Polyamines (PAs) are small, aliphatic amines that are found in all living cells. In plants, putrescine, spermidine, spermine, and thermospermine are known as ubiquitous PAs. They are involved in various physiological processes and environmental stress responses, including pathogen infections. Several studies have demonstrated that PAs and their catabolic products, such as H$_2$O$_2$ produced by diamine oxidases and polyamine oxidases, are closely involved in the activation of host defense mechanisms. This minireview briefly summarizes recent advances regarding the function of PAs during disease resistance in plants.

Keywords: disease resistance, H$_2$O$_2$, polyamine, polyamine oxidase

INTRODUCTION

Polyamines (PAs) are aliphatic, polycationic compounds that are present in all living organisms. The most common PAs in plants are diamine putrescine (Put), triamine spermidine (Spd), and tetraamine spermine (Spm). Additionally, thermospermine (T-Spm), a structural isomer of Spm, was recently identified as a ubiquitous PA in plants (Takano et al., 2012). PAs are involved not only in developmental processes, such as cell division, embryogenesis, organogenesis, xylem development, and leaf senescence, but also in various environmental stress responses, including plant-microbe interactions (Kusano et al., 2007; 2008). A number of studies have provided evidence that PA metabolism is drastically changed by pathogen infections (Walters, 2000; 2003a; 2003b). Moreover, several transgenic plants exhibited increased tolerance to various pathogens when their endogenous PA levels were altered by overexpressing PA metabolic genes (Waie and Rajam, 2003; Prabhavathi and Rajam, 2007; Moschou et al., 2009; Fu et al., 2011; Gonzalez et al., 2011; Hazarika and Rajam, 2011). These findings indicate that PAs regulate the activation of defense responses in plants. In this review, I briefly summarize current knowledge of the role of PAs in disease resistance. More comprehensive reviews of PAs in biotic stress responses, including pathogen and beneficial interactions, are available elsewhere (Jiménez-Bremont et al., 2014).

POLYAMINE BIOSYNTHESIS

The PA biosynthetic pathway has been thoroughly investigated, and two Put synthesis pathways are usually conserved in plants. The first is the single-step conversion of ornithine to Put, which is catalyzed by ornithine decarboxylase (ODC); however, some plant species, including members of the genus Arabidopsis, have lost this pathway (Hanfrey et al., 2001). The other pathway comprises three sequential reactions in which arginine is converted to agmatine by arginine decarboxylase (ADC), agmatine is converted to N-carbamoylputrescine by agmatine iminohydrolase, and N-carbamoylputrescine is converted to Put by N-carbamoylputrescine amidohydrolase. Put is then successively converted to Spd by Spd synthase (SPDS), and then to Spm or T-Spm by Spm synthase (SPMS) or T-Spm synthase (TSPMS) (also known as ACAULIS5), respectively. These reactions involve the addition of aminopropyl groups supplied from decarboxylated S-adenosylmethionine (dcSAM) that is formed from SAM by SAM decarboxylase (SAMDC) (Fig. 1).

POLYAMINE CATABOLISM

Cellular PA levels are controlled not only by biosynthesis pathways, but also by catabolic pathways. In plants, two classes of enzymes, copper-containing amine oxidases (AOs) and flavin-containing PA oxidases (PAOs), are involved in PA catabolism. AOs catalyze the oxidation of Put and Spd to their corresponding amino aldehydes, with the concomitant production of ammonia and H$_2$O$_2$ (Cona et al., 2006; Angelini et al., 2010; Planas-Portell et al., 2013). However, information regarding PA oxidation is still fragmentary because of the 10 putative AO genes that have been identified in Arabidopsis, only four have been characterized biochemically (Møller and McPherson, 1998; Planas-Portell et al., 2013). PAOs are classified into terminal catabolism and back-conversion types based on their reaction modes. The former reaction converts Spd or Spm to 4-aminobutanal or...
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\[ N-(3\text{-aminopropyl})-4\text{-aminobutanal, respectively, along with} \]
\[ \text{the production of 1,3-diaminopropane and H}_2\text{O}_2 \] (Šebela et al., 2001). The latter reaction is known as the opposite re-
\[ \text{action of PA biosynthesis, and it converts tetraamines to} \]
\[ \text{Spd, and Spd to Put, and produces 3-aminopropanal and} \]
\[ \text{H}_2\text{O}_2 \] (Kusano et al., 2008) (Fig. 1). In \textit{Arabidopsis}, f i v e \]
\[ \text{PAO genes are conserved, and all AtPAOs have back-} \]
\[ \text{conversion activity, although their substrate specificities} \]
\[ \text{differ slightly (Tavladoraki et al., 2006; Kamada-Nobusada} \]
\[ \text{et al., 2008; Moschou et al., 2008; Takahashi et al.,} \]
\[ \text{2010; Fincato et al., 2011; Ahou et al., 2014). In contrast, both} \]
\[ \text{types of PAOs are present in monocotyledonous plants} \]
\[ \text{(Cona et al., 2006; Ono et al., 2012; Liu et al., 2014).} \]

