

A review on: Actions of polyamine on abiotic stresses in rice

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Abstract—The abiotic stresses in environment are the main cause for the growth, development and production of rice (*Oryza sativa*) loss worldwide. Polyamines are small, low molecular weight and positively charge molecules that are present in all living organisms and have strong binding capacity to negatively charged molecules (DNA, RNA and Proteins). Naturally occurring polyamines are involved in rice abiotic stress response. Molecular studies at transcriptional, translational and transgenic plants have shown that polyamines play an important role in controlling the cell cycle, protecting the cell, acting as signaling and modulating rice plants tolerance to abiotic stresses, specially the activities of polyamines biosynthesis enzymes. This review highlights how polyamines act in rice during abiotic stress and how to design new strategies to survival rice plants in advance environment.

Index Terms— Polyamines, rice (*Oryza sativa*), abiotic stress, transgenic rice, stress tolerance

1 INTRODUCTION

Rice (*Oryza sativa*) is one of the main important food crops in the world. Almost half of the population depends on rice as their staple food in the world (Coffman et al. 1987). Rice growth, cultivation, development and productivity are decreased by environmental stresses, of which salinity and drought represent some of the most devastating ones. Erosion, soil degradation and salinization affect approximately 3.6 billion of the world's 5.2 billion ha of dry-land used for agriculture (Riadh et al. 2010). 10% of the land surface (950Mha) and 50% of all irrigated land (230Mha) are salt-affected (Ruan et al. 2010). Global annual losses from soil salinity are estimated at US\$ 12 billion (Qadir et al. 2008). Most high-yielding rice cultivars developed for irrigated conditions are highly susceptible to drought stress as well (Lafitte et al. 2007). Drought is another abiotic stress with a reduction of productivity up to 35% (Jongdee et al. 1998). The estimated average annual loss of rice production due to drought conditions world-wide is about 18 million tons, or 3.6 billion US\$ (O'Toole et al. 2004). Drought delays the development of the rice plant (Puckridge et al. 1980), and strongly affects morphology (O'Toole et al. 1980, 1981, 1982) as well as physiological processes like tran-

assimilates to the grain (Turner et al. 1986; Fukai et al.1995). Polyamines (PAs) are small, positively charged, organic molecules that are ubiquitous in all living organisms. The three common

PAs in plants are putrescine (Put), spermidine (Spd) and spermine (Spm). Polyamines are also associated with responses of plants to abiotic stresses, including mineral nutrient deficiencies, osmotic and drought stress, salinity, heat, chilling, hypoxia and environmental pollutants (Groppa et al. 2008; Alcazar et al. 2010; Gill et al. 2010). Therefore, polyamines are thought to play an essential role in the abiotic stress tolerance of rice. However, the physiological function of polyamines under abiotic stress conditions is not clear (Ma et al. 2005; Capell et al. 2010). Polyamines are positively charged at physiological pH and are therefore able to interact with negatively charged molecules, such as nucleic acids, acidic phospholipids, proteins and cell wall components such as pectin (Bouchereau et al. 1999; Martin et al. 2000; Kakkar et al. 2002). The multiple suggested roles of polyamines encompass involvement in protein phosphorylation, conformational transition of DNA (Martin et al. 2001), and maintenance of ion balance, prevention of senescence, radical scavenging, membrane stabilization (Bouchereau et al. 1999) and regulation of gene expression by enhancing the DNA-binding activity of transcription factors (Panagiotidis et al. 1999).

2 POLYAMINES BIOSYNTHESIS AND METABOLISM IN RICE

Approximately 21 genes encoding enzymes involved in poly-

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spiration, photosynthesis, respiration and translocation of

