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PEROXIDASES AS A MECHANISM OF ANTIOXIDANT RESPONSE IN TEOSINTE AND MAIZE

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ABSTRACT

Oxidative stress from environmental sources and developmental transitions such as seed maturation involves the formation of reactive oxygen species (ROS) in plant cells. The modified oxide-reduction changes that follow are central events in cellular responses. Plant peroxidases are involved in numerous cellular processes in plant development and in response to stress. In maize, eight peroxidases of different classes have been identified, four of which have been characterized linked to the plasma membrane in the roots of *Zea mays* L. In teosinte there is very little information about the mechanisms of response to oxidative stress; in this field, the most recent work relates the concentrations of peroxidases in seedlings subjected to saline stress, thermal stress and stress by infection with a plant pathogen, with the possible role that these enzymes can have in these conditions and in a fairly early period of development of the plant. The high synthesis of peroxidases at high temperatures and stress with NaCl could be interpreted as an indicator of resistance in teosinte to hot environments and certain types of soils with certain salt concentrations. Current and future climate and environmental changes force us to do research on the mechanisms of resistance of plants to adverse factors and, in this sense, the present revision aims to motivate fellow researchers to do work in that area.

INTRODUCTION

Their ability to respond to fluctuations in their environment is one of the crucial functions of plant cells. The understanding of the connections between the initial responses of a plant and subsequent events that constitute a successful adjustment to its altered environment is one of the great challenges of plant biology (Grene, 2002). Aerobic metabolism uses molecular oxygen as an electron acceptor in energy-producing oxidations that allow the impressive complexity of higher organisms, but the reduction of O_2 to H_2O implies several drawbacks (Barranco, 2006).

The process of transforming molecular oxygen into water is divided into four stages (Figure 1). Initially, an external energy input allows oxygen to destabilize to form superoxide anion (O_2^-), a highly reactive intermediate with a relatively short half-life (2-4 μs) (Smirnoff, 2001). This radical can spontaneously generate hydrogen peroxide (H_2O_2) and/or react with transition metals such as iron (Fe) or copper (Cu) present in certain molecules, through Haber-Weiss or Fenton reactions, to form hydroxyl radical (OH^-) (Halliwell, 2006). H_2O_2 is an intermediate activated state which, unlike the rest, has a longer half-life (1 ms) and is capable of diffusing from its place of production (Willekens *et al*., 1997), is also reduced to OH^- radical.

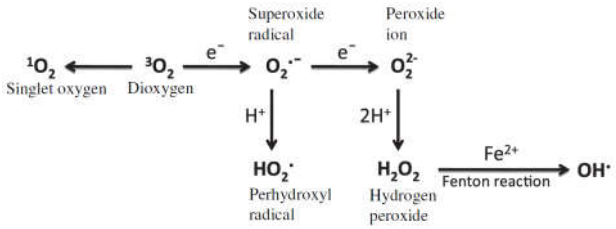

Figure 1 Generation of ROS by energy transfer (Gill and Tuteja, 2010).

This radical is considered one of the most powerful oxidants known, since the cell has no enzymatic mechanisms to eliminate this reactive species and its excess usually leads to cell death. However, when the reduction is incomplete, the inevitable consequence of aerobic metabolism is the formation of reactive oxygen species (ROS) as well as reactive nitrogen species (RNS) (Barranco, 2006). These intermediate products

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have a high and diverse reactivity and due to the presence of unpaired electrons in their valence layer are less stable than O_2 or water (Foyer and Noctor, 2013).

Finally, the OH^-radical is reduced spontaneously to form a stable molecule such as H_2O. Alternatively, O_2 can accept the excess energy of photooxidation to form singlet oxygen ($^1O_2$) (Gill and Tuteja, 2010), a very unstable intermediate state and whose production is restricted to the chloroplast. Many of these oxidized reactive forms are capable of inactivating enzymes by oxidizing their thiol groups or by producing redox changes in the metals of their active sites, they also cause DNA breaks and mutations by reducing the aromatic compounds of this molecule and altering the functionality of the lipid membranes upon reacting with lipids to form hydroperoxides (Dat *et al*., 2000).

Production of ROS in plants

ROS are generated in cell compartments as a byproduct of a variety of processes such as photosynthesis in chloroplast, photorespiration and beta oxidation of fatty acids (AG) in peroxisomes and glyoxysomes (Del Río *et al.*,2003 y De Pinto *et al.*,2006) mitochondrial respiration or the production of H_2O_2 and O_2^- by peroxidases (Pe) and nicotinamide adenine dinucleotide phosphate reduced (NADPH) oxidoreductases of the wall and cell membrane respectively (Mittler *et al*., 2004 and Del Río *et al*. 2009).

