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REVIEW

Antioxidant defense responses: physiological plasticity in higher plants under abiotic constraints

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Abstract Environmental stresses (salinity, drought, heat/cold, light and other hostile conditions) may trigger in plants oxidative stress, generating the formation of reactive oxygen species (ROS). These species are partially reduced or activated derivatives of oxygen, comprising both free radical ($O_2^{\cdot-}$, $OH\cdot$, $OH_2\cdot$) and non-radical (H_2O_2) forms, leading to cellular damage, metabolic disorders and senescence processes. In order to overcome oxidative stress, plants have developed two main antioxidants defense mechanisms that can be classified as non-enzymatic and enzymatic systems. The first class (non-enzymatic) consists of small molecules such as vitamin (A, C and E), glutathione, carotenoids and phenolics that can react directly with the ROS by scavenging them. Second class is represented by enzymes among them superoxide dismutase, peroxidase and catalase which have the capacity to eliminate superoxide and hydrogen peroxide. In this review, we have tried to explore the related works, which have revealed the changes in the basic antioxidant metabolism of plants under various abiotic constraints.

Keywords Antioxidant defense · Abiotic constraints · Enzymes · Reactive oxygen species · Vitamins · Glutathione · Phenolics

Introduction

In higher plants, abiotic constraints (salinity, drought, heat/cold, light) are responsible of oxidative stress caused by an

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unbalance between pro-oxidants and antioxidants in favor of the formers (Sreenivasulu et al. 2007; Farooq et al. 2008). In fact, a common denominator in all these adverse conditions is the over production of the reactive oxygen species (ROS) within different cellular compartment of the plant cell (Pinheiro et al. 2004). ROS formation is initiated by the univalent reduction of molecular oxygen using either one, two or three electrons generating superoxide, hydrogen peroxide (H_2O_2) or hydroxyl radical ($OH\cdot$) respectively or by the formation of singlet oxygen ($^1O_2$) by transfer of excess excitation energy to O_2 (Alscher et al. 2002; Eva and Dean 2003; Wu et al. 2008). ROS are divided in two main classes consisted of non-radical species (H_2O_2) or free radical forms ($O_2^{\cdot -}, OH\cdot, OH_2\cdot$). Accumulation of high concentrations of ROS is potentially detrimental to plants cells causing damage to valuable biomolecules like DNA, proteins, lipids, chlorophyll, membrane etc (Blokhina et al. 2003). Generated at low amounts, ROS are involved as early messenger molecules in signaling cascades of reaction activated by several external and development stimuli and ROS serve also in defense reactions in apoplast (Asada and Takahashi 1987; Abbasi et al. 2007).

In higher plants, dissipation of excess photochemical energy is an immediate and finely turned response, which occurs through heat irradiation, alternate sinks for photosynthetic elements and down regulation of photosystem II (Foyer et al. 1994; Megdiche et al. 2008). The photoreduction of oxygen is an important alternative sink for the consumption of excess energy but it is associated with an increase in the generation of ROS such as H_2O_2, $O_2^{\cdot -}$, $OH\cdot$ and $^1O_2$ (Foyer and Harbinson 1994; Nicolas et al. 2006; Tahkokorpi et al. 2007). Superoxide can also be formed during the conditions of photoinhibition where by an electron from photosystem I is accepted by dioxygen (Simontacchi et al. 1993; Petropoulos et al. 2008; Hong-Bo et al. 2008a). Stress condition also results in an elevated rate of single electron transfer from the elements of the photosynthetic electron transport chain to molecular oxygen resulting in the formation of superoxide radical and consequently H_2O_2 and $OH\cdot$ production (Less and Galili 2008; Hong-Bo et al. 2008b, c).

Free radicals can be formed via enzymatic reaction from non-autooxidizable substances such as halo alkanes, phenols, nitro compounds and aromatic amines (Dalmia and Sawhney 2004; Jaleel et al. 2006; Massacci et al. 2008). Free radicals are also formed when cell constituents are exposed to ionizing radiation (Davenport et al. 2003). The presence of oxygen in the cellular environment represents a constant oxidative threat to cellular structure and process (Pand and Khan 2003; Martinez et al. 2007). Generation of ROS have greater toxicity potential on biomolecules and membranes (Scandalios 1997; Miller et al. 2007).

