown to respond during injuries (Guan and Scandalios 2000; Mittler et al. 2004; Rentel et al. 2004; Serres and Mittler 2006; Dias et al. 2011; Kumar et al. 2011; Soares et al. 2011; Choudhury et al. 2013; Golldack et al. 2014). The plants respond to the pathogenic attacks by employing emergency defenses and ROS impose hypersensitive reactions (HR), systemic acquired resistance, acclimation and stress hormone production therein inducing defensive characteristics (Apel and Hirt 2004; Vellosillo et al. 2010; Karuppanapandian et al. 2011; Tripathy and Oelmuller 2012).

‘ROS gene network’ is the genetic trigger behind the roles fulfilled by ROS in the plant cells. More than 152 genes have been identified in Arabidopsis to be closely associated forming a large gene network regulating the production, effects and scavenging by ROS (Mittler et al. 2004). Surprisingly, plants have been found to stimulate the ROS expression through the ROS generating enzymes that are homologous to eukaryotic NADPH oxidases for signaling processes in common under multiple stress conditions (Serres and Mittler 2006). The protective mechanisms work as an interconnected as the antioxidant’s ability to scavenge cells from ROS toxicity in turn further enhances the plant tolerance to abiotic stresses (Zaefyzadeh et al. 2009). The antioxidant levels have been modified in certain crop transgenic lines to shift the focus on stress – induced oxidative stress tolerance (Faize et al. 2011).

3. Pathophysiology of plant- fungal interactions

Pathogens of different nature work their ways out differently in causing infections. Fungal species also have some characteristic patterns both physical and cellular while they attack the plant cells which in turn trigger the defense mechanisms to take place. So, to better evaluate the role of ROS and the futuristic benefits out of it, understanding the ways by which fungi infect the plant, its consequences on the plant structures and then the plant physical defenses counteracted for salvation becomes necessary.

Fungal infections from spores mostly enter the plant either through the anticlinal walls of epidermal cells via stomata openings or wound openings in the form of hyphae that are specialized structures for extracting nutrients. After entering, fungal cells can exhibit intracellular or intercellular growth. The biotrophic fungus derives its nutrition from compatibility with living plant cells by developing characteristically different hyphae respectively (Bailey 1986). Fungal pathogens have been found to specifically inhabit particular plants, their tissues or parts attributing to genetic makeup (aka host resistance) as well as the cellular physical barriers imposed by plants (aka non-host resistance). The infection pattern can spread from the surface or within the cells after tissue decays. The fungal infection impacts plant growth, lead to changes in hormonal levels, and suction of nutrients without membrane destructions by specialized haustoria are found in biotrophic fungi (Schulze-Lefert and Panstruga 2003). Severe cases during necrotrophic infections causes’ plant cell and tissue death by continuous secretion of virulence and pathogenic factors instead of any infection extensions (Van Kan 2006).
Hemi biotrophic fungi are characterized as the ones exhibiting an early biotrophic and late necrotrophic life phases (Gebrie 2016).

The cell wall degrading enzymes (cellulases, pectinases, proteases) released by fungi during infection are the virulence factors that release plant cell wall fragments and oligogalacturonides working as DAMP molecules that initiates the immune responses (Montesano et al. 2005; Leon and Montesano 2013). The initiation of hypersensitive reactions (HR) in plant cells is crucial in establishing a protective barrier after fungal entrance in the cells and a fungal hairpin encoding gene hrpN eliciting HR responses leads to enhanced virulence causing maceration and leaf cell death (Ponce de Leon et al. 2007). Fungal cells not just tend to extract the nutrients and sugars (energy resources) from the plant cell sap but greatly disturb the metabolism of the host plants (Morkunas and Ratajczak 2014).

