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Taqi Ahmed Khan, Aligarh Muslim University
Mohd Mazid, Aligarh Muslim University
Firoz Mohammad, Aligarh Muslim University

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Potential of Ascorbic acid against oxidative burst in plants under biotic stress: A Review

Taqi Ahmed Khan¹, Mohd Mazid²*, Firoz Mohammad²

¹ Department of Biochemistry, Faculty of Life Sciences, AMU, Aligarh, India. 202002.
² Plant Physiology Division, Department of Botany, Faculty of Life Sciences, AMU, Aligarh, India. 202002.
*Corresponding author, Phone:+91-0571-2702016, E-mail: mazidmohd699@gmail.com

ARTICLE INFORMATION

ABSTRACT

Since, plants vary to a greater extent in their physiological response to various kinds of environmental stress. To prevent damage caused by pathogenic attack and to acclimate to change in their environment, plants have evolved direct and indirect mechanism for sensing and responding to pathogenic stimuli. Presently, ascorbic acid (AA) has gained significant place in plant science, mainly due to its properties (antioxidant and cellular reductant etc.), and multifunctional roles in plant growth, development, and regulation of remarkable spectrum of plant cellular mechanisms against biotic stress induced by pathogenic infection and herbicidal and pesticidal treatments. As it is evident from the present review, recent progress on AA potentiality in tolerance of plants to biotic stress has been impressive to a greater extent. AA produced in plants as indirect response against biotic stress at different sites in plants and its intertwined network cause changes in nuclear gene expression via retrograde signaling pathways, or even into systemic responses, all of which are associated with biotic stress resistance. The role of AA in mediating tolerance to biotic stress will establish much consideration in nearest future as in terms of agriculture re-thinking. Moreover, AA might provide attacking targets to production of crops which have high severity to pathogenesis and herbicidal treatments.

Keywords

Ascorbic acid
pathogenesis
plant hormones
ROS signaling
PR protein

Introduction

Oxidative stress, which frequently accompanies by several kinds of biotic stress, may cause denaturation of functional and structural proteins (Naem et al. 2011; Khan et al. 2011a; Mazid et al. 2011a). Plants respond to the stress in part by modulating gene expression, which eventually leads to the restoration of cellular homeostasis, detoxification of toxins and recovery of growth. As a consequence, these diverse environmental stresses often activate similar cell signalling pathways and cellular responses, such as the production of stress proteins, up regulation of antioxidant and accumulation of compatible solutes (Shinozaki and Yamaguchi-Shinozaki 2000; Zhu 2001; Mazid et al. 2011b). Biochemical adaptation in plants involves various changes in the biochemistry of the cell. These changes include the evolution of new metabolic pathways, the accumulation of low molecular weight metabolites, the synthesis of special proteins, detoxification mechanisms and changes in plant hormone levels. Adaptation represents the ability of living organisms to fit into a changing environment, at the same time improving its chances of survival and reproducing itself (Fujita et al. 2006; Smirnoff 1995; Khan et al. 2011b; Khan et
The complex plant responses to pathogenic stresses, which involves expression of many genes, biochemical and molecular mechanisms.

AA is a small antioxidant molecule, fulfills essential metabolic functions in the life of animals and plants. As it is a small, water soluble, reduce the sugar acid with antioxidant properties and acts as a primary substrate in the cyclic pathway for enzymatic detoxification of a number of reactive oxygen species (ROS) such as H$_2$O$_2$, and many other, harmful to normal functioning of plant metabolism (Mazid et al. 2011c). AA is an essential cofactor for α-ketoglutarate-dependent dioxygenases (e.g. prolyl hydroxylases) important for formation of covalent adducts with electrophilic secondary metabolites in plants (Traber and Stevens 2011; Khan et al. 2011d). In addition, it acts directly to neutralize superoxide radicals (O$_2^-$), singlet oxygen (O') or hydroxyl radical (OH') simply by acting as a secondary antioxidant during reductive recycling of the oxidized form of α-tocopherol (Noctor and Foyer, 1998). L-AA serves as a co-factor for many enzymes (Amigioni and De-Tullio 2000) and it contributes to the detoxification of ROS (Sims and Wheeler 2000; Conklin 2001; Conklin and Barth 2004). This antioxidant activity of AA is associated with resistance to oxidative stress and longevity in plants (Mazid et al. 2011d; Mazid et al. 2011e). Moreover, the endogenous level of AA has recently been suggested to be important in the regulation of developmental senescence and plant defense against pests (Pastori et al. 2003; Barth et al. 2004; Pavet et al. 2005). A recent plethora of evidences suggests that it may play a role in protection of plant against several biotic stresses such as pesticides, and pathogenesis (Shalata and Neumann 2001; Vwiko et al. 2008).