It is also known that plants resist to the stress-induced production of ROS by increasing component amounts of their defensive system (Foyer et al. 1994; Zabalza et al. 2008). Plant cells are normally protected against such effect by a complex antioxidant system as non-enzymatic and enzymatic antioxidants (Smirnoff 1995; Ali et al. 2008). The non-enzymatic antioxidants include two general classes (1) lipid soluble membrane associated antioxidants (e.g., α-tocopherol and β-carotene), and (2) water soluble reductants (e.g., glutathione, ascorbate and phenolics). Enzymatic antioxidants comprise superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR), which are believed to scavenge H_2O_2 in chloroplast and mitochondria. The other enzymatic antioxidants, catalase (CAT) and peroxidase (POX), are capable of removing H_2O_2, neutralizing or scavenging free radicals and oxyintermediates (Karpinski and Muhlenbock 2007; Sang et al. 2007). Without this defense mechanism, plants could not efficiently convert solar energy to chemical one. Among these enzymatic antioxidants, CAT and SOD are the most efficient antioxidant enzymes and their combined action neutralize the potentially dangerous $O_2^{\cdot -}$ and H_2O_2 to H_2O (water) and molecular oxygen (O_2) thus converting cellular damage (Scandalios 1997). Two key antioxidants in chloroplast involved in reactive oxygen radical scavenging are ascorbate and α-tocopherol (Smirnoff and Wheeler 2000). The ROS are produced in the young senescing leaf cells excessively under stressful condition and are removed by complex non-enzymatic [ascorbate (AA), glutathione (GSH), α-tocopherol] and enzymatic (CAT, APX, glutathione peroxidase, SOD and GR etc) antioxidant systems (Scandalios 1997). GR and glutathione dehydrogenase participate together with APX in the AA–GSH cycle. Both enzymes catalyze reactions that maintain the large pool of GSH and AA, and are essential for the appropriate functioning of the antioxidant system in plants (Davenport et al. 2003). The activities of antioxidant enzymes such as APX, CAT and SOD are upregulated in response to several abiotic stresses such as drought (Sankar et al. 2007; Jaleel et al. 2007a, b, c, 2008a; Manivannan et al. 2007, 2008a), salinity (Jaleel et al. 2007d, e, f, g, 2008b, c, d; Manivannan et al. 2008b), ozone (Puckette et al. 2007), SO_2, UV-B (Rajendiran and Ramanujam 2004) and temperature (Ali et al. 2005).

Non-enzymatic antioxidants

The term antioxidant refers to the activity possessed by numerous vitamins, secondary metabolites and other phytochemicals to serve as protection against the damaging effects of highly reactive molecules known as the radicals (McDermott 2000; Eraslan et al. 2007; Hong-Bo et al. 2008d). The non-enzymatic system of defense against oxidative stress consists of the antioxidant molecules corresponding to glutathione, AA, α-tocopherol, carotenoids and phenolic compounds (Blokhina et al. 2003; Seong et al. 2007). These molecules play a key role in scavenging free radicals in plants by donating electron or hydrogen (Asada 1999).

α-Tocopherol

α-Tocopherols (vitamin E) are lipophilic antioxidants synthesized by all plants. α-Tocopherols interact with the polyunsaturated acyl groups of lipids, stabilize membranes and scavenge and quench various ROS and lipid soluble byproducts of oxidative stress (Wang and Quinn 2000). Singlet oxygen quenching by tocopherols is highly efficient, and it is estimated that a single α-tocopherol molecule can neutralize up to 120 singlet oxygen molecules in vitro before being degraded. Because of their chromanol ring structure, tocopherols are capable of donating a single electron to form the resonance—stabilized tocopheroxyl radical (Yamaguchi et al. 2001). α-tocopherol was consumed predominantly as radical scavenging antioxidant against the lipid peroxidation as observed in the soybean membrane system (Clement et al. 2002). α-Tocopherol levels increase in photo-synthetic plant tissues in response to a variety of abiotic stresses (Munne-Bosch and Algere 2003).