3.1. Plant physical and chemical defenses

Plants identify the conserved MAMP’s, PAMP’s or DAMP’s through their PRR’s that is a trigger for initiating PAMP triggered plant immunity (aka PTI) along with the factors like fragments of cell wall, lipopolysaccharides, peptidoglycan and chitin released by pathogenic attacks (Hadwiger 2013; Malinovsky et al. 2014). PTI works against host specific and non-host pathogens. Effector triggered immune responses including hypersensitive responses (HR) and systemic acquired resistance (SAR) targets the pathogenic virulent effector proteins that are meant to disrupt PTI components (Tsuda and Katagiri 2010; Coll et al. 2011). These mechanisms lead to expression of specific genes that in turn activates the signaling pathway networking (Leon and Montesano 2013). These signals in turn are responsible for multitudes of plant defensive mechanisms like cell wall protection by lignification or callose deposition, xylem vessel plugging by tyloses, release of antimicrobial compounds like phytoalexins, pathogenesis related (PR) proteins and defensive hormones for example salicylic acid, ethylene, jasmonic acid (Nicaise et al. 2009; Zipfel 2009). Callose is a β-(1,3)-glucan polymer that deposits in the cell wall forming papillae or appositions working as a barrier while pathogen invades and serves as the site for amassing proteins like antimicrobial metabolites & thionins, phenolics, ROS, and polymers offering innate immunity to plant cells (Luna et al. 2011; Schwessinger and Ronald 2012). The biochemical composition of papillae differs with respect to the plant species and invading pathogen. During potential fungal attacks, papillae offer an entry barrier and then impart time for the internal defense machinery to come in action (Voigt 2014). The accumulation of reactive oxygen species in addition to the mentioned mechanisms at the site of pathogen invasion in papillae is the first line defense action adopted by plants to primarily restrict the cell wall vulnerability to fungal degradation enzymes and then acting in intracellular spaces serving as a member of the surveillance system that will be focused in the coming sections (Lamb and Dixon 1997; Voigt 2014).

4. ROS mediated defense mechanisms during fungal attacks

Reactive oxygen species are the unwanted cost paid by living cells as by-products from the aerobic processes and resides in several cellular compartments including peroxisomes, chloroplasts, mitochondria and recently identified apoplasts (Jubany-Mari et al. 2009; Daudt et al. 2012). Plant cell require molecular oxygen in ground state to carry out energy production and around 1 to 2% of it gets converted to ROS in the cellular compartments by energy transfer reactions whereas the rest gets reduced to water (Scandalios 2005; Halliwell 2006). The benefits posed by ROS and harms due to its shift to oxidative burst are illustrated in Figure 1.

Under their optimal concentrations, reactive oxygen species act as cofactors during redox reactions occurring in the cells and this way they are indirectly involved in regulation and management of several pathways occurring during plant defenses (Torres 2010). The evolutionary studies have been suggestive of the mechanisms behind ROS scavenging to have evolved prior to its role as an indirect antimicrobial agent in signaling pathways (Mittler et al. 2011). ROS mediated defenses are exhibited mostly through oxidative bursts that occur primarily within few minutes of infection in both, resistant as well as susceptible plant host cells and second burst occurs after several hours but only during resistant interactions (Baker and Orlandi 1995; Lushchak 2014). ROS accumulates around the penetration sites of the cell walls, the plasma membrane, the intracellular inoculation sites such as mitochondria and chloroplasts and during late infection stages it tends to participate in programmed cell death of the infected tissues so as to restrict the infection spread (Fillinger and Elad 2015). 2A protein phosphatases (PP2A) have been recently shown to control the ROS production and regulation (Rahikainen et al. 2016). Overall, it can be rightfully stated that ROS molecules perform many protective roles acting as signaling messenger, antimicrobial and cell wall strengthener and can no more be looked upon as an undesirable cellular production. The cellular basis of ROS is being revealed gradually and much more needs to be done for establishing a clear pathway governing ROS stimulation, production, regulation and scavenging.

4.1. ROS in first line of defense

ROS is present during the first line of defense in papillae extensions of cell walls to drag away the fungal cells. The apoplastic ROS oxidative burst is produced by the plasma membrane NADPH oxidases when the membrane receptor kinases sense any pathogen attack (Savatin et al. 2014; Rahikainen et al. 2016). In fact, a controlled ROS burst and callose deposition have been characterized as the foremost defense responses towards any pathogenic invasion in plant cells (Torres et al. 2006; Ellinger et al. 2013). The reinforcement of these appositions has been found to be established by peroxidases that use hydrogen peroxides for connecting the phenolic and glycoprotein components (Brown et al. 1998; Jones and Dangl 2006; Voigt 2014). The outcome is the overall strengthening of the cell wall and subsequent transmission of signals for the defense signaling networks to start their work and the internal hypersensitive response to eradicate any fungal or other pathogenic components from intracellular and intercellular spaces (Leon and Montesano 2013).