AA signaling and plant hormones

Plant responses to stress can be viewed as being orchestrated through a network that integrates signaling pathways characterized by the production of ET, Ck, JA, SA, ABA and GA$_3$ (Mazid et al. 2011; Mazid et al. 2010). The identified regulatory step in the network involves transcription, protein interaction and targeted protein damage. Molecular and genetic studies present the notion that the cross talk between AA and various plant hormones exists. It includes alternation in the expression of hormones biosynthetic genes and/or signaling intermediates. Studies of such interaction have examined changes in endogenous levels of other hormones, described synergistic effects with exogenous AA treatment (Mazid et al. 2011g).

The Combined synergistic effect of AA induced ABA and GA$_3$ in signal transduction has been extensively studied using the cereal aleurone layer (Lovegrove and Hooley 2000). Evidence suggests that these hormones are perceived at the plasma membrane and that phospholipases and G-proteins are involved in the early signaling events. Through these systems, GA$_3$ and ABA regulate the expression of a number of proteins in the aleurone layer, including α-amylase. However, GA can also promote cell death in this system (Bethke et al. 1999), a protectant involves AOS, and notably H$_2$O$_2$, which is produced in glyoxysomes by the activity of a flavin-containing acyl CoA oxidase (Mazid et al. 2011h). ABA can present cell death by promoting high activities of enzymes that destroy ROS. ABA represents a good example of a combination of genetic, molecular and biochemical approaches can lead to the elucidation of a complex biosynthetic pathway. ABA biosynthesis increases when plant cells lose turgor, raising the question of which step in the pathway is activated by various environmental stresses. The promoters of the peroxidases respond to ABA and to redox signals (Fryer et al. 2003; Baier et al. 2004; Khan et al. 2011e). APX is synergistically induced by ABA and oxidative stress (Fryer et al. 2003) while other peroxidases (2CPA) is oxidatively induced by wounding and photo-oxidation. Studies of ET signaling in Arabidopsis indicate that receptor gene families in plants may function similar to many of their animal counterparts, increasing their flexibility at responding to stressful environments. Also, studies in the past few years have contributed to the accumulating evidence that ET signaling has a substantial role in disease resistance (Chang and Sockeye 1999). The bacterial spot disease symptoms were greatly reduced in one line of tomato deficient in ET synthesis (ACC deaminase/and two lines impaired in ET perception (Nt/Nr and 14893) in comparison to the wild type cultivars (Lund et al. 1998). Hence, the fact that oxidative stress is a common facet of many cellular biotic stress responses that elucidating those intracellular signaling processes mediating AA signaling is of potential significance to any programme targeting improving crop resistance against biotic stress.