α-Tocopherols also function as recyclable chain reaction terminators of polyunsaturated fatty acid (PUFA) radicals generated by lipid oxidation (Girotti 1998; Jaleel et al. 2007h). α-Tocopherols scavenge lipid peroxy radicals and yield a tocopheroxyl radical that can be recycled back to the corresponding α-tocopherol by reacting with ascorbate or other antioxidants. α-Tocopherols are major lipid soluble antioxidant present in the PUFA enriched membranes of chloroplasts and are proposed to be an essential component of the plastid antioxidant network. The most attributed function of tocopherols is their involvement by various mechanisms in protecting PUFAs from oxidation (Sandorf and Hollander-Czytko 2002). ROS generated, as by-products of photosynthesis and metabolism are potential sources of lipid peroxidation in plant cells. Synthesis of low-molecular-weight antioxidants, such as α-tocopherol, has been reported in drought-stressed plants (Munne-Bosch and Algere 2003). Oxidative stress activates the expression of genes responsible for the synthesis of tocopherols in plants (Sandorf and Hollander-Czytko 2002).

α-Tocopherol plays a unique role as an antioxidant and a stabilizer for biological membranes. α-Tocopherol is lipid soluble antioxidant associated with biological membrane of cells, especially the membrane of photosynthetic apparatus (Lawlor 2002; Kanwischer et al. 2005). It is synthesized in chloroplasts and protoplastids and located in membranes of the cells, especially the thylakoid membranes of the chloroplasts. The structure and location of α-tocopherol determine its function as a membrane stabilizer (Smirnoff 1995). α-tocopherol incorporated into the lipid portion of cell membranes and other molecules, protecting these structures from oxidative damage and preventing the propagation of lipid peroxidation (Mc Dermott 2000). The ROS formed at the membrane of wheat leaves under water stress was efficiently removed upon rehydration with increase in the content of α-tocopherol and β-carotene (Bartoli et al. 1999).

Ascorbic acid

Ascorbic acid is one of the most extensively studied antioxidant and has been detected in majority of plant cell types, organelle and apoplast (Smirnoff 2000; Giovannoni 2007). AA also has been implicated in regulation of cell elongation (Srivalli et al. 2003). A pathway for AA biosynthesis featuring GDP-mannose and L-gabetose has recently been proposed for plants. GDP-mannose phosphorylase provides GTP-mannose, which is used for cell wall carbohydrates biosynthesis as in pea and soybean (Shams-El-Din 2000).

The AA is an important component of plant antioxidant system (Smirnoff and Wheeler 2000). AA plays a protective role in plants against ROS that are formed from photosynthetic and respiratory processes (Guo et al. 2005). AA is linked to cell growth, being involved in the cell cycle and other mechanisms of plant cell growth and division as well as acting as a co-factor for many enzymes (Lee and Kader 2000). AA has effects on many physiological processes including the regulation of growth, differentiation and metabolism in plants (Mehlhorn et al. 1996). AA influences many enzyme activities and minimizes the damage caused by oxidative process through synergic function with other antioxidants (Asada 1999; Foyer et al. 1994). AA scavenges many types of free radicals affecting many enzyme activities and it is also required for regeneration of α-tocopherol (Smirnoff 2000).

In the ascorbate–glutathione cycle, two molecules of AA are utilized by APX to reduce H_2O_2 to water with concomitant generation of monodehydroascorbate (MDHA). MDHA is a radical with a short lifetime and can disproportionate into dehydroascorbate (DHA) and AA. The electron donor is usually NADPH and catalyzed by MDHA reductase (MDHAR) or ferredoxin in water–water cycle in the chloroplasts (Asada 1999). In plant cells, the most important reducing substrate for H_2O_2 removal is AA. H_2O_2 removal by ascorbate is also important in the apoplast (Blokhina et al. 2003). A direct protective role for AA has also been demonstrated in rice, where partial protection against damage caused by a release from flooding conditions was provided by the prior addition of AA (Chen and Gallie 2004). AA can also directly scavenge $^1O_2$, $O_2^{\cdot -}$ and OH· and regenerate tocopherol from tocopheroxyl radical, thus providing membrane protection (Laing et al. 2007). AA also acts as a co-factor of violaxanthin de-epoxidase, thus sustaining dissipation of excess excitation energy (Smirnoff 2000). Antioxidants such as AA and glutathione are involved in the neutralization of secondary products of ROS reactions (Conklin 2001). AA scavenges $O_2^{\cdot -}$ and $^1O_2$, reduces thiol radicals and dismutases H_2O_2 through the conversion of MDHA or DHA to ascorbate by the action of GR in a NADPH-dependent reaction (Hamada 2000; Tanaka et al. 1999).