4.2. ROS as signal molecules

The fungal elicitors when come in contact with the plant resistance (PR) products, the primary and secondary
signaling molecules begin to be released triggering the activation of the entire signaling cascade (Gebrie 2016). The complex cascade of networking is made possible by expression of multitudes of genes. The well-known oxidative response to stress conditions is a resultant of WRKY53 transcriptional network (Triplett et al. 2016). ROS entities are involved in regulating hormonal responses, interactions of host with pathogen and developmental processes through redox balances that further assist the expression of transcription factors (Barna et al. 2012). ROS production leads to ionic influxes and protein phosphorylation and works in association with other signal molecules like salicylic acid and nitric oxide (Torres et al. 2006). The ROS apoplastic responses against fungal pathogens has shown to suppress plant immunity extensively (Caplan et al. 2015; Zabala et al. 2015). The well documented signaling network keys i.e. salicylic acid and its regulators NPR1 and TGA transcription factors get induced by ROS (Fu and Dong 2013). Normally, NPR1 is nitrosylated by enzyme S-nitroso-glutathione (GMSO) and present as polymers at cysteine in the cytoplasm. But, during stress the thioredoxins reduce the disulfide bonds when salicylic acid accumulates and redox state alters (Lehmann et al. 2015). Interestingly, at times ROS do not induce these salicylic acid dependent signals even on longer accumulation but only induces PR proteins suggesting the other controlling factorials that still remain unknown (Peleg-Grossman et al. 2012). For signaling, hydrogen peroxide is a more diffusible and stable preference than superoxide ion. In fact, ROS and calcium ions are co-produced during signal pathways in a way that they tend to take part in regulation of each other making the mechanistic understanding more complicated (Wrzaczek et al. 2013; Choi et al. 2017).

4.3. ROS in hypersensitivity reactions (HR)
Hypersensitive reactions (HR) are a series of reactions that ultimately lead to programmed cell death. ROS in adequate concentration directs the invaded plant cells towards apoptosis so as to restrict the fungal infection spread by depleting them of nutrient supply especially with biotrophic fungus (Bastas 2014). In contrast, the necrotrophic fungi get a chance to enhance its infection and colonization during HR as these fungal cells target the cell and plant issue death for its colonization. HR comes into action by DNA cleavage, condensation of chromatin, blebbing of the membrane resulting into destruction of the membrane and exposure of the cellular contents (Li et al. 2006).

4.4. Mechanical responses
ROS have been found to play crucial roles in mechanosen-sing mechanisms that have been found to offer immunity to plant cells being involved in gravitropism,
morphogenesis, seed development and microbial inter-
actions (Benikhlef et al. 2013; Jayaraman et al. 2014; Land-
rein et al. 2015). ROS along with calcium mediates mecha-
nosensing that makes the plant resistant towards fun-
gal infections and it has been depicted during the infection of
Botrytis cinerea in Arabidopsis plants (Chehab et al. 2012; Bene-
louajehajri et al. 2013).

4.5. ROS defense and localization in plant parts

ROS is localized throughout the plant body and is functional as de-
sensive entities irrespective of the location of action. ROS pro-
duction in leaves is well documented through studies on
A. thaliana but the recent evidences suggest its defensive ac-
tions against root fungi very well. It is evident by the study con-
ducted on infection caused by a significant root infecting fungus Fusarium oxysporum (infests essential food crops like banana, tomato) whereby immunity was found to be greatly enhanced in pub22/pub23/pub24 U-box type E3 ubiquitin ligase triple mutants of Arabidopsis thaliana that produced more ROS in contrast to their over expressing strains for transcription factor ERF72 (Chen et al. 2014). These triple mutant strains exhibiting enhanced MAMP response through MAP-kinase activity, oxidative burst, MAMP genes and transcriptionally activated ROS; are able to resist the fungal pathogenic infections by Pseudomonas syr-
ingae, HyaIoperonospora arabidopsisidis, Piriformospora indica (Jacobs et al. 2011).

However, not just plants employ ROS production as a de-
sense but even the fungus does so during infection and it is
evident from the metabolic studies on Botrytis cinerea
where H2O2-generating NADP oxidases in association with
peroxiredoxins produces hydrogen peroxide in conidial cells during initial infection cycle making ROS a virulence factor destructing the host plant cells (Choquer et al. 2007; Breitenbach et al. 2015). The ultimate infection causation then depends on the balance between the ROS produced in infecting plant parts and the fungal cells (Breitenbach et al. 2015).