ROS levels in plants

Under normal growth conditions ROS cellular production is low (240 µM s^{-1} O_2- and a level of 0.5 µM H_2O_2 in chloroplasts) (Polle, 2001), which implies that in basal conditions the cell has, in general, a reducing environment that prevents the oxidation of proteins, lipids or DNA and guarantees vital functions. This homeostasis is a consequence of the presence of ROS elimination systems (antioxidant systems) capable of maintaining the production of reactive oxygen species under control (Noctor and Foyer, 1998).

However, different physiological phenomena or situations of stress such as drought and dehydration, salinity, cold, high temperatures, heavy metals, ultraviolet radiation, atmospheric pollutants such as ozone and SO_2, nutrient shortage, pathogen attack or excessive light radiation among others , cause changes in the levels of ROS that can generate disturbances in this equilibrium and the consequent extra increase in free radical levels, triggering a situation of oxidative stress (Dat *et al*., 2000, Rodríguez- Serrano *et al*., 2006, Romero-Puertas *et al*., 2007, Rasmussen *et al*., 2013 and Zhao and Yi, 2014). In this way, the production of ROS can be increased in the cellular environment up to three times in the form of an O_2^- radical and 10 to 30 times in the form of the H_2O_2 intermediate with respect to its basal conditions (Gill and Tuteja, 2010).

Resistance to ROS in plants

Different situations of stress and physiological phenomena causespace-time changes in the levels of ROS that behave as important signals that regulate growth, development, tolerance to abiotic stress factors, an adequate response to pathogens and programmed cell death (Vacca, 2004, Tyburski *et al.*,2009, Lariguet *et al.,* 2013 y Wu *et al.,* 2013). In this way, depending on the concentration of ROS in the cell, the oxidative effect can be dominated against the signifier or vice versa. High concentrations of ROS can damage macromolecules, saturate the cell's antioxidant capacity and promote mechanisms of programmed cell death (Vacca, 2004).

In addition, not only is cellular ROS concentration important. The different types of ROS produced and the balance between the levels of them can also be of special relevance in determining the response and are subject to the interaction between the different generating sources and the different elimination systems, which can change radically depending on the physiological conditions of the plant and of the integration of the different environmental, developmental and biochemical stimuli (Noctor *et al*., 2007 and Møller and Sweetlove, 2010).

Antioxidant systems in plants

The plants have developed an elaborate antioxidant system formed by enzymes and metabolites to remove reactive oxygen molecules or control their excess before causing damage to metabolism and cell structure (Thirupathi *et al*., 2011). Each cell compartment has more than one antioxidant system that eliminates a particular ROS, however, the apparent partial redundancy of these systems together with the ROS producing enzymes explains the complexity in the regulation of oxidative and redox homeostasis, which must be accurately adjusted according to the needs of the cell (Gadjev *et al*., 2006 and Gechev *et al*., 2006). The antioxidant systems are classified by their capacity of catalysis in enzymatic and non-enzymatic (Ortíz, 2015).

Enzymatic antioxidant systems

Enzymatic systems, made up of low molecular weight proteins such as catalases (CAT), peroxidases, superoxide dismutases (SOD) and ascorbate-glutathione cycle enzymes such as ascorbate peroxidase (APX) and glutathione reductase (GR) (Thirupathi *et al*., 2011) catalyze the ROS elimination process through the regeneration of reductors; in this way, the radicals O_2^- and H_2O_2 are essentially eliminated enzymatically.

Metabolic cycles within the aqueous phase of peroxisome, chloroplast, cytosol and mitochondria oxidize and successively reduce glutathione and ascorbate, using NADPH as the ultimate electron donor. Glutathione ascorbate, reduced (GSH), ascorbate peroxidase (APX), glutathione reductase (GR), superoxide dismutase (SOD) and monodehydroascorbate reductase (MDHAR) are involved in plant cell antioxidant regeneration through several routes. The enzymes involved are of a hydrophilic nature, although in some cases they are slightly associated with the membranes where the ROS are generated. Different isoforms of antioxidant enzymes are found in different subcellular compartments. Evidence to date suggests a coordinated response to ROS among different members of the different SOD gene families (Grene, 2002).

Non-enzymatic antioxidant systems

Non-enzymatic systems are able to cushion the ROS by reducing them directly. Thus, free radicals $O_2^-$and OH are mainly controlled by non-enzymatic systems (Ortíz, 2015) such as biochemical and molecular mechanisms activated or deactivated by the action of metals; however, such systems have only been partially studied (Thirupathi *et al*., 2011).

Ascorbic acid, glutathione and α-tocopherol act as antioxidants in the detoxification of ROS. These compounds have central and interrelated roles, which act both in non-enzymatic form and substrates in enzyme-catalyzed detoxification reactions (Foyer, 1993, Hausladen and Alscher, 1994, Winkler *et al*., 1994, Chaudiere and Ferrari, 1999). An anti-ROS response includes the induction of genes belonging to ROS elimination mechanisms (Grene, 2002).

