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Review

Mechanisms of oxidative stress in plants: From classical chemistry to cell biology

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ABSTRACT

Oxidative stress is a complex chemical and physiological phenomenon that accompanies virtually all biotic and abiotic stresses in higher plants and develops as a result of overproduction and accumulation of reactive oxygen species (ROS). This review revises primary mechanisms underlying plant oxidative stress at the cellular level. Recent data have clarified the 'origins' of oxidative stress in plants, and show that apart from classical chloroplast, mitochondrial and peroxisome sources, ROS are synthesized by NADPH oxidases and peroxidases. ROS damage all major plant cell bio-polymers, resulting in their dysfunction. They activate plasma membrane Ca^{2+}-permeable and K^+-permeable cation channels as well as annexins, catalyzing Ca^{2+} signaling events, K^+ leakage and triggering programed cell death. Downstream ROS-Ca^{2+}-regulated signaling cascades probably include regulatory systems with one (ion channels and transcription factors), two (Ca^{2+}-activated NADPH oxidases and calmodulin) or multiple components (Ca^{2+}-dependent protein kinases and mitogen-activated protein kinases). Intracellular and extracellular antioxidants form sophisticated networks, protecting against oxidation and 'shaping' stress signaling. Research into plant oxidative stress has shown great potential for developing stress-tolerant crops. This can be achieved through the use of directed evolution techniques to prevent protein oxidation, bioengineering of antioxidant activities as well as modification of ROS sensing mechanisms.

Contents

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1. Introduction

Virtually all environmental and biotic stresses trigger a generalised stress response called an oxidative stress which can damage cell components and cause their dysfunction. This is induced by over-production and accumulation of molecules containing activated oxygen and called 'reactive oxygen species' (ROS). The reasons causing an oxidative stress mainly include: (i) an imbalance between ROS generation and detoxification due to disturbance of 'normal' cell physiology; (ii) ROS biosynthesis *de novo* as a constituent part of stress signaling and immunity response needed for defence and adaptation. These mechanisms co-exist, because stress factors directly producing ROS (transition metals, ultraviolet or ozone) additionally stimulate ROS generation by NADPH oxidases and peroxidases (Rao et al., 1996; Ranieri et al., 2003; Apel and Hirt, 2004; Zhang et al., 2010; Nawkar et al., 2013).

It is believed that the effect of O_2 derivatives is one of the oldest stresses on the planet (Dowling and Simmons, 2009). Plants have dealt with this for at least 2.7 billion years, i.e. since they started producing O_2 from CO_2 and H_2O. The constantly increasing level of O_2 has both directed species evolution and determined the biochemistry of modern plants and animals (Dowling and Simmons, 2009). Intriguingly, plants evolved the ability to employ an oxidative stress (or at least ROS biosynthesis) for signaling needs and sensing other stresses, regulation of growth, polarity and death (Demidchik et al., 2003, 2010; Foreman et al., 2003), sensing hormones and regulatory agents such as amino acids and purines (Murata et al., 2001; Demidchik et al., 2004, 2009; Krishnamurthy and Rathinasabapathi, 2013), generating gravitropic response (Joo et al., 2001) and a number of other processes that are not primarily related to stress or oxidation.

This review summarises and evaluates classical and some new concepts in the field of plant oxidative stress and ROS metabolism. A particular emphasis of this review is on the chemistry of individual ROS, cell and membrane mechanisms leading to ROS generation, amplification and regulation of ROS-mediated signals and programed cell death.

2. Definitions

The term ROS embraces substances containing one or more activated atoms of oxygen but are not necessarily radicals (for example H_2O_2 is not a radical). Free radicals are any chemical species that exist independently and contain unpaired electron(s). Some free radicals do not have oxygen atoms (for example, transition metals or carbon-centered radicals). Both ROS and free radicals promote oxidative stress through oxidation of cell compounds. The term 'oxidative stress' has several meanings. Firstly, it is the 'physiological state' (or conditions) when loss of electrons (oxidation) exceeds gain of electrons (reduction) leading to chemical (oxidative) damage of cell compounds. Oxidative stress is therefore associated with severe and long-term redox (reduction/oxidation) imbalance due to the lack of electrons. Secondly, it is one of 'stress factors' (similar to salinity, drought and others) damaging cells and triggering signaling and defence reactions. These definitions are related and can be combined.

In most cases oxidative stress starts from the activation of triplet oxygen (O_2). This makes O_2 more active or 'reactive'; therefore it is also often defined as the stress caused by 'reactive oxygen species', 'reactive oxygen intermediates', 'oxygen-derived species', 'free oxygen radicals' etc. Reactive nitrogen species (RNS) are another important class of substances potentially involved in oxidative stress (in this case, sometimes called 'nitrosative stress'). However experimental data are insufficient yet to understand the mechanisms of plant nitrosative stress; therefore this will not be discussed here in greater detail.

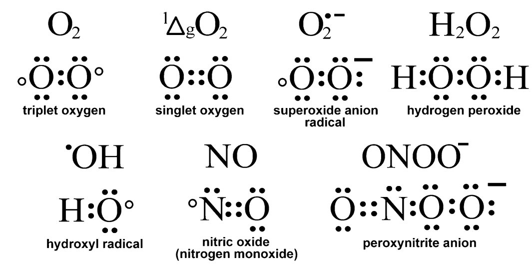

Fig. 1. Lewis dot structures of molecular oxygen (triplet oxygen) and key reactive oxygen/nitrogen species.

3. Chemistry of oxidising species

Oxygen is the most abundant element in the Earth's crust (Guido, 2001). Comprising about 89% of the mass in H_2O, oxygen is also the most abundant (by mass) element in living organisms. It is the second most powerful oxidiser known in chemistry after fluorine, which is far rarer than oxygen (Renda et al., 2004; Dowling and Simmons, 2009). Major atmospheric form of oxygen is O_2. This molecule has two unpaired electrons ($O_2^{2\bullet}$) and can exist as a free molecule; therefore it is a free radical. Both electrons in O_2 have the same spin numbers or 'parallel spins' which limit (restrict) the number of O_2 targets to those that have two similar electrons with antiparallel spins. This phenomenon is called a 'spin restriction' and decreases the reactivity of O_2. O_2 is not very chemically active and not toxic to aerobic organisms. To 'acquire' higher reactivity, O_2 requires an input of energy to remove the spin restriction. This energy comes from a number of chemical and biochemical reactions, highly energised electrons in electron transport chains (ETC), ultraviolet, ionising irradiation etc. Among many ROS found in biological systems, singlet O_2 ($^1\Delta_gO_2$), hydroxyl radical ($^\bullet OH$), hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet -}$) and nitric oxide ($NO^\bullet$) (Fig. 1) are crucially important for induction of oxidative stress (Apel and Hirt, 2004). A number of other ROS could also be involved, such as peroxyl, alkoxyl and hydroperoxyl radicals, peroxinitrite, ozone and hypochlorous acid.

3.1. Superoxide radical

3.1.1. Chemistry of superoxide and measurements of superoxide production in plants

Triplet oxygen (O_2) can lose its 'spin restriction' by accepting a single electron, for example, due to the 'leak' of electrons in plant ETC or functioning of NADPH oxidase. This leads to formation of $O_2^{\bullet -}$ which is more reactive than O_2. It is called 'superoxide anion radical', 'superoxide radical anion', 'superoxide radical' or just 'superoxide'. The half-life of superoxide is typically from 1 to 1000 μs which only allows it to diffuse for few micrometers from site of the generation (Kavdia, 2006). $O_2^{\bullet -}$ participates in a