4.6. ROS in the prime PTI response

The oxidative burst refers to the release of several ROS species in the cellular environment and frequently observed playing central roles in PTI responses towards attacking fungal enti-
ties by a homologous NADPH oxidase (Daudi et al. 2012; Malinovsky et al. 2014). RbohD (respiratory burst oxidase homologue D) in the leaves of Arabidopsis sp. is one such NADPH oxidases that are activated through calcium and phosphorylation by calcium dependent protein kinas
es CDPK5 factors (Kimura et al. 2012; Dubiella et al. 2013). Around ten such Rboh sequences have been identified in A. thaliana, of which D, E and F are crucial for ROS for-
mation in leaves, B in seed and C in roots (Marino et al. 2012). Similarly, potato counterpart, StrRbohD is phosphory-
lated by StCDPK5 and induces ROS that renders plants more resistant to hemibiotrophic fungi such as Phytophthora infestans whereas susceptible towards necrotrophic fungi like Alternaria solani (Kobayashi et al. 2007). However, PTI response mechanisms are dependent on the activation of CDPK and MAP-Kinase cascades but ROS burst is indepen-
dent of these factors (Rasmussen et al. 2012; Xu et al. 2014).

4.7. ROS overly synthesis can also be scavenging

ROS production and accumulation is a natural response of plant cells and due to this, even the fungal cells get exposed to oxidative stress by ROS as it is over produced during stressed conditions (Lehmann et al. 2015). An efficient scavenging also occurs in fungal cells through molecules like ascorbic acid, carotenoids, flavonoids, glutathione and enzymes such as peroxidase, catalase, and superoxide dismu-
tase that prevent any restriction for fungus in infecting the host plant cells and has been detected using cellular imaging and florescent markers (Samalova et al. 2014). The identifi-
cation of yeast AP-1 like protein and ATF/CREB homologues i.e. YAP-1 and Moafl in Ustilago maydis and Magnaporthe grisea respectively that protects the fungus from oxidative stress were detected and their mutant strains depleted of these special characteristics were found to be significantly deficient in their virulence capacity towards the host crops like rice (Molina and Kahmann 2007; Guo et al. 2010).

Further, the study extended by suppression of host cell NADPH oxidases using diphenyleneiodonium (DPI) which was found to restore the virulence. Dis-
functioning of any scavenging system from fungal cells is a way to restrict the infection spread. It can be stated here that both the conditions, the ROS release under normal state as well as it’s over production during stress can be exploited as proliferative defensive approaches to savior the crop plants from fungal spoilage.

4.8. ROS defense v/s miRNA mediated vulnerability

ROS has been shown to link with miRNA levels that renders the plants mostly resistant towards fungal infections but mir396 miRNA has been detected to render the plant vulner-
able towards fungal infection, the exact mechanisms behind which are largely unknown (Soto-Suárez et al. 2017). An Ara-idopsis strain MIM396 was selected with reduced miRNA (miR396) activity that demonstrated enhanced broad resist-
ance coverage from potent fungal members Plectosphaerella cucumerina, Botrytis cinerea, Fusarium oxysporum (Soto-
Suárez et al. 2017). ROS hydrogen peroxide accumulation as well as callose deposition was identified as major mecha-
nisms in MIM396. Host reprogramming was observed in the strain due to expression of growth regulation factor transcription factors that is explicit in many important crops like rice, tomato and maize (Karlova et al. 2013; Gao et al. 2015). It is a notable mechanism of defense priming and such molecular studies are substantial in widening the knowledge of disease resistance in plants at the minutest cellular level (Martinez-Medina et al. 2016).
5. ROS defenses towards root fungus *Verticillium dahliae* for some major crop cultivars

*Verticillium dahliae* is a vascular, fungal, soil-borne pathogenic member that infects a broad range of more than 200 economically significant crop hosts including ornamentals, fruits, and vegetables causing vascular wilts. The infection is severe as the fungus has the ability to create infection reservoirs in the typical non-host cereals and micosclerotia remaining dormant in soil for long times (Heale 1988). It destroys huge toll of crops as well as cereal cultivars rendering large amounts of economic losses and any efficient control strategies are lacking currently. A recent hope is incurred by the transcriptome analysis in several plant species that have been carried out to identify the potential resistance genes and creating genetically engineered inter-related and intra-related crop species lately. Interestingly, ROS encompasses a common defensive phenomenon amongst all the transgenic varieties that will be discussed in the succeeding sections. Figure 2 summarizes the basic ROS mediated responses from major plant cultivars fighting off *Verticillium* wilts.

