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REVIEW ARTICLE

GROWTH RESPONSES OF PLANTS UNDER WATER STRESS: INVOLVEMENT OF REACTIVE OXYGEN SPECIES (ROS)

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Abstract

Plant growth is a vulnerable process being affected by several factors under natural conditions. All types of stresses encountered in natural environment affect plant growth and ultimately reduce productivity of crop plants. Recent global climatic changes made the situation more serious by causing problems like water deficit, high salinity, heat stress and different diseases caused by fungi, pest or bacteria as fallout. Water stress is considered as one of the major abiotic stress factors that limit plant growth and ultimately reduces the productivity of crop plants up to 80% of total production. A huge amount of land of our country is suffering from poor irrigation or irregular rainfall. Such problem calls for a demand for water use efficient or water resistant varieties of crop plants. To develop water resistant varieties, it is important to understand the growth mechanism of crop plants under water limited condition. Keeping in view of these problems this review work is focused light to the understanding of the role of Reactive Oxygen Species (ROS) in growth responses of plant under normal as well as water stress condition.

Plant responses to water stress and Reactive Oxygen Species (ROS)

Under water stress condition plants can only survive if they reduce the water loss and/or increase water uptake. Plants are adapted to reduce water loss by inhibiting shoot growth and closing their stomata while, on the other hand, increase water uptake by promoting root growth under water stress condition. Water stress generally inhibits both root and shoot growth of plants, root growth being less inhibited compared to shoot growth (Spollen et al., 1993; Sharp, 2002). However, low level of water stress (mild stress) promoted root growth even over control (Sharp and Davies, 1989; Das and Kar, 2013). Mild water stress induced root growth promotion and shoot growth inhibition, which is being considered as one of the adaptive mechanisms of plants to survive under water limited condition. There are different factors associated with water stress induced plant growth responses; Reactive Oxygen Species (ROS) are one of them.

During last two decades the role of reactive oxygen species (ROS) has been extensively studied on plant growth and development. ROS is a collective term for free oxygen radicals and some non-radical derivatives of oxygen that are capable of independent existence and contain unpaired electrons. They are highly reactive and their overproduction may cause cellular death (Apel and Hirt, 2004; Foyer and Noctor, 2005). Under normal physiological condition ROS are being generated at basal level and this basal level of ROS is scavenged by plants using antioxidant system.

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Under drought condition plants accelerate generation of ROS and this excess ROS may be harmful and even causes cellular death of plants; however, generation of a minimal level of ROS is indispensible for growth and development of plants under water stress condition (Foyer and Noctor 2005; Gill and Tuteja 2010; Singh et al., 2014; Dey et al., 2021). Production of ROS, including hydroxyl radical ($^{\cdot}OH$) and superoxide ($O_2^{\cdot -}$), has been reported during the development of seeds and seedlings (Bailly, 2004; Oracz et al., 2009) and the alleviation of dormancy (Oracz et al., 2007). The mode of action of ROS could be either indirect (cellular signaling; Oracz et al., 2009) or direct (e.g. scission of polymers), but the latter was often regarded as a "negative role," causing toxicity and deterioration (Bailly, 2004; Winterbourn, 2008). Among ROS H_2O_2 can travel across the membrane through aquaporins (Bienert et al., 2007) underlining its role as a suitable molecule for cell-to-cell signalling (Schmidt et al., 2014). It was revealed that all the biologically active ROS i.e. superoxide ($O_2^{\cdot -}$), hydroxyl radical ($OH^{\cdot}$), hydrogen peroxide (H_2O_2) have significant role during root and shoot growth under normal as well as water stress condition (Das and Kar, 2016).

ROS involvement in different physiological and growth processes of plants

Involvement of ROS during plant growth responses has been observed by different workers. ROS including hydroxyl radical ($OH^{\cdot}$), superoxide ($O_2^{\cdot -}$) and hydrogen peroxide (H_2O_2) are also being implicated recently for having a vital role in plant growth and development as well as plant adaptation to biotic and abiotic stress (Sagi and Fluhr 2001; Oracz et al., 2009; Singh et al. 2014). Superoxide ($O_2^{\bullet -}$) formation is also an unavoidable event of certain metabolic steps requiring oxygen reduction. $O_2^{\bullet -}$ can be converted into the less reactive H_2O_2 spontaneously or via the action of superoxide dismutases (SOD) (Kar, 2011; O'Brien et al., 2012). Hydrogen peroxide (H_2O_2) has a half-life of 1 millisecond and the diffusible property of H_2O_2 across membranes (Bienert and Chaumont, 2014) makes them a perfect molecule for signalling both intracellular as well as intercellular. Another important feature of H_2O_2 and $O_2^{\bullet -}$ is the production of $OH^{\bullet}$ which is considered to be the most destructive ROS. Hydroxyl radical ($OH^{\bullet}$) has a half life of only 1 ns and can react with anything that come across (Halliwell and Gutteridge, 2007). Recent findings have proposed a significant role of $OH^{\cdot}$ in regulating growth mechanism when it was produced in the apoplast and participate in the scission of cell wall polysaccharides effecting wall loosening and extension growth of plants. The roles of different ROS on the growth responses of plant under normal as well as water stress conditions are discussed as below.