Response of plant system to pathogenesis

Plants are attacked by many diseases-causing organism including bacteria, fungi, viruses and nematodes. These pathogens cause large crop losses and probably since the agriculture have contributed to human hunger and malnutrition. Plant resist pathogens attacks both with performed defenses such as antimicrobial secondary compounds and by including defense responses (Hammond-Kosak and Jones 2000; Heath 2000). Inducible defences can be activated upon recognition of general elicitors such as bacterial flagellin and even host cell fragments released by pathogen damage (Gomez-Gamez and Boller 2002). However plants have developed a variety of sophisticated defense mechanisms to cope with an environment in which many different microbes live by detecting proteins producing infections.
To combat invasion by microbial pathogens and herbivores insects effectively, plants make use of pre-existing physical and chemical barrier as well as inductive defense mechanism that become activated upon attack. The activation of plant defense state is correlated with a stimulation of three pathogenesis related (PR) proteins, such as chitinase, ige-1, 3-glucanase and peroxidase which are molecular markers of SAR (systemic acquired resistance) (Roth et al. 2000), which is triggered by necrotizing pathogens, induced systemic resistance (ISR), which is activated upon colonization of roots by selected strains of non-pathogenic rhizobacteria and wound induced defense, which is typically elicited upon tissue damage such as that caused by feeding insects. Induced defense responses are regulated by a network of inter connecting signal transduction pathways in which the hormonal signals SA, JA and ET play a major role, and other hormones such as BRs and ABA also be involved (Dong 1998). Results of Dias et al. (2011) confirmed that AA is the main precursor of oxalic acid in susceptible and resistant cacao (Theobroma cacao L.) infected by the hemibiotropic fungus Moniliophthora perniciosa. Oxalic acid help in synthesis of H₂O₂ in plant-pathogen interaction play a role in inhibition of growth of biotrophic pathogens and could help in prevention of the infection/colonization process of plants by necrotrophic pathogens. Moreover, Katay et al. (2011) reported that the effect of ascorbigen and 1-methyl ascorbigen on the disease resistance in bean against fungal pathogen Uromyces phaseoli and also suggests that effectiveness of protection depended on the dosage of the applied 1-methylascorbigen and on the time interval between the chemical pre-treatment and inoculation. Studies of Bala and Thukral (2011) established that AA along with glycerol found to be most effective in increasing the phytochemical potential of spirodela polyrrhiza L. In addition, Belide et al. (2011) also suggested that hyperhydration and necrosis of Agrobacterium-infected cotyledons found to be effectively controlled by using AA along with L-cysteine and iota-carrageenan.

Indeed, AA acting simply as an antioxidant in the apoplastic space, but however it is to be involved in a complex phytohormone mediated signaling network that ties ozone and pathogen responses and influences the onset of senescence. Now it has become increasingly clear that AA function is intertwined in a complex network that meshes the plant response to pathogens and the onset of senescence. Acute exposure to ozone (150-300 p.p.b.) for a short time period (4-6h) cause necrotic lesion on leaves and induce plant reaction that resemble the hypersensitive response (HR), suggesting similarities between ozone and pathogen induce responses (Kangasjarvi et al. 1994; Sharma and Davies 1994; Sandermann et al. 1998; Rao-Koch and Davis 2000a). In a large number of studies associated with stress mitigation/tolerance in plants by adding the different natural and synthetic compounds such as PPGs (phenypropanoid glycosides), AA is used as a reference compound (Lopez-Munguia et al. 2011). Similarly, studies of Da Silva et al. (2011) suggesting that in phosphonolibenium assay, the Anadenanthera Colubrina (ACHE) Libidibia ferrea (LFHE) and Pityrocarpa moniliformis (PMHE) showed increased antioxidant activity in relation to AA against ROS respectively. Pathogen-induced HR is a rapid oxidative burst at the site of microbial infection. Moreover, ROS production during HR (and recognition of the invading pathogen), are mediated by a nicotinamide adeninedinucleotide hydrogen phosphate (NADPH) oxidase localized in the plasma membrane (Levine et al. 1994; Rao and Davis 2001) and induced signal transduction network appear to involve a mitogen activated protein kinase (MAPK) signaling cascade pathways (Vranova et al. 2002; Mazid et al. 2012) (Figure 1).

![Figure 1](image.png)

Figure 1. Induction of defence response through ascorbic acid signaling pathway involving ROS, MAPK, SA and JA induced gene expression against pathogen attack.