amine biosynthesis in the rice genome. For 17 of these genes for expression (ADC1, 2 and 3, AIH, CPA1, 2, 3 and 4, ODC1, and 3, SAMDC1, 2, and 4, SPD/SPM1, 2, 3 and 4). The biosynthesis and degradation pathway of PAs in rice is well documented in figure 1. The first step in polyamine biosynthesis is decarboxylation of ornithine or arginine, catalyzed by ornithine- or arginine decarboxylases (ODC, ADC), to yield the diamine putrescine. The ADC pathway leading to putrescine synthesis consists of three enzymatic steps catalyzed by the sequential action of ADC, agmatine iminohydrolase (AIH) and N-carbamoylputrescine amidohydrolase (CPA). Higher molecular weight polyamines spermidine and spermine are formed by sequential addition of aminopropyl groups to putrescine and spermidine, respectively by the activity of spermidine synthase and spermine synthase. The aminopropyl groups are generated from S-adenosylmethionine (SAM) by SAM decarboxylase. SAM is also a precursor of ethylene, which is produced from SAM via 1-aminocyclopropane-1-carboxylic-acid (ACC) by ACC synthase and ACC oxidase. Genes encoding some of these enzymes have been cloned and characterized in different plant species. However, genes encoding sequences for all the above-mentioned enzymatic activities, with the exception of ODC, have only been characterized in Arabidopsis. This plant has no detectable ODC activity (Hanfrey et al. 2001), indicating that putrescine is produced exclusively through the ADC pathway. In the Arabidopsis genome there are two genes encoding ADC (ADC1 and ADC2), and one single gene respectively for AIH and CPA (Janowitz et al. 2003, Piotrowski et al. 2003). There are also two genes for spermidine synthase (SPDS1 and SPDS2), two for spermine synthase (SPMS1 and SPMS2) (Hanzawa et al. 2000; Panicot et al. 2002) and at least four for SAM decarboxylase (SAMDC1, SAMDC2, SAMDC3 and SAMDC4) (Urano et al. 2004). Put is catabolized by diamine oxidases (DAOs), in a reaction that converts put into Δ^1 -pyrroline and generates ammonia and H_2O_2 as byproducts. DAOs are preferentially localized in plant cell walls, and hydrogen peroxide resulting from Put catabolism may be important in lignifications and cross-linking reactions under normal and stress conditions. Following the oxidation of Put, Δ^1 -pyrroline is catabolized into γ -aminobutyric acid (GABA), which is ultimately converted, into succinic acid, a component of the Krebs cycle (Eller et al. 2006). Polyamines is their double-edged role, as being both sources of ROS and potential ROS scavengers and playing role as redox homeostasis regulators in plants (J. Saha et al. 20015). Both the catabolism and back-conversion of polyamines by DAO and PAOs result in the production of H_2O_2 in the apoplast and per-oxisomes (I. Pottosin et al. 2014). H_2O_2 has long been known as a signal molecule. It is able to mediate various processes, such as stomatal closure, directly due to its ability to influence ion channels, while it can also activate specific stress response processes through the MAPK cascade (P. N. Moschou et al. 2008). Polyamines, especially spermidine, also induce superoxide anion (O_2^-) production by the activation of NADPH-oxidase. However, (O_2^-) dismutates spontaneously or enzymatically to H_2O_2 . The ratio of (O_2^-) to H_2O_2 is an important

signal in transcription (E. A. Andronis et al. 2014), and might be the mediator of polyamines in plant adaptation to unfavorable conditions. Ono et al. (2012) have recently reported seven PAO isoforms (OsPAO1 to OsPAO7) from *Oryza sativa*. They cloned and overexpressed OsPAO3, OsPAO4, and OsPAO5 in *E. coli* to examine their enzymatic activities. Their work revealed that OsPAO3 favored Spd as substrate followed by thermospermine and Spm and showed a full PA back-conversion activity. OsPAO4 substrate specificity was similar to that of OsPAO5 preferring Spm and thermospermine, but not Spd. Those enzymes also converted Spm and thermospermine to Spd, again indicative of PA back conversion activities. Moreover, similar to the report of Moschou et al. (2008c), they showed that OsPAO3, OsPAO4, and OsPAO5 are localized in peroxisomes.