Role of superoxide ($O_2^{\cdot -}$):

Among ROS, superoxide ($O_2 \bullet^-$) is reported to participate in many physiological processes of plants. Thus $O_2 \bullet^-$ production is essential for the growth of etiolated wheat seedlings (Shorning et al., 2000) and leaf elongation of maize (Rodríguez et al., 2002). Metabolism of apoplastic $O_2 \bullet^-$ is also indispensible for axis growth of *Vigna radiata* (Singh et al., 2014). It was proposed that in plants a plasma membrane oxidase, catalysing the reduction of molecular oxygen to $O_2 \bullet^-$ at the expense of NAD(P)H, similar to the inducible NADPH oxidase in the plasma membrane of mammalian phagocytes (Segal and Abo, 1993), appeared as an early response to pathogen attack (Wojtaszek, 1997). The second mechanism for apoplastic $O_2^{\cdot -}$ production in plants, which can be different from the phagocyte-type oxidase, is possibly by the NAD(P)H oxidizing activity of peroxidase localized in the cell wall (or at the plasma membrane) (Askerlund et al., 1987). Root growth during early seedling stage of *Vigna radiata* and mild water stress induced promotion of root growth also depends on $O_2 \bullet^-$ production (Das and Kar, 2016).

Role of Hydrogen peroxide (H_2O_2):

Besides $O_2 \bullet^-$, H_2O_2, which is also a product of $O_2 \bullet^-$ metabolism either spontaneously or through activity of superoxide dismutase (SOD), has been reported to play role in growth and development (Foreman et al., 2003). Hydrogen peroxide (H_2O_2), one of the important ROS, may act as a signalling molecule and it has important roles in series of processes including plant development, stress responses, and programmed cell death (Pei et al., 2000; Apel and Hirt, 2004; Foyer and Noctor, 2005). Root growth of early grown seedlings was also found to be dependent on H_2O_2 generated due to SOD activity (Das and kar, 2016).

Role of hydroxyl radical ($OH^{\cdot}$):

It is well established that cell wall loosening is one key factor for extension growth of plant cells. Hydroxyl radicals ($^{\cdot}OH$), a highly reactive ROS, have been proposed as plant cell wall-loosening agent (Schopfer, 2001). Investigation carried out in vivo condition demonstrated $^{\cdot}OH$ production and oxidation of cell wall polysaccharides in tissues of germinating cress (*Lepidium sativum*) seeds and maize (*Zea mays*) seedlings. Both germination and seedling elongation are two distinct developmental processes that require wall loosening for elongation growth or tissue weakening. Hydroxyl radical ($OH^{\cdot}$) produced by the reduction of H_2O_2 with Fe^{2+} ions (Fenton's reagent) has been shown to decompose cell-wall materials such as straw and sawdust (Halliwell, 1965). Indeed, cell-wall polysaccharides such as pectin and xyloglucan can be broken down in vitro by $OH^{\cdot}$ generated in a Fenton-type reaction, e.g. by the reduction of O_2 with ascorbate in the presence of Cu^{+2} ions (Miller, 1986; Fry, 1998). Depending on the above findings Fry (1998) suggested that $OH^{\cdot}$, produced in the apoplastic space of plant tissues, could act as a site-specific oxidant targeted to play a useful physiological role in cell-wall loosening processes underlying cell expansion, fruit ripening and organ abscission. Reports are there demonstrating the cleavage of cell wall polysaccharides by $OH^{\cdot}$ that may be produced in the apoplastic space in growing tissues, non-enzymatically or enzymatically, i.e. the activity of peroxidase from $O_2 \bullet^{-}$ and H_2O_2 (Fry, 1998; Schopfer, 2001; Liszkay et al., 2004). Water stress-induced root growth of *Vigna radiata* seedling also seems to be driven by $OH^{\cdot}$, which was produced by cell wall peroxidase (Das and Kar, 2016).

Water stress induced ROS production

ROS production under stress is mainly occurring due to increased photorespiration, oxidation of fatty acids and activity of the mitochondrial electron transport chain (mETC). Excess amount of ROS has potentially damaging effects on cellular components, but in very low amount ROS can also play vital roles in cellular signalling and in mediating plant responses to environmental stresses (Torres et al. 2005; Miller et al. 2009). On the other hand, apoplastic $O_2 \bullet^{-}$ production and its metabolism was found necessary during axis growth of germinating *V. radiata* seeds (Singh et al., 2014). Therefore, it is quite likely that similar ROS metabolism is instrumental in causing root growth induced by water stress. Indeed, extracellular production of $O_2 \bullet^{-}$ in intact roots of *Vigna radiata* was higher under water stress condition compared to control (Das and Kar, 2016).

Water stress induced NADPH oxidase (NOX) activity

NADPH oxidase (NOX) is an enzyme that catalyzes the production of superoxide ($O_2^{\bullet -}$) by transferring electrons from NADPH to molecular oxygen, with secondary generation of H_2O_2 in the apoplastic region of plant cells. NADPH-oxidase generated ROS