Generally, ROS formed during HR (Leon et al. 1995; Ryals et al. 1996) activate ethylene, SA and JA signaling pathways, serve to induce defense gene expression to counteract the invading pathogen and to minimize lesion formation in plants exposed to oxidative stress like O₂⁻ET synthesis (Overmyer et al. 2000). ET triggers programmed cell death (PCD) in the accelerated cell death mutant (acdl) (Greenberg and Ausubel 1993), and is involved in regulating PCD in plant pathogen interaction (Bent et al. 1992). SA signaling is regulated for ozone-induced cell death responses (Overmyer et al. 2003), induction of pathogens related proteins (PR) (Greenberg 1996;
Dempsey et al. 1999), and SAR (SAR increased to subsequent infection by a broad range of pathogens) (Ryals et al. 1996; Shah and Klessing 1999). Therefore, these plant hormones do not act independently in response to pathogens but rather in a complex signaling network (Dong 1998; Rao and Davis 2001). In a study of Pastori et al. (2003), vtc1 (AA deficient mutant of Arabidopsis) is subjected to a large-scale microarray analysis to identify genes that are differentially expressed in the AA-deficient mutant relative to the wild type in the absence of added ROS. One hundred and seventy one transcripts that were either increased or decreased in vtc1 versus wildtype were identified. Specifically, the most dramatic changes in transcript abundance were observed in genes involved in plant defense responses against pathogenesis. PR proteins such as PR-1, PR-2, PR-5 and lytic enzymes, such as β-glucanases and chitinases are significantly increased in vtc 1 compared to wild type. Many disease resistance proteins of plants detect the presence of disease-causing bacteria, viruses or fungi by recognizing specific pathogen effectors molecule that is produced during the infection process. Effectors are often pathogen proteins that probably evolved to subvert various host processes for promotion of the pathogen life cycle. Five classes of effectors-specific R proteins are known and their sequences suggest the roles in both effector recognition and signal transduction. Although some R proteins may act as primary receptor of pathogens effectors proteins, most appear to play indirect roles in this process. New technologies arising from the genomics and proteomics revolution will greatly expand our ability to investigate the role of R proteins in plant disease resistance.

In contrast, major antioxidant enzymes such as CAT and APX are largely unaffected in vtc1. Interestingly, when the AA content is artificially elevated by feeding with 10 mM ascorbate resulting in AA levels similar to wild type treated equally, the transcript abundance is reversed in vtc1, indicating that low AA induces defense response and high ascorbate suppresses the induction of defense genes. Thus, one would predict that constitutively induced defense gene expression in vtc 1 might correlate with resistance to pathogens. Barth et al. (2004) tested this hypothesis with vtc 1 and wild type using the bacterium *Pseudomonas syringae* Pv maculicola ES4326 and the virulent fungus *Peronospora parasitica* Pv Noco, the cause of downy mildew and found that induction of the PR genes in vtc1 may be due to an SA-dependent pathway as the total SA content is found to be approximately six fold higher in vtc 1 than in wild type. In addition, hyphal development and fungal conidiophores production is significantly reduced in vtc1 and also vtc 2, a second non-allelic AA-deficient mutant. PR-1 and PR-5 proteins are of higher abundance in vtc 1 than in wild type, particularly within the first 24 h post-inoculation with *Pseudomonas syringae* as revealed by western blot analysis. Virulent pathogens have been repeated to induce non-specific resistance responses via the induction of SA synthesis and PR proteins (Glazebrook et al. 1997). However, the defense responses elicited by virulent pathogens are activated more slowly and/or they are activated lower levels than the defense response induced by virulent pathogens.

Furthermore, PR gene induction in the AA deficient mutant may occur via altered SA-dependent signaling. However, these are also evidence for the possible involvement of other phytohormone signaling pathways (Pastori et al. 2003). Many recent studies suggest the specific requirement of AA as a cofactor for the activity of 2-oxo acid-dependent dioxygenases, a class of enzymes that includes those regulating the synthesis of hydroxyl proline containing proteins and hormones in plants (Arrigoni and De Tullio 2000). As already stated before that studies of Conklin and Barth (2004) evidence that AA involved as a cofactor in the synthesis of ABA, GA, ET and AA-dependent dioxygenases are involved in ABA biosynthesis. Specifically, NCED, a dioxygenases catalyzing the formation of Xanthoxin, the precursor of ABA, can be activated before addition of AA and Fe(III) (Schwartz et al. 1997). ABA has been demonstrated to induce PR genes in several other plant species, such as in rice (Agarwal et al. 2001) and in Lithospermum (Yu et al. 1999). AA is also strictly required by some enzymes that are involved in GA biosynthesis (Arrigoni and De Tullio 2000). A role of GA in pathogen defense has been suggested, for example, in tomato and in arbuscular mycorrhiza plants of *linium Usitatissimum* when infected by fungal pathogens (Dugassa et al. 1996). ET like SA, ABA and GA also plays a role in the pathogen response and specifically in the induction of PR genes. In ET biosynthesis, ABA is required for 1-amino cyclopropane-1-carboxylate (ACC) oxidase that forms ET (Dong et al. 1998) (Table 1). In last, taken together, analysis of the vtc1 mutant suggests that AA affects cell signaling during pathogenesis induced resistance. Presumably, the availability and/or the redox status of AA regulate enzyme activity directly or modulate redox-sensitive proteins which trigger signaling cascades (Pignocchi and Foyer 2003). Thereby, AA modulates the content of several signaling molecules like SA, ABA, ET and GA.