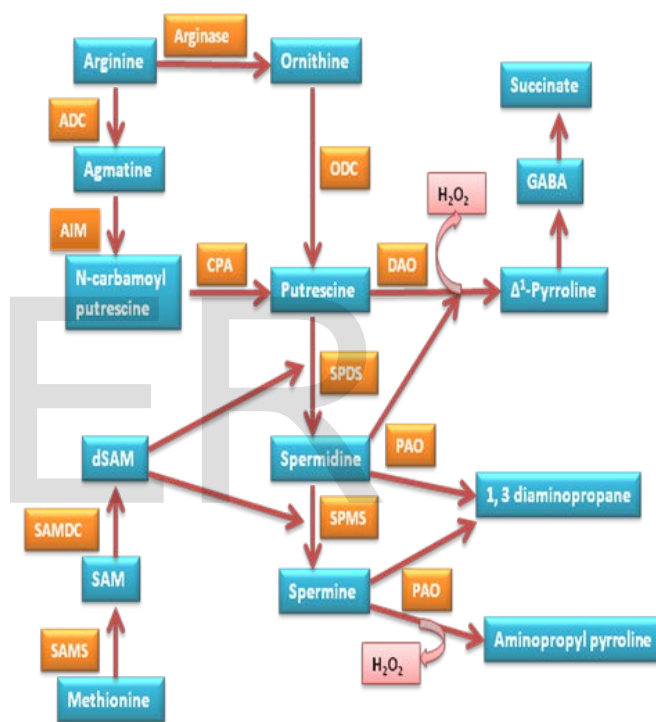


Fig. 1 General pathway for the biosynthesis and metabolism of polyamines in rice.

ADC: Arginine decarboxylase, AIM: Agmatine iminohydrolase, CPA: N-Carbamoyl putrescine amidohydrolase, DAO: Diamine oxidase, ODC: Ornithine decarboxylase, PAO: Polyamine oxidase, SPDS: Spermidine synthase, SPMS: Spermine synthase, SAMDC: S-adenosylmethionine decarboxylase, SAM: S-adenosyl methionine, GABA: γ -aminobutyric acid

3 SALINITY STRESS

Salt and drought stress are the two major abiotic stresses in agriculture and reduced water potential is a common consequence of both of them. Salinity is a complex environmental constraint that presents two main components: an osmotic component due to the decrease in the external osmotic potential of the soil solution, and the ionic component linked to the

accumulation of ions which become toxic at high salt concentrations (mainly Na^+ and Cl^-). A high salt concentration disrupts the integrity of cellular membranes, the activity of various enzymes and the function of the photosynthetic apparatus. Plants respond to changes in this unfavorable environmental accumulating low molecular-weight osmolytes such as proline (Kishore et al. 1995; Zhu et al. 1998) and PAs (Flores et al. 1991). Until now, it remains unclear which component of salt stress is responsible for PAs accumulation, despite numerous reports have tried to elucidate this essential clue for many years and differences in PAs content (Fig. 1) and in the activity of biosynthetic enzymes have been reported among and within many species (Flores et al. 1991; Tiburcio et al. 1997; Bouchereau et al. 1999; Capell et al. 2004; Zapata et al. 2004). The measurement of PAs levels in different rice cultivars showed that salt-tolerant rice cultivars maintains a high level of higher PAs, e.g. Spd and Spm, whereas salt-sensitive rice cultivars maintains only a high level of Put (Krishnamurthy and Bhagwat, 1989; Basu and Ghosh, 1991). The salt tolerant cultivars AU1, Co43, and CSC1 were effective in maintaining high concentrations of Spd and Spm, while the content of Put was not significantly altered in the growth stages analyzed when plants were exposed to salinity. The salt sensitivity in rice was associated with excessive accumulation of Put and with low levels of Spd and Spm in the shoot system of the salt-sensitive cultivars Co36, CSC2, GR3, IR20, TKM4, and TKM9 under saline conditions (Krishnamurthy and Bhagwat, 1989). Root plasma membranes of rice salt-tolerant cultivars Nonabokra and Pokkali were rich in $\text{Spm}=\text{Spd}$, whereas the root plasma membranes of sensitive cultivars (M-1-48 and IR8) were rich in Put only (Roy et al. 2005). However, salinity caused a significant increase in Spd and Spm in almost all the plant species studied. This meant that the pool of Put was directed to Spd and Spm synthesis. The $(\text{Spd} + \text{Spm}) = \text{Put}$ ratio increased with salinity, which would be in agreement with the idea of a protective role of higher PAs (Spd and Spm) against salt stress. Moreover, Mansour and Al-Mutawa (1999) indicated that the cellular alterations induced by NaCl in wheat roots were alleviated by low concentrations of Spd or Spm, whereas Put was ineffective. El-Shintinawy (2000) also indicated that salinity greatly enhanced the accumulation of Spm and Spd associated with a decrease in Put content in wheat cultivars. However, 200mM NaCl did not significantly change the OsSPDS2 (a SPDS gene) mRNA levels in rice plants (Imai et al. 2004).