**FREE POLYAMINES IN DISEASE RESISTANCE**

Plants have evolved defense mechanisms to cope with a wide variety of pathogens. The defense reaction involving localized cell death, known as the hypersensitive response (HR), is important for limiting the spread of pathogens. The activation of the defense response is initiated by the host receptor-mediated recognition of pathogen-associated molecular patterns, or by the recognition of pathogen race-specific avirulence factors by a corresponding resistance protein in the plant (Dangl and Jones, 2001; Chisholm et al., 2006). Many researchers have shown that PA metabolic enzymes are activated and PAs accumulate during disease resistance, including during the HR (Walters, 2000; 2003a). Incompatible powdery mildew fungus (\textit{Blumeria graminis} f. sp. \textit{hordei})-infected barley leaves exhibit increased levels of PA metabolic enzymes, such as ODC, ADC, SAMDC, AO, and PAO, as well as free Put and Spm and the conjugated forms of Put, Spd, and Spm (Cowley and Walters, 2002). Similar results have been observed in tobacco leaves that induce the HR in response to tobacco mosaic virus (TMV) infection (Negrel et al., 1984; Torrigiani et al., 1997; Marini et al., 2001). Various PAs accumulate during disease resistance, and the role of free Spm has been investigated extensively. Yamakawa et al. (1998) found that a TMV-induced HR increased the levels of free Spm in the intercellular spaces of tobacco leaves, and the exogenous application of Spm to tobacco leaves, which mimics the apoplastic accumulation of Spm upon infection with an incompatible pathogen (i.e., a pathogen that induces the HR), induced the expression of pathogenesis-related proteins and additional TMV resistance. Subsequent studies showed that exogenous Spm induces the activation of two mitogen-activated protein kinases, SIPK and WIPK, which are strongly activated during the TMV-induced HR, as well as the expression of some HR marker genes in tobacco leaves (Takahashi et al., 2003; 2004a; 2004b; Uehara et al., 2005). In \textit{Arabidopsis}, exogenous Spm also induces a number of disease-related genes, and further suppresses the replication of avirulent cucumber mosaic virus (CMV) (Mitsuya et al., 2009). These findings indicate that Spm acts as a signaling molecule to regulate the expression of various defense-related genes during incompatible pathogen infections in plants. Importantly, Spm-mediated signaling pathways are inhibited by AO and PAO inhibitors, which suggests that H\textsubscript{2}O\textsubscript{2} derived from Spm oxidation is involved in these pathways. Recently, the accumulation of various defense-related genes, as well as biotrophic pathogen resistance, was also confirmed in \textit{SPMS-overexpressing Arabidopsis} plants (Gonzalez et al., 2011).

The function of another tetraamine, T-Spm, is also similar to that of Spm. Exogenously applied T-Spm restricts CMV replication by inducing the expression of a subset of defense-related genes in \textit{Arabidopsis} (Sagor et al., 2012). T-Spm treatment and \textit{TSPMS} expression in

![Fig. 1 Polyamine metabolic pathways in plants. Biosynthetic and catabolic processes are indicated by black and gray arrows, respectively.](image)
Arabidopsis plants increased resistance to Pseudomonas viridiflava (Marina et al., 2013). The authors suggested that T-Spm oxidation is crucial for eliciting plant resistance. Recently, the functions of longer, uncommon PAs, such as caldopentamine, caldohexamine, homocaldopentamine, and homocaldohexamine, have also been shown to be similar to those of tetraamines (Sager et al., 2013).

Put and Spd were also shown to be involved in disease resistance. Eggplants expressing the oat ADC gene exhibited tolerance to the wilt-causing fungus Fusarium oxysporum (Prabhavathi and Rajam, 2007). In contrast, an Arabidopsis adc2 knockout mutant showed enhanced susceptibility to Pseudomonas syringae pv. tomato DC3000 (Kim et al., 2013b). Additionally, sweet oranges overexpressing the apple SPDS gene were less susceptible to Xanthomonas axonopodis pv. citri (Fu et al., 2011). Yoda et al. (2003; 2006) showed that HR cell death caused by TMV infection or cryptogein, an oomycete-derived elicitor, is partly mediated by H₂O₂ production via Spd catabolism. They suggested that Spd is a substrate for H₂O₂ production because Spd, but not Spm, accumulates in apoplasts during the HR. Indeed, the substrate specificities of plant PAOs are broad (Moscou et al., 2008; Takahashi et al., 2010; Fincato et al., 2011; Ahou et al., 2014).

