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Review article

The impact of environmental contamination on the generation of reactive oxygen and nitrogen species – Consequences for plants and humans

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ABSTRACT

Environmental contaminants, such as heavy metals, nanomaterials, and pesticides, induce the formation of reactive oxygen and nitrogen species (RONS). Plants interact closely with the atmosphere, water, and soil, and consequently RONS intensely affect their biochemistry. For the past 30 years researchers have thoroughly examined the role of RONS in plant organisms and oxidative modifications to cellular components. Hydrogen peroxide, superoxide anion, nitrogen(II) oxide, and hydroxyl radicals have been found to take part in many metabolic pathways. In this review the various aspects of the oxidative stress induced by environmental contamination are described based on an analysis of literature. The review reinforces the contention that RONS play a dual role, that is, both a deleterious and a beneficial one, in plants. Environmental contamination affects human health, also, and so we have additionally described the impact of RONS on the coupled human – environment system.

1. Introduction

Environmental pollutants such as heavy metals, nanomaterials, and toxic metal oxides affect plants, among others by inducing the formation of reactive oxygen and nitrogen species (RONS) within them. Over the last 30 years, metal toxicity and the tolerance of plants against that toxicity have been studied intensely (Prasad, 1995; Hall, 2002; Shah et al., 2010; Møller et al., 2007). Moreover, soil contaminants induce the oxidative stress in organisms. In soil, pesticides generate RONS intensively (Gülçin et al., 2007). In addition to pesticides, cadmium and lead are soil contaminants, also. The main sources of cadmium in soil contamination are industry (by atmospheric pollution, waste disposal) as well as phosphorus and waste fertilizers used in agriculture (Salmanzadeh et al., 2016; Gallego et al., 2012; Besson-Bard et al., 2009). The oxidative stress is the specific plant response to different environmental factors, including a deficit of some mineral salts, for example phosphate (Gill and Tuteja, 2010). Lead, released into the environment as a result of smelting activities and mining, is one of the most potent environmental pollutants (Shah et al., 2010). Plants take up lead, mainly through their root systems (Kaur, 2014). Lead causes the heavy-metal-induced oxidative stress in plant cells (Kaur, 2014).

In the 18th century, studies by Antoine Laurent Lavoisier revealed the toxicity of oxygen. The control of ROS levels in organisms is very important (Mittler, 2017), because these species are crucial for life of all living organisms. On the other hand, ROS are toxic compounds. Exemplary, ROS affect the cellular oxy-reduction processes (Pranczk et al., 2014).

The endogenous sources of RONS include auto-oxidant reactions, xanthine oxidase, redox cycles, inflammations, oxidative reactions in phagocytic cells and cytochrome P450 reactions. However, RONS may be also delivered to plants by exogenous sources such as environmental toxins, chemicals and smog (Wang et al., 2015). Another very important source of ROS is biochar. It is produced from municipal waste or sewage sludge. The photogeneration of ROS induced in the biochar suspension was already confirmed (Fang et al., 2017).

It is important to recognize the consequences of recent environmental and climatological changes on plants and humans. In this review, the impact of the environment on the generation of RONS in plant and human organisms is studied. Moreover, environmental factors that induce RONS production in plants are analyzed taking account their impact on the metabolism of RONS in the development stages of plants. The functions of RONS in plant and human biochemistry, considering their roles in cells, are evaluated. Knowledge on the importance of RONS for the proper functioning of plant and human organisms as well as a recognition of the mechanisms associated with the oxidative stress allow a better understanding of the pathophysiology of many diseases in which an increased activity of RONS plays a key role. The subjects discussed in the review confer knowledge on the mechanisms through which RONS are generated, for example as a result of agricultural development, and on the mechanisms that underpin their destructive

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impact on the oxidative stress in cells. The oxidative stress has been proven to promote the development of diseases of various etiologies and to complicate treatments (Mittler, 2002; Apel and Hirt, 2004; Torres, 2010). For this reason, understanding of generation processes and the activity of RONS in plant and human environments is very important.

2. The plant - environmental system

2.1. The physiological production of RONS in plants

Some plant organelles, such as chloroplasts or mitochondria, can produce RONS (Minibayeva et al., 2012). About 2% of the oxygen in mitochondria takes part in the formation of hydrogen peroxide (Becana et al., 2000). The apoplast is one of the main sites of the RONS formation, which is induced by NADPH oxidase (Potocký et al., 2012). Abiotic and biotic stresses in plants lead to the formation of RONS. Environmental factors such as salinity, temperature, nutrient levels, and chemicals cause abiotic stress, while pathogens, allelopathy, and wounding are factors that cause biotic stress. The superoxide anion radical is formed by the release of electrons during the respiratory chain, and it is produced by neutrophils and macrophages during the killing of bacteria with oxygen (Minibayeva et al., 2012). The superoxide anion radical can also be formed as a product of photo-oxidation reactions, photorespiration in glyoxysomes and peroxisomes, and in the Mechler reaction (Karuppanapandian et al., 2011). Among RONS species, hydroxyl radical has the highest reactivity and is the most toxic form (Pranczk et al., 2014). Hydrogen peroxide participates in the oxidation of thiol groups (Kemp et al., 2008; Davies, 2016). ·NO reacts with proteins that contain iron-sulphide centers (Lindermayr et al., 2005). ·NO induces multiple metabolic pathways with the participation of guanylate cyclase, aconitase, second messengers, Ca^{2+} cations, cyclic guanosine monophosphate, and cyclic adenosine diphosphate-ribose (Beligni and Lamattina, 2000; Neill et al., 2003; Lamattina et al., 2003). Recent studies have focused on the role of ·NO in programmed cell death. The effects of ·NO on plant cells, which depend on its concentration, are described in Table 1. Plants adapt to environmental changes (Franks et al., 2014; Osakabe et al., 2013), and the result of such adaptations are changes in the ·NO concentrations of plant cells. ·NO regulates the process of receiving and responding to environmental stimuli and stimulates the closing of stomata. The latter function is especially vital during droughts, when water management is most important: closed stomata reduce transpiration. Furthermore, ·NO modulates light-induced processes. This function enables stimulation of germination, inhibition of the hypocotyl, as well as elongation of internodes. The mechanism of endogenous ·NO production has not yet been fully elucidated. Studies on wheat seedlings treated with ·NO have shown that these seedlings exhibit a partial etiolation. ·NO takes part in the developmental processes of plants (Sanz et al., 2015). Small amounts of ·NO are present in the flesh of ripe fruits. The concentration of ·NO decreases during maturation processes. Delayed wilting of carnations has been observed following treatment with high levels of ·NO. A reduced loss of water and chlorophyll has been observed in the case of broccoli exposed to ·NO (Leitner et al., 2009; Wendehenne et al., 2004).