4 DROUGHT STRESS

Under drought stress, the concentration of the polyamine degradation product β -alanine was not changed, while GABA levels were clearly increased (Fig. 2). GABA is a degradation product of Put and Spd via D1-pyrroline (Bagni et al. 2001), which was not present in our samples in detectable quantities. This makes a high degradation rate of Put or Spd rather unlikely, although we cannot exclude that D1-pyrroline is degraded too rapidly to accumulate to detectable levels. GABA levels can also be influenced by other metabolic pathways (Fait et al. 2008). The pool size of arginine, the main substrate for polyamine biosynthesis, increased under drought condi-

tions, indicating that this pathway was not substrate limited. The other possible substrate, ornithine was increased in roughly half of the cultivars and decreased in the others. Arginine is also a precursor of proline biosynthesis (Yang et al. 1999; Hsu et al. 2003), where it is converted to ornithine through the activity of arginase (Brown et al. 1966). Polyamine catabolism not only eliminates cellular polyamines, but enzymes and products of polyamine catabolism also contribute to important physiological processes (Martin et al. 1997; Sebela et al. 2001). However, very little is known about polyamine catabolism under stress conditions. Phuc et al (2013) indicated that Put and Spd levels decreased under drought stress, while Spm increased in all investigated cultivars, making it the most abundant polyamine under drought stress. The accumulation of Spm is in accordance with previous results in rice (Krishnamurthy et al. 1989; Maiale et al. 2004; Yang et al. 2007). Furthermore, transgenic rice over-expressing the *Datura stramonium* ADC gene exhibited higher drought tolerance due to the conversion of Put to Spd and Spm (Capell et al., 2004). Rice plants expressing SAMDC from *D. stramonium* showed unaltered levels of Put and an increase in Spm at the expense of Spd, leading to similar drought symptoms as in the wild type, but a more robust recovery upon return to well-watered conditions (Peremarti et al. 2009). Bouchereau et al. (1999) proposed that sensitive organisms generally accumulate Put under stress conditions and are unable to accumulate Spd and Spm. ADC is thought to be the enzyme primarily responsible for abiotic stress-induced Put accumulation (Tiburcio et al. 1997; Galston et al. 1997) In response to drought stress, the expression level of ADC2 was up-regulated, with the exception of the two most sensitive cultivars. This is in accordance with observations in Arabidopsis (Urano et al. 2003; Soyka et al. 1999) and in mustard (Mo et al. 2002), where also only ADC2 is up-regulated in response to osmotic, drought and salt stress, respectively. Induction of SAMDC has been shown under drought conditions in rice (Li ZY et al. 2000; Kawasaki et al. 2001; Rabbani et al. 2003; Shiozaki et al. 2005) and under salt stress in wheat (Li Z-Y et al. 200). However, the induced SAMDC gene identified by Li and Chen in rice is homologous to SAMDC1, which was not induced by stress in the present study (Li ZY et al. 2000).

5 COLD STRESSES

The important role of PA biosynthetic pathway has been observed in rice plant (Fig. 2) in response to cold stress (Cook et al. 2004; Usadel et al. 2008; Alcázar et al. 2011). It has been observed that cold-tolerant varieties show higher endogenous PA levels in response to low temperature than non-tolerant ones (Groppa and Benavides 2008). Theocharis et al. (2012) have reviewed the involvement of PAs in low temperature stress. In Arabidopsis, accumulation of free Put has been observed within 24 h of cold exposure, while no changes in Spd levels were detected (Cuevas et al. 2008). Quantitative expression analyses of both ADC1 and ADC2 genes show that transcription is induced as early as 30 min after cold exposure, ADC1 showing greater amplitude (Cuevas et al. 2008). The presence of CRT/DRE (C-repeat/Dehydration-Responsive

Element) in the promoter of ADC1, which confer responsiveness to cold, desiccation, and salinity, can mediate the early and transient ADC1 up regulation under cold stress (Yamaguchi-Shinozaki and Shinozaki 1994; Hummel et al. 2004). Similar observation was obtained from rice (Lee et al. 1997). They revealed the accumulation of Put during cold stress as a result of increased ADC1 and ADC2 activities. Vogel et al. (2005) had reported a cold inducible C₂H₂ zing finger transcription factor Zat12 to be involved in this upregulation. Put in turn activates zeaxanthin leading to accumulation of ABA. ABA-responsive elements (ABRE) present in most stress responsive elements are further activated culminating in synthesis of protective metabolites and cold acclimation (Vogel et al. 2005).