Peroxidases

Peroxidases are enzymes that catalyze the reduction oxide between H_2O_2 and a large variety of hydrogen donors such as phenols, aromatic amines and others by the reaction $H_2O_2 + AH_2 \rightarrow 2H_2O + A^-$. These enzymes utilize various peroxides (ROOH) as electron acceptors to catalyze said oxidation reaction. There are 15 classes in the enzymatic code cataloged by the International Union of Biochemistry and Molecular Biology that have been incorporated into reactions catalyzed by peroxidases (Passardi *et al*., 2007). They are classified into two large superfamilies, one including plant, fungal and bacterial peroxidases, and another superfamily structurally unrelated to the former constituted by animal peroxidases (Hiraga *et al*., 2001). In turn, within the superfamily of plant, fungal and bacterial peroxidases three classes have been defined based on their differences in amino acid sequence (Table 1) (Welinder, 1992).

Table 1 Classification of the vegetable peroxidase superfamily. Modified from Hiraga *et al*., (2001).

Superfamilia	Clase	Miembro (número EC)	Origen	Peso molecular (kDa)
Peroxidasas de plantas	I	Citocromo c peroxidasa (EC 1.11.1.5)	Levaduras y bacterias	32-63
		Catalasa-peroxidasa (EC 1.11.1.6)	Bacterias y hongos	150-240
		Ascorbato peroxidasa (EC 1.11.1.11)	Plantas	30-58
	II	Manganeso peroxidasa (EC 1.11.1.13)	Hongos	43-49
		Ligninasa (EC 1.11.1.14)	Hongos	40-43
	III	Peroxidasa (EC 1.11.17, POX)	Plantas	28-60

Teosinte, direct wild ancestor of maize

As a result of extensive studies of its taxonomic and morphological characteristics, teosinte is currently considered the wild and direct predecessor of maize (*Zea mays* spp. *mays*). Archaeological evidence of microfossils indicates that the first maize that were used as food were very similar to the current hybrids, but their ancestry was not clarified except when the teosinte was analyzed evolutionarily (Piperno *et al*., 2009).

Six species of teosintes are known, which from the taxonomic point of view are grouped into two sections based on morphological characters of the male inflorescence, under the assumption that this structure has not been subject to the selective pressure of man as it has been the female inflorescence: Luxuriantes Section (Doebley and Iltis, 1980) and Section *Zea* (*Zea mays* L, *Zea mays* ssp. *mexicana*, *Zea mays* ssp. *parviglumis*, *Zea mays* ssp. *mays*). Of the latter, Zea parviglumis is the closest to maize (Espíndola, 2010).

Although *Zea diploperennis* is the teosinte most genetically remote to maize, its direct defenses are more conserved due to its lesser exposure to selective breeding involving the domestication process (Rosenthal and Dirzo, 1997). And although the current use of *Zea diploperennis* falls into two basic categories: cattle stubble and maize breeding (Benz *et al*., 1990), its kinship with maize has allowed to study some limiting aspects that modify its development, such as the attack of certain pathogens and the mechanisms of defense before them, dwarfism, adaptation to drought and oxidative stress (Matías, 2016).

Peroxidases in teosinte

The high reduction of hydrogen peroxide in healthy *Zea diploperennis* teosinte seedlings and the null reduction in healthy seeds indicate that the expression of peroxidases is more related to germination processes (as established by Haslekas *et al*., 2015) than to latency in seeds. In thermal stress, the activity of peroxidase in healthy teosinte at 4 °C is lower than in non-stressed teosinte and, in turn, lower than in stressed plants at 37 °C; this higher concentration of peroxidases is interpreted as a greater resistance of seedlings treated at 37 °C, an aspect that is related to climates exclusively dry or very little wet, in which *Zea diploperennis* grows wild. In saline stress with Nacl and $CdCl_2$, the synthesis of peroxidases is elevated compared to healthy coleoptilo, where it is lower, which indicates that, to these conditions this species responds by producing antioxidant enzymes that would form part of its mechanism of response to those characteristics of certain types of soils. Similarly, seedlings infected with *Ustilago maydis* (the fungus to which it is most susceptible and causing common carbon) present a slightly higher enzymatic activity than healthy coleoptile, which can be translated as an activation of its mechanism of resistance to oxidative stress by means of peroxidase enzymes (Matías and Pérez, 2017).

Oxidative stress by low temperatures in maize

Maize plants subject to temperatures below 20 °C are prone to physiological and biochemical changes. The damage is increased according to the duration and severity of the cooling conditions. For example, in plants growing steadily in the range of 15 to 17 °C (day/night), the growth is severely retarded and its vegetative period elongated and the activities of metabolic enzymes are reduced (Hirt and Shinozaki, 2004).