Reduced glutathione

Glutathione is a tripeptide (α-glutamyl cysteinylglycine), which has been detected virtually in all cell compartments such as cytosol, chloroplasts, endoplasmic reticulum, vacuoles and mitochondria (Jimenez et al. 1997). Glutathione also occurs predominantly in the reduced form (GSH) and its concentration is the highest in the chloroplasts (1–4 mM) (May et al. 1998). The glutathione pool is an important redox component in plant cells. Changes in intercellular glutathione status may therefore be expected to have important consequences for the cell, through modification of the cell metabolic functions associated with glutathione regulated genes (Noctor et al. 2002). Glutathione takes part in the control of H_2O_2 levels (Alscher et al. 2002). The change in the ratio of its reduced (GSH) to oxidized (GSSG) form during the degradation of H_2O_2 is important in certain redox signaling pathway (Pastori et al. 2000).

Glutathione is the major source of non-protein thiols in most plant cells. The chemical reactivity of the thiol group of glutathione makes it particularly suitable to serve a broad range of biochemical functions in all organisms. The nucleophilic nature of the thiol group also is important in the formation of mercaptide bonds with metals and for reacting with select electrophiles. This reactivity along with the relative stability and high water solubility of GSH makes it an ideal biochemical to protect plants against oxidative stress, heavy metals and certain exogenous and endogenous organic chemicals (Noctor et al. 2002). It has been suggested that the GSH/GSSG ratio, indicative of the cellular redox balance, may be involved in AOS perception (Noctor and Foyer 1998). GSH acts as an antioxidant and is involved directly in the reduction of most active oxygen radicals generated due to stress. Pastori and Foyer (2002) reported that glutathione, as an antioxidant, helped to withstand oxidative stress in transgenic lines of tobacco.

GSH content vary in different subcellular compartments, according to the intensity of stress (Pei et al. 2000). The increase in GSH can be correlated with its ability to scavenge single oxygen, peroxides and hydroxyl radicals and is involved in recycling of acetic acid in the ascorbate–glutathione pathway in chloroplasts (Foyer et al. 1994). The major water-soluble antioxidant metabolite glutathione and AA are primarily in the cytoplasm and mitochondria. Many enzymes also catalyze the reaction between glutathione and H_2O_2 to form water and oxidized glutathione (Liang et al. 2007). Glutathione is necessary for the cell to enter the G_1 phase, the pre-mitotic phase of the cell cycle in which capable of responsing to extracellular stimuli that determine whether it will enter the S-phase, or enter quiescence, differentiation or death (May et al. 1998).

Phenols

Among antioxidants, AA, glutathione and phenolic acids (simple polyphenols) are particularly important. Polyphenolic structure has the ability to eliminate radical species and to function as metal chelators (Ksouri et al. 2008). It has been suggested that peroxidase could act as an efficient H_2O_2 scavenging system in plant vacuoles in the presence of phenolics and reduced ascorbate (Zancani and Nagy 2000).

Santiago et al. (2000) hypothesize a cycle where H_2O_2 is scavenged by phenolics through a peroxidase; phenolics are oxidized to phenoxyl radicals which can be reduced by AA. This cycle can occur in both the apoplast and in the vacuole, where phenolics are particularly concentrated. Antioxidant activity correlates well with total phenolics content and anthocyanin content in blueberry (Ehlenfeldt and Prior 2001; Prior et al. 1998; Kalt et al. 2000). Salicylic acid is a phenolic hormone that plays a crucial role in stress resistance in plants (Alvarez 2000). Conner et al. (2002) reported antioxidant activity may be assayed directly or indirectly by using total phenolic content as a surrogate measure of antioxidant activity among blueberry cultivars. The high antioxidant capacity of blueberries has been highly correlated to their anthocyanin and total phenolic content (Kalt et al. 2000).