**Response of plant system to pesticides and herbicides application**

Pesticide may be a chemical substance or biological agent (such as a virus or bacteria) used against pests including insects, plant pathogens, weeds, molluscs, birds, mammals, fish, nematodes and microbes that compete with humans for food, destroy property, spread disease or are a nuisance. Modern pesticides are designed to ensure the effectiveness against target organism. Many
Pesticides have been developed to target specific biochemical reactions within their target organism. However, it is of great concern to understand their effects on non-targeted crops they are meant to protect.

Table 1. Plant disease resistance (R) proteins.

<table>
<thead>
<tr>
<th>Plant Name</th>
<th>pathogen</th>
<th>Effector/R-protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lycopersicon esculentum</td>
<td>Pseudomonas syringae</td>
<td>Avr pto/pto</td>
</tr>
<tr>
<td>Arabidopsis thaliana</td>
<td>P. S. parasitica</td>
<td>Avr/-/RPP1</td>
</tr>
<tr>
<td>Arabidopsis thaliana</td>
<td>P. Syringae</td>
<td>AvrRps4/RPS4</td>
</tr>
<tr>
<td>Lycopersicon esculentum</td>
<td>Cladosporium fulvum</td>
<td>Avr2/CF-2</td>
</tr>
<tr>
<td>Oryza sativa</td>
<td>Xanthomonas oryzae</td>
<td>Avr2/Xa21</td>
</tr>
<tr>
<td>Arabidopsis thaliana</td>
<td>Raestonia Solanacearum</td>
<td>Avr2/RRS1-R-</td>
</tr>
</tbody>
</table>

As their persistence in the geosphere may cause problems in the biosphere, their presence in soil and water is continuously monitored. Current standard procedures for pesticides determination in soil and water samples (HPLC and GC/MS) are accurate but rather time-consuming and beyond the analytical capacities of smaller water works as they require expensive instrumentation. Consequently, immunological methods are being widely investigated as an alternative analytical procedure and in fact, some cases have already been successfully adapted to environmental analyses (Sadik and Von Emon 1996).

AA is reported to be effective in reducing damage caused by pesticides. AA along with other two chemicals viz., thioare and thiamine capable of potentiating-SH turnover and improve growth and productivity of maize (Sahu et al. 1993). It was further noted that foliar spray of thioare (1000ppm) and AA (100 ppn) significantly increased leaf area index (LAI), number of green leaves plant\(^{-1}\) and biological yield ha\(^{-1}\) in maize. This improvement appeared to have resulted from increased biosynthetic efficiency and canopy photosynthesis on account of the biological activity of –SH group (Sahu et al. 1993).

Phytotoxic effect on cucumber leaves of nine pesticides, including three herbicides (Paraquat, fluzifop-p-butyl, and Haloxyfop), three fungicides (flusilazole, cuproxt and cyazofamid) and three insecticides (imidacloprid, chlorpyrifos, and abamectin) has been examined. Plants treated with paraquat showed the severest phytotoxic symptoms with the highest reduction in net photosynthetic rate (Pn), while other pesticides except flusilazole inhibited Pn to various degrees. The inhibition of Pn by cuproxt was accompanied by declines both in stomatal conductance and intercellular CO\(_2\) concentration whereas decreased Pn for the cyazofamid was associated with increased intracellular CO\(_2\) concentration was increased or unaffected. Interestingly, inhibitions of Pn were alleviated by AA pre-treatment, as for the pesticides except paraquat and flusilazole. Chlorophyll a (Chl) level, chl a/chl b ratio, photosynthetic rate (Pn) and transpiration rate (Tr) significantly increase, whereas chl b and stomatal conductance (gs) have no obvious change after exogenous AA treatment.