also pertinent to the photosynthetic apparatus. In fact, variation of thylakoid-associated PAs have been observed during plant response to various external stresses such as salinity, UV-B radiation, ozone, heavy metal, water stress, or chilling (Kaumar et al. 1997; Jantaro et al. 2003; Alcázar et al. 2006; Sfichi et al. 2004). It was also observed that high CO₂ concentrations increased the thylakoid bound put (Alcázar et al. 2006). However, UV-B radiations increased the thylakoid-associated Spm (Sfichi et al. 2004). Some reports have shown that Put, exogenously added during salt stress, enhances the level of the photochemical efficiency of PSII (Zhang et al. 2009). Moreover, the application of PAs during stress-induced senescence prevented chlorophyll loss and preserved the thylakoid membranes structure (Cohen et al. 1979; Popovic et al. 1979).

7 OXIDATIVE STRESSES

PAs are known to have a function in oxidative stresses. The antioxidative effect of PAs is probably due to a combination of their anionic and cationic-binding properties in radical scavenging, inhibiting properties of lipid peroxidation, metal-catalyzed oxidative reaction, and production of H₂O₂ by DAO and PAO (Groppa and Benavides, 2008). H₂O₂ produced by PA catabolism may cause activation of antioxidative defense responses. Phenylpropanoid-PA conjugates can act as antioxidants against ROS and reactive nitrogen species in response to stress conditions (Yamasaki and Cohen, 2006). ROS characterized by the accumulation of toxic molecules O^{•−}, H₂O₂, and OH[•] in tissues is a common plant response under abiotic stress (Miller et al. 2008) capable of causing damage to plant cell membranes and macromolecules (Apel and Kirt 2004). Plants have ROS scavenging enzymes such as superoxide dismutase (SOD), different peroxidases (POD), catalase (CAT), glutathione reductase (GR), glutathione peroxidase (GPX); lipoxygenase (LOX), and ascorbate peroxidase (APX) (Roychoudhury et al. 2011). The generation of ROS by PAO is tightly linked to catabolic processes of PAs (Cona et al. 2006), which is associated with plant defense and abiotic stress responses (Roy et al. 2005).

8 POLYAMINE ACCUMULATING TRANSGENIC RICE PLANT AND ABIOTIC STRESS TOLERANCE

It is possible to evaluate the PA biosynthesis genes and identify their roles in abiotic stresses by molecular biology and genetic engineering techniques in recent year (Groppa and Benavides, 2008). It is observed that PAs have different types of role in environmental stresses such as water stress (Capell et al. 2004), low and high temperatures (Hummel et al. 2004) and salinity (Maiale et al. 2004; Roy et al. 2005; Liu et al. 2006). Over-expression of PA biosynthetic genes like ADC (Capell et al. 2004, Roy and Wu, 2001) and SAMDC (Roy and Wu, 2002) in plants like *O. sativa* has increased tolerance to various abiotic stresses (Table 1). For example, in a recent study, transgenic rice plants expressing the *Datura stramonium* ADC (arginine decarboxylase) gene produced higher levels of Put under

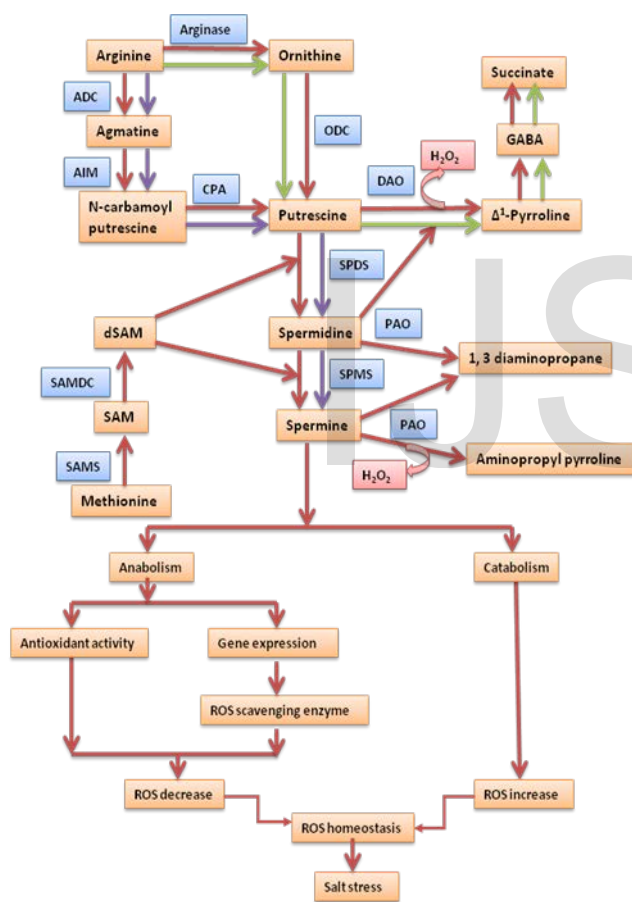


Fig. 2 Polyamine metabolism in rice to response salt (red arrow), drought (green arrow) and cold (blue arrow) stresses.