5.1. ROS mediated resistance against *V. dahliae* through Ve locus in *Solanum lycopersicum*

There are two linked genes of Ve locus namely Ve1 and Ve2. The former codes for leucine zipper motifs and latter for PEST sequences that induce receptor mediated endocytosis (Kawchuk et al. 2001). The roots of transgenic resistant tomato lines constructed by engineering these genes were inoculated with *V. dahliae* and found to exhibit an early enhanced hydrogen peroxide production along with peroxidase and phenylalanine ammonia lyase activities whereas the susceptible lines did not induce an early production of the same (Gayoso et al. 2010). There was a second response also seen by production of hydrogen peroxide inducing systemic pathogenesis related gene expression and signal cascades by salicylic acid production (Hu et al. 2005). Co-relation of peroxidase activity was not similar with the ROS production and it decreased with time (Gayoso et al. 2010). This exemplary finding in tomato can also be utilized to render other *Solanaceae* members resistant to *Verticillium*.

5.2. ROS awaits defensive establishment in *Solanum melongena* L. against *V. dahliae*

Similar to tomato crops, *V. dahliae* is active against other members of *Solanaceae* such as eggplants and causes wilts that take away a huge toll of crop yield annually. A significant study on small RNA profiling have suggested the involvement of miRNAs and RNA silencing pathways in incurring defense mechanisms in several plant species and was one of the ever-conducted study for economically significant *S. melongena*.

![Figure 2. ROS mediated Defensive Responses induced in several cultivars during *Verticillium dahliae* infection.](image-url)
(Yang et al. 2013). On sequencing the small RNA libraries for mock infected and V. dahliae infected eggplant seedlings, comparative study of miRNA from different documented species was carried out. 38 miRNAs were found to be conserved in the family, 8 were variable along with some conserved in un-related plant species were found in eggplant transcriptome (Yang et al. 2013). 33 of these RNAs were involved in cellular processes and signal transduction pathways against V. dahliae infection where 28 were suppressed and 5 were over expressed suggesting the prospective analysis of these specific non-conserved and conserved miRNAs with respect to the cellular defense mechanisms such as ROS burst, cell wall reinforcement and more (Axtell et al. 2007).

However, documentation of ROS being involved in defenses against V. dahliae in S. melongena L. is lacking but salicylic acid signal induction has been studied that is greatly induced by ROS burst during any stress condition. SA is well known now in inducing systemic responses conferring resistance to eggplant seedlings in addition to improvement in germination and seedling vigor (Mahesh and Sharada 2014). Lately, SA involvement in inducing growth related factors such as chitinase, MPK-1, GPX and in resistance induction via PR proteins has been well defined (Mahesh et al. 2017). An innovative study awaits the establishment of the roles incorporated by ROS entities during eggplant defenses as the works so far clearly indicates a connection.

5.3. ROS induced by V. dahliae prior to Olea Europaea L. roots

Recently, wilts caused by Verticillium in woody olives have gained attention due to their treatment complexities and transcriptomes of both were obtained characterizing six sub-clusters from olive and V. dahliae as differentially expressed genes. Jimenez-Ruiz et al in 2017 carried out this study whereby noticeably they deduced that ROS is induced primarily in pathogen V. dahliae within two days followed by the host i.e. olive roots within seven days. In resistant olives, Ca/Zn superoxide dismutase and three antioxidant glutathione peroxidases from sub-clusters B and C of olive were found to be over-expressed under biotic attack where the former produces hydrogen peroxide as defense and the latter oxidizes glutathione for converting hydrogen peroxide to water (Jimenez-Ruiz et al. 2017). This indicates both; the induction of ROS based defense mechanism as well as protective mechanism against pathogenic ROS production. ROS and NO concentrations in collaboration have been found in high concentrations in olive seedling roots strongly fighting off the pathogenic V. dahliae infections that enabled the differentiation of the synergistic mycorrhizal associations where defense reactions are suppressed (Espinosa et al. 2014).

5.4. Genes exhibiting ROS bursts confer immunity against V. dahliae in Gossypium hirsutum

Several studies have been conducted on understanding the metabolic changes that happens during interaction between cotton roots and its pathogen V. dahliae and their protein production during the same to enhance the transgenic production expressing defensive genes. The proteomic studies have deduced that ROS related proteins are over expressed during infection and others related to cell wall synthesis and normal metabolism are down regulated (Xie et al. 2013). PR-10 proteins, S-adenosyl methionine synthetase (involved in synthesis of an antioxidant glutathione), ascorbate peroxidase and phosphoglycerate kinase; all of which are indicators for oxidative burst seemed to be upregulated during infection in cotton roots suggesting a key role of ROS in defense and then scavenging in the hosts (Xie et al. 2013).