POLYAMINES CONJUGATION

PAs often occur as free molecular bases, but they can also be associated with small molecules, such as phenolic acids, or macromolecules, such as proteins. They are most commonly conjugated with cinnamic acids, such as p-coumaric, ferulic, and caffeic acids, and the resulting conjugates are known as hydroxycinnamic acid amides (HCAAs) (Walter, 2000; 2003a). They can act directly as antimicrobial agents, and they can be incorporated into the plant cell wall to strengthen it against microbial-induced degradation. A number of studies have examined how HCAAs in plants respond to pathogen infection, and it was shown that there is a good correlation between the accumulation of HCAAs and pathogen resistance (Walter, 2000; 2003a). Recently, it was shown that tomato plants expressing tyramine N-hydroxycinnamoyltransferase, the key enzyme in HCAA synthesis, accumulated salicylic acid and exhibited enhanced resistance to Pseudomonas syringae pv. tomato (Campos et al., 2014).

PAs are also conjugated to proteins by transglutaminase (TGase), which catalyzes their covalent binding to the γ-carboxamide groups of protein endoglutamine residues (Folk, 1980; Del Duca et al., 2014; Cai et al., 2015). The two terminal amino groups of PAs are conjugated to one or two glutamine residues, thereby giving rise to either mono-(γ-glutamyl)-PAs (mono-PAs) or bis-(γ-glutamyl)-PAs (bis-PAs). The additional positive charges of the protein-bound PAs may induce protein conformational changes. Moreover, bis-PA derivatives can form both intra- and intermolecular cross-links. Del Duca et al. (2007) analyzed TGase activity during the HR in the tobacco-TMV interaction, and revealed that TGase activity was enhanced during the HR and gave rise to mono- and bis-PAs. Overall, our knowledge of conjugated PAs is much less than that of free PAs.

PROTEIN-PROTEIN INTERACTIONS

Many plant pathogens inject effector proteins into plant cells, where they may directly manipulate host innate immunity. Recently, studies have reported that PA metabolites are targeted by pathogen derivatives. Arabidopsis SPDS2 was identified as a target protein of 10A06, one of the effector proteins in the cyst nematode Heterodera schachtii (Hewezi et al., 2010). The C2 protein of beet severe curly top virus was shown to attenuate the degradation of SAMDC1 in Arabidopsis via a physical interaction, which resulted in the suppression of host DNA methylation-mediated gene silencing, further facilitating viral replication (Zhang et al., 2011). The Xanthomonas campestris pv. vesicatoria effector AvrBsT induces hypersensitive cell death in the pepper Capsicum annuum. Kim et al. (2013a) demonstrated that AvrBsT interacts with pepper ADC1 (CaADC1), and that the transient co-expression of AvrBsT and CaADC1 in Nicotiana benthamiana leaves specifically enhanced AvrBsT-induced cell death, which was accompanied by an accumulation of PAs, and burst of nitric oxide (NO) and H₂O₂. NO has emerged as a key mediator of plant defense responses, and it is known that Spm and Spd are potent NO inducers (Tun et al., 2006; Wimalasekera et al., 2011a). Although further studies are needed to determine the NO generation mechanism in disease resistance, it has been reported that a knockout mutant of CaAO1, one of the AO genes in Arabidopsis, showed an impaired PA-induced NO release (Wimalasekera et al., 2011b).

CONCLUDING REMARKS

Recent studies have increased our knowledge of the roles of PAs in disease resistance. Some PAs function as signaling molecules in disease resistance, and PA oxidation and the resulting reaction products, such as H₂O₂, are at least partially involved in disease resistance. Although gain-of-function and loss-of-function analyses have been performed in Nicotiana species (Moscou et al., 2009; Yoda et al., 2009), some important findings regarding PA oxidation in the host defense response have been obtained using AO and PAO inhibitors. Generally, it is suggested that apoplast PA oxidation is important for disease resistance; however, all of the Arabidopsis PAOs are localized to peroxisomes and the cytoplasm (Tavladoraki et al., 2006; Kamada-Nobusada et al., 2008; Moscou et al., 2008; Fincato et al., 2011; Ahou et al., 2014), and an apoplast-localized tetraamine-oxidation enzyme has not yet been identified. Loss-of-function analyses of each AO and PAO in Arabidopsis using T-DNA knockout mutants would help to further clarify the role of PA oxidation in disease resistance, including the HR. Moreover, the function of conjugated PAs and other PA-mediating factors, such as NO, are poorly understood. It is clear that PAs are functionally important molecules in disease resistance in plants; however,
much more information is required to obtain an overall picture of the role of PAs in plant-microbe interactions.

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