In addition, pesticides application impairs the photosynthesis of cucumber seedlings, while AA pre-treatment can increase the resistance of plants to pesticides, which might be mediated by enhanced activities of CO\(_2\) assimilation. Organophosphate enhanced the rate AA of oxidation in aqueous solution and shows antioxidant activity. Results of Rehfeld and Pratt (1969) indicate that the phosphate moiety of malathione (an organophosphate) is responsible for antioxidant activity and, it might be due to the phosphate’s ability to chelate metabolism (Cu\(^{2+}\)). The physiological role of the pyridine nucleotide monodehydroascorbic acid reductase and of the ascorbic acid-monodehydroascorbic system in photosynthesis is indicated by the findings that the illumination of chloroplast suspensions supplemented with AA and an AA oxidising agent markedly slow down the role of AA oxidation and thus, supporting the hypothesis of a participation of AA, as an electron carrier in the oxidative-phosphorylative chain functioning in the illuminated chloroplast (Marre and Arrigoni 1958).

Moreover, some herbicides, commonly called weed killers, are a type of pesticides used to kill unwanted plants. Selective herbicides kill specific targets while leaving the desired crop relatively unharmed. Some of these act by interfering with the growth of the weed and are often synthetic “imitations” of plant hormones. They are widely used in agriculture and in landscape turf management. In the U.S., they account for about 70% of all agricultural pesticides use. Plants have developed resistance to Atragine and to ALS-inhibitors and more recently, to glyphosate herbicides. Mareastil is one weed that has developed glyphosphate resistance. Also herbicides application to potato fields limits harmful effects of weeds. However, they can have some effects on changes in the chemical composition of potato tubers (Leszczynski 2002). From the aspect of consumption, AA is one of the most important constituents of a potato tuber. Therefore, it makes table potatoes as the cheapest and commonest source of AA (Leszczynski 2000). Studies of Zarecka and Gugala (2003) suggest that the application of herbicides to potato fields caused an increase in the content of AA in comparison with the control. The statistical analysis showed a significant effect of potato cultivars on AA concentrations.

Furthermore, a significantly higher concentration of AA was determined after application of some...
herbicides as sencor 70WG, sencor 70WG+ Fusilade super and Basagram600 SL+Focus ultra. Some authors (Zarzecka and Gasiorowska 2000) reported positive effects of pesticides on the content of AA. Bladex (Cyanazine), sencor (metribuzin) and potaran (Metobromuron) reduced the content of AA in potato tubers while Hamouz et al (1996b) did not find any significant influence of cultivation methods on AA concentration. As AA has a critical role in photosynthesis, as the high concentration in stroma of chloroplast (10-25mM) (Foyer et al. 1983), and it has been shown to have important functions in photosynthesis, such as in the protection of the photosynthetic apparatus against the oxygen radicals and H₂O₂ that are found during photosynthetic activity (Asada 1994), and against photo-inactivation; Since it is a cofactor of carotenoid-de-epoxidation (Siefermann and Yamamoto 1974). Mostly herbicides kill plants (weeds) by blocking PS-II of photosynthesis like paraquat. Also, AA in photosynthesis works in its three biochemical modes. Firstly, it acts as an antioxidant by removing H₂O₂ formed by oxygen photoreduction in PS-I (Mehler reaction), catalysed by APX, and some of which is bound to thylakoids where it can scavenge H₂O₂ as it forms. Secondly, MDA, formed by APX can act as a direct electron acceptor to PS-I. Thirdly, it is a cofactor for violaxanthin de-epoxidase. The de-epoxidase, which is bound to the lumen side of the thylakoid membrane, is dependent on ascorbate as a cofactor (Neubauer and Yamamoto 1993). Ascorbate thus contributes to electron flow and to formation of zeazanthin, which act as a photoprotectant.

Conclusion

AA can act efficiently in plants as immunomodulators when applied at the appropriate concentration and the current stage of plant development. AA is implicated in plant responses to biotic stress and to undergo profound changes in plants interacting with pathogens. AA regulated stress response as a result of a complex sequence of biochemical reactions such as activation or suppression of key enzymatic reactions, induction of stress responsive proteins synthesis, and the production of various chemical defense compounds. Due to its essential function as a co-factor for the biosynthesis of GA, ABA, SA and ET, AA appears to influence not only the endogenous level but also signaling of these plant hormones, and thus affect responses against the biotic stress. In addition, AA also open up new approaches for plant resistance against hazardous biotic stress conditions. However, there are obviously still large gaps to fill in order to elucidate the precise role of AA in enhancing the tolerance of plant to a number of biotic stresses during development of plant systems.

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