A homologous tomato Ve gene i.e. Gbve1 in cotton has shown resistance towards deadly defoliating as well as non-defoliating extracts of V. dahliae (Zhang et al. 2012). Effectively resistant transgenic cotton against V. dahliae was produced by incorporating antimicrobial hairpin protein Hcm1 from Xanthomonas oryzae and cercopin-A-melittin, an insect origin chimeric protein (Zhang et al. 2016). Verticillium as well as Fusarium wilts were found to be greatly suppressed as the hairpin protein enhanced ROS burst specifically hydrogen peroxide content, which further assisted in micro hypersensitive response & PR protein production and signaling causing effective stress imprinting that mediates memory responses for future attacks (Zhang et al. 2016). Increased expression of the inherent GbRLK receptor-like kinases, plant defending NaD1 & hypersensitive response inducing Hpa1 and also incorporated Arabidopsis NPR1 confers significant resistance in cotton roots against Verticillium wilts (Miao et al. 2010; Parkhi et al. 2010; Gaspar et al. 2014; Zhao et al. 2015). Since apoplasts comprise the first defense line in plants and primary sites for releasing ROS, a proteomic study conducted for comparing the control and V. dahliae infected cotton roots further affirmed the over production of ROS related proteins and GbNRX1 (a thioredoxin) was concluded to be a significant regulator of the apoplastic ROS homeostasis (Li et al. 2016).

5.5. ROS mediated HR and SA signal pathway offer resistance to Helianthus annuus against V. dahliae

Subjecting to the deficit of any chemical controlling methods for V. dahliae infections in crops, selection of resistant genotypic lines has been considered the most effective strategy in defying the economic losses. Similar to tomato and cotton, transcriptome profiling for sunflower plant has also revealed the predominant defense mechanisms i.e. salicylic acid transduction networking and hypersensitive reactions (HR) to be working during V. dahliae infections (Guo et al. 2017). HR were found to be directly linked with ROS and nitric oxide mediated signaling that were in turn activated by respiratory burst oxidase homologue (RBOH), flagellin- sensitive 2 (FLS2) and cyclic nucleotide-gated ion channels (CNGC) respectively (Guo et al. 2017). In the treated resistant sunflower crops, the expression of RBOH & CNGC genes was up-regulated whereas FLS2 was down-regulated.

5.6. ROS dependent cytoskeletal rearrangement necessary for Arabidopsis resistance against Verticillium toxins

The study of defense gene expression in control and atrbohD and atrbohF Arabidopsis mutants displayed its control by hydrogen peroxide modulation as signal molecule of the dynamic microtubule cytoskeleton (Yao et al. 2011). These defensive molecules are essential in combating toxins produced by V. dahliae. AtrbohD and atrbohF encodes two different NADPH oxidases that produce ROS and are found
in guard and mesophyll cells of Arabidopsis respectively and are essential for H₂O₂ production for defense against VD-toxins such that their mutants cannot conserve the cytoskeleton, are not able to produce PR proteins and are unable to show any ROS mediated defense response (Yao et al. 2011).

6. Conclusion

ROS is maintained under a delicate relationship in plants by regulation of its production and protection from its deleterious effects. The recent advent of studies towards the beneficial roles played by ROS are paving ways for better understanding of intra cellular communication, the mechanisms balancing the sudden production and balancing of these excited oxygen species, the interlinking of ROS molecules with established signaling molecules. The biochemical assays in conjunction with genetic tools and analysis along with the advanced imaging technologies give hope to unveil the aspects related to accurate ROS biological functioning and factors influencing their specific sub-cellular production in near future. This will aid in deciphering the key roles of ROS in signaling and henceforth the defense mechanisms especially against fungal pathogenic attacks. Similar to the most common and dangerous plant disease *Verticillium* wilt affecting commercially important crops that has been discussed in preceding sections; case studies can be employed for other fungal members and an overall study on the effective genes and their outcomes will aid in grabbing insights towards ROS related processes and combating the global food deficits to large extents. Novel drugs targeting specifically the most vulnerable target sites or development of bioengineered resistant strains of crop cultivars are some of the numerous implications. These insights will definitely prove proliferative for scavenging crops from damages and further increasing their yields and as a result dealing with the ever-rising demands of increasing population worldwide.

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