Photoxidative stress is considered the main cause of freezing damage in species susceptible to stress due to low temperatures. Inhibition of photosynthesis is the first event observed in these conditions. Under optimal growth conditions, the energy absorbed by the leaves is used primarily for the assimilation of carbon in the photosynthesis process (Burdon, 1999). When plants undergo suboptimal growing temperatures in the field, the light absorbed by the leaves cannot be efficiently used by photosynthesis and becomes potentially harmful by the excess of electrons that react with the abundant presence of oxygen (Taiz and Zeiger, 2006). Photoinhibition increases H_20_2 levels and produces damage to the cell membrane. It also increases the range of electron transporters of O_2 (Smirnoff, 2005). Several studies confirm the change in antioxidant enzymes present in plants exposed at low temperatures (Inzé and Van Montagu, 2002).

The process for tolerating low temperatures is complex. Cellular and metabolic changes that occur during cold acclimatization also include increased levels of sugars, soluble proteins (some with cryoprotective activity), as well as the appearance of protein isoforms and the alteration of the lipid composition of the membrane (Burdon, 1999). Many of these events are regulated by changes in the expression of the response genes at low temperatures (LTR). The ability to acclimatise to tolerate cold is under genotypic control (Kang and Gauch, 1996).

Membrane-bound peroxidases in maize roots

The work of Mika *et al*. (2009) demonstrates the involvement of class III peroxidases bound to the membrane of maize seedlings (*Zea mays* L.) of 5 days of growth in the responses to stress for the first time. The applied treatments consisted of puncture stress and stress with different signal compounds to investigate different forms of oxidative stress; the effects of a wide range of compounds (H_2O_2, methyl jasmonate, salicylic acid, maize pathogen extracts, chitosan and cantharidine) that participate in multiple signaling cascades in plants were investigated. The total peroxidase activity of corn root and the concentration of proteins in four peroxidase evaluated (pmPOX1, pmPOX2a, pmPOX2b and pmPOX3) were modified after five or more types of treatments applied (indicating strict control and adjustment of the enzymes to multiple stress functions).As a first hypothesis, the large amount of peroxidase isoenzymes and their narrow, differential and superimposed regulation seem to have evolved to cope with all possible stress situations (Passardi *et al*., 2005). Applying the strongest stressors on pmPOX as guidelines, the results of the study indicate a regulation of all four pmPOX by methyl jasmonate and salicylic acid signaling. Available data showed that the four membrane-bound peroxidases are involved in the defense of pathogens with different responses to each of the inducers and, probably, different roles. For example, pmPOX2b showed the broader response of all four enzymes, reacted to each stressor and effector used, and revealed the highest uptake by H_2O_2 treatment. Therefore, the study suggests a broad function of peroxidases in oxidative stress. In the future, more detailed analysis approaches could shed light on the complex functional network of plasma membrane, apoplastic and cell wall peroxidases (Mika *et al*., 2009).

Peroxidases linked to axial roots of maize

The work of Li *et al*. (2014) on axial roots of maize plants subjected to phosphate-free treatment (main source of fertilizer), in which the protein profiles obtained from four stages of response to the deficiency of phosphate (Pi)were compared, localizes 4 spots that relate to different peroxidases: a glutathione peroxidase of 18.7 kDa, an anion peroxidase of 37.8-38.3 kDa, a peroxidase type 2 of 35.5-42.6 kDa and a peroxidase type 1 of 38.5-44.5 kDa with 348 aa, and from which their expression increases, or they appear, when the seedlings were subjected to stress due to absence of phosphate.

CONCLUSIONS

The detection of peroxidase in teosinte (*Zea diploperennis*), as well as the identification of peroxidases in maize (*Zea mays* L.) suggests the active participation of this wide range of enzymes in the antioxidant response that activates the plant cell to several types of stress; be biotic like infection with pathogens such as *Ustilago maydis*; or abiotic, such as salt stress, by temperature, acid-base type, by H_2O_2, methyl jasmonate, chitosan, cantharidine or by the absence of any nutrient, such as phosphate.

In maize, it is hypothesized that membrane-bound peroxidases are involved in the defense of pathogens and in the regulation of H_2O_2 levels. In teosinte, the peroxidases participate in the defense against infection by *Ustilago maydis* (common charcoal fungus or huitlacoche in maize and teosinte), in the germination process during the first 6 days of in vitro growth and in the regulation of the levels of H_2O_2 during saline stress with NaCl and $CdCl_2$ as well as during heat stress.

The specific involvement of peroxidases in grasses has not yet been studied in detail, however, recent work suggests an extensive role of peroxidases in oxidative stress.

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