Table 1
The role of ·NO in plant cells.

Positive effects	Negative effects
Regulation of lignification of cell wall	Cell membrane damage
Stimulating of closing of stomata	Reaction with redox center in proteins
Modulation of proper functioning of aconitase	Formation of toxic peroxynitrite by reaction with superoxide anion radical
chlorophyll biosynthesis	
Cell signaling	
Participation in defense mechanisms	

NO participates in programmed cell death. Increase of the ·NO concentration in plant cells contributes to the activation of programmed cell death. ·NO is indispensable to a systemic resistance upon infections. Moreover, ·NO takes part in processes that limit the invasiveness of pathogens. During droughts, aqueous stress induces an increased production of intrinsic proteins that are generated only in the presence of ·NO. Interestingly, ·NO may react antagonistically against RONS (Tanou et al., 2009; Lounifi et al., 2013). ·NO occurs as an antioxidant in cytotoxic conditions in plant cells.

Plants reduce RONS levels by using special enzymes, such as ascorbate in the chloroplast stroma (enzyme concentration 2–3 mM), or secondary metabolites, such as the hypecins in *Hypericum hirsutum* (Mazimba et al., 2013; Ashraf, 2009; Foyer et al., 1994; Noctor and Foyer, 1998). The physiological concentration of the superoxide anion radical is considered to be ca. 10^{-11} M (D'Autréaux and Toledano, 2007), while the value for hydrogen peroxide is ca. 10^{-7} M (Karuppanapandian et al., 2011), for hydroxyl radical ca. 10^{-10} M (D'Autréaux and Toledano, 2007), and for singlet oxygen ca. 10^{-9} M (Krieger-Liszkay, 2005).

In our opinion, although the role of enzymes involved in the scavenging of RONS is well defined, many threads related to RONS detection mechanisms and methods of controlling the balance between production and scavenging of RONS are still to be examined. Researchers have to do more to investigate these issues.

2.2. The role of RONS in plant metabolism

RONS play essential roles in the metabolism of plants. For example, they contribute to disease resistance (Kranner et al., 2010), control cell death processes (Blokhina and Fagerstedt, 2010), regulate plant growth (Arasimowicz-Jelonek et al., 2011), initiate mitogen-activated protein kinase cascades (Jaspers and Kangasjärvi, 2010), and moreover alleviate seed dormancy (Oracz et al., 2009; Oracz et al., 2007; Tanou et al., 2009, 2012; Lounifi et al., 2013). However, many reports describe ROS as toxic for plants because they disturb the natural metabolism processes of their cells (Mittler et al., 2004; Garg and Manchanda, 2009).

(a) The role of RONS in cell signaling in plants

In recent years the biochemistry of plants has been further elucidated, and a major achievement was the identification of the respiratory burst oxidase homologues (Rbohs) (Cheng et al., 2001). The *Arabidopsis* genome has been examined and ten of the NAPDH oxidase genes were shown to occur there, however, only three NADPH oxidase homologues have been identified in the leaf and root plant tissues (Mittler et al., 2004). Moreover, the studies of the *Arabidopsis* rbohD and rbohF mutants confirmed the role of some types of proteins as the sources of the ROS oxidative burst (Kobayashi et al., 2007). Furthermore, hormonal interactions were investigated and the regulation of progress of the ROS-dependent cell death was examined (Fig. 1) (Van Breusegem and Dat, 2006).

Many enzymes, such as Rbohs, may produce ROS (Mittler et al., 2004) (1).

$$2\,O_2 + NADPH \rightarrow 2\,O_2^{-\cdot} + NADP^+ + H^+ \quad (1)$$

In the next step the superoxide anion radical is reduced to hydrogen peroxide and oxygen (2). This process is catalyzed by superoxide dismutase (Garg and Manchanda, 2009).

$$2\,O_2^{-\cdot} + 2H^+ \rightarrow H_2O_2 + O_2 \quad (2)$$

Subsequently, hydrogen peroxide undergoes the Fenton reaction (3) (Garg and Manchanda, 2009). During this reaction hydroxyl radical is produced. Hydroxyl radicals are highly reactive and take part in many