6 HEAT STRESS

In heat tolerant cotton and rice, substantial increase in free and conjugated PAs and long chained PA as well as higher accumulation of PAOs and PA biosynthesizing ADC were observed during heat stress (Evans and Malmberg, 1989; Cona et al. 2006). In callus of heat-tolerant rice cultivars, an increase in ADC and PAO activities were detected (Roy and Ghosh, 1996). It is now well accepted that these adaptation mechanisms are

drought stress than wild type plants, which led to higher levels of Spd and Spm and improved drought tolerance. In contrast, wild-type *Datura stramonium* exhibit increased endogenous Put levels on the onset of drought stress but this Put level is not enough to trigger the conversion of Put into Spd and Spm (Capell et al. 2004). Another example is the introduction of the *Tritordeum* SAMDC (S-adenosylmethionine decarboxylase) gene into rice, which resulted in a three to four-fold increase in Spd and Spm levels in transformed plants, which then had normal growth and development even under NaCl stress (Roy and Wu, 2002). Recently, Peremarti et al. (2009) generated transgenic rice plants constitutively expressing heterologous SAMDC gene from *Datura stramonium* to dissect the roles of Put from higher polyamines Spd and Spm. In another set of experiments, ADC expressing transgenic rice plants produced higher levels of Put, Spd and Spm and exhibited drought tolerance. Further, it has been proposed that Put may reflect the sub optimal growth conditions while Spd and Spm may help detoxifying free radicals (Larher et al. 2003). These results confirmed the involvement of polyamines in drought stress and further attributed individual roles to Put, Spd and Spm. Interestingly, introduction of a single polyamine biosynthesis gene has been shown to confer tolerance to multiple stresses.

Table 1. Transgenic rice expressing polyamines in abiotic stress tolerance

Gene	Source	Transgenic Plant	Accumulated PA	Tolerance	References
ADC (Arginine decarboxylase)	<i>Avena sativa</i>	<i>Oryza sativa</i>	Put	Salt	Roy et al. 2001
ADC (Arginine decarboxylase)	<i>Datura stramonium</i>	<i>Oryza sativa</i>	Put, Spd, Spm	Drought	Capell et al. 2004
SAMDC (S-adenosyl methionine decarboxylase)	<i>Tritordeum urgidum</i>	<i>Oryza sativa</i>	Spd, Spm	Salt	Roy et al. 2002
SAMDC (S-adenosyl methionine decarboxylase)	<i>Dianthus stramonium</i>	<i>Oryza sativa</i>	Spd, Spm	Drought	Peremarti et al. 2009

CONCLUSIONS AND FUTURE PROSPECTS

Rice is one of the main food crops in the world that are differently affected by abiotic stresses and their productivity is decreasing every year by global environmental changes (GEC). GEC causes salinity, drought, flooding, soil acidification, soil salinization, extremely low and high temperatures, and other adverse environmental conditions. These GEC factors directly or indirectly affect rice production. According to FAO, the world population will be nine billion by 2050 and needs 70% more food. About 23% of the calories consumed by human are provided by the rice. Thus, it is very necessary to improve stress tolerant rice variety. Polyamines have a lot of physiological and cellular functions such as seed germination, cell division, somatic embryogenesis and differentiation, de-

velopment of flowers and fruits, dormancy breakdown of tubers, protect photosynthetic apparatus. Therefore, a lot of work is required specially molecular biology and genetic engineering techniques to modify plant PAs levels are developed, including exogenous PAs and addition of specific inhibitors to intact plants (microarray, transcriptomics, and metabolomics, reverse genetics approaches) and PAs transgenic rice to response in abiotic stress tolerance. The PAs biosynthesis genes encoding the enzymes will also be helpful for increasing the abiotic stress tolerance in rice.

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