Antioxidant enzymes

Plants have developed antioxidant enzymes such as APX, DHA reductase (DHAR), POX, GR, CAT, SOD for scavenging the ROS (Vranova et al. 2002). Key enzymes involved in the detoxification of ROS are namely SOD, CAT, peroxidase (POD), APX and other enzymes implicated in the Halliwell and Asada cycle (ascorbate–glutathione pathway). Under stress condition that enhanced activity of almost all these enzymes (Zaka et al. 2002; Zhao et al. 2008). SOD and CAT required for destruction of super oxide and H_2O_2 (Davis and Swanson 2001). SOD, CAT, APX and GR are present in isoforms with specific subcellular localization. The enzymes of glutathione–ascorbate cycle have been implicated in mitigating the effect of ROS (Gara et al. 2000; Molina et al. 2002; Porcel et al. 2003). A large number of studies deal with various oxidative stress factor in plants, and describe how exposed plant adjust their detoxifying enzyme activities (Ahmadi and Baker 2001; Akashi et al. 2001; Sgherri et al. 2003; Agarwal et al. 2006; Jaleel et al. 2007a, b, 2008a, b). APX and CAT represent the major enzymes of H_2O_2 degradation and it is interestingly to note that apoplast of barley leaves has been shown to contain substantial amount of SOD, CAT and APX required for superoxide and H_2O_2 detoxification (Vanacker et al. 1998).

Superoxide dismutase

Superoxide dismutase is a metal-containing enzyme that catalyzes the dismutation of superoxide radical to oxygen and H_2O_2. Dismutation to H_2O_2 by SOD initiates subsequent formation of hydroxyl radical by the Fenton reaction (Foyer et al. 1994). The combined action of SOD and CAT abate the formation of the most toxic and highly reactive oxidant, the hydroxyl radical (·OH), which can react in discriminately with all macromolecules. Although there are not known direct scavengers of single oxygen $^1O_2$ or the hydroxyl radical (·OH), SOD is believed to function in their elimination by chemical reaction (Alvarez 2000).

Superoxide dismutase has been found in all aerobic organisms examined, where it plays a major role in the defense against toxic reduced oxygen species, which are generated as by products of many biological oxidations. The generation of oxygen radical can be further exacerbated during environmental adversity and consequently SOD has been proposed to be important for plant stress tolerance (Apel and Hirt 2004). The source of superoxide radical generation may be natural—i.e., byproducts of metabolic activities, including the electron-transport chain—or reduced by external agent including ozone, UV-B, gamma rays, light-induced photoinhibitory conditions, or chemical like paraquat or methyl viologen (Raychaudhuri and Deng 2000).

An important function of SOD is to prevent radical mediated chain oxidation of GSH, thereby enabling GSH to act physiologically as a free radical scavenger without concomitant oxidative stress to the cell. The combination of SOD and GSH plays a significant role in intracellular antioxidant defense (Asada 1999). SOD classification is based on the metal ion in their active site and they are copper and zinc (Cu/Zn SOD) containing SOD which is the most efficient scavengers of the superoxide anion and as essential component of ascorbate–glutathione cycle for the detoxification of toxic oxygen species (Chew et al. 2003).

Inside a cell, the SOD constitutes the first line of defense against ROS (Alscher et al. 2002). The interaction of the SOD involvement in scavenging ROS is very complex and also involves other peroxidases (Scandalios 1997). Many stress situations caused an increase in the foliar SOD activity (Pastori et al. 2000). Antioxidants, which inhibit the oxidation of organic molecules, are very important not only for food preservation, but also for the defense of living systems against oxidative stress. Oxidative damage alleviation was reported in salt stressed *Catharanthus* plants through the action of SOD in all parts (Jaleel et al. 2007e, 2008d) indicating that there might be an efficient active oxygen scavenging system.

Ascorbate peroxidase

Ascorbate peroxidase is one of the most important antioxidant enzymes of plants that detoxify H_2O_2 using ascorbate for reduction. Different isoforms of APX are active in chloroplasts, cytosol and microsomes. In different plant species, APX activity increases in response to a variety of biotic and abiotic stresses (Asada 1999). APX in combination with the effective ascorbate–glutathione cycle functions to prevent the accumulation of toxic levels of H_2O_2 in photosynthetic organisms (Asada 1999; Shigeoka et al. 2002). APX is more specific and use AA as electron donor, but to a lesser extent, can also use guaiacol or other substrates (Mehlhorn et al. 1996; Jaleel et al. 2008e).

Ascorbate peroxidase utilizes H_2O_2 to oxidize AA to MDHA radical, which disproportionate to DHA non-enzymatically. MDHAR regenerate AA at the expense of nicotinamide adenine dinucleotide phosphate (NAD(P)H) and DHAR regenerate AA utilizing GSH to form GSSG. GSH is regenerated at the expense of NADPH by the action of GR, until getting the rate of limiting step of the cycle (Hoekstra et al. 2001; Gopi et al. 2007). The high level of endogenous APX is essential and effectively maintains the antioxidant system that protects plants from oxidative damage due to biotic and abiotic stresses (Shigeoka et al. 2002). APX and CAT represent the major enzymes of H_2O_2 degradation (Vanacker et al. 1998). APX isoenzymes have high specificity for AA as an electron donor especially in the case of chloroplastic APX and mitochondrial APX isoenzymes (Leonardis et al. 2000).

The AA/GSH cycle constitutes an important detoxification pathway for dissipation of H_2O_2 and other reactive oxygen radicals in chloroplasts (Sgherri et al. 2003). It is assumed that the increased activities of the enzymes of AA/GSH pathway, especially that of APX confer general resistant to array of environmental stresses (Gara et al. 2000). APX activity would increase the demand for AA regeneration. In this context, it is believed that a simultaneous increase in several components of the antioxidative defense system would be necessary in order to obtain an increase in plants protective mechanisms (Foyer et al.

1994). APX are implicated in the protection of membranes from salt damage by scavenging toxic oxygen radicals. Enhanced production of oxygen free radicals is responsible for peroxidation of membrane lipids and the degree of peroxidase damage of cells was controlled by the potency of peroxide enzyme system (Sreenivasulu et al. 2007).

Catalase

Catalase is tetrameric heme containing enzymes that catalyze the dismutation of H_2O_2 into water and oxygen. The enzyme is abundant in the glyoxisomes of lipid-storing tissues in germinating barley, where it decomposes H_2O_2 formed during the β-oxidation of fatty acids (Fazeli et al. 2007) and in the peroxisomes of the leaves of C_3 plants, where it removes H_2O_2 produced during photorespiration by the conversion of glycolate into glyoxylate (Foyer and Fletcher 2001; Jayakumar et al. 2008). This is also due to the fact that there is proliferation of peroxisomes during stress, which might help in scavenging of H_2O_2, which can diffuse from the cytosol (Lopez-Huertas et al. 2000). A third class of CAT is located in vascular tissues and may be involved in protection against environmental stress (Fu and Huang 2001). The H_2O_2 scavenging system represented by APX and CAT are more important in partitioning tolerance than SOD as reported in oxidative stressed wheat varieties (Asada 1999; Lafitte et al. 2007).

Peroxidase

Peroxidase, CAT and APX appear to play an essential protective role in the scavenging process when coordinated with SOD activity. They scavenge H_2O_2 generated primary through SOD action (Chaitanya et al. 2002). POX involves in various metabolic steps such as auxin catabolism the formation of iso di–tri bridges in the cross-linking of cell wall proteins, the cross-linking of pectins by diferulic bridges in tobacco (Amaya et al. 1999; Jaleel et al. 2008e, f) and the oxidation of cinnamyl alcohols prior to their polymerization, during lignin and suberin formation (Whetten et al. 1998). Auxin treatments affected a sharp increase in the POX activity in the roots of *Psoralea corylifolia* (Rout et al. 2000). Water deficit stress increased the POX activity in soybean plants (Zhang et al. 2006).

Concluding remarks

The future will determine more precisely how ascorbate, glutathione and tocopherol as well as antioxidant enzymes are involved in initiating and controlling redox signal transduction and how they trigger the gene expression of other related responses to optimize survival strategies under stress. In addition, other problems are how antioxidants coordinate growth and development of higher plants in a constantly changing environment, how redox signaling is linked with hormonal regulation, nutrient status and redox potential of higher plants, and how their redox signaling is cooperated with inter- and intracellular signaling, transport capacity, developmental and environmental cues to maintain an appropriate dynamic homeostasis for stress tolerance and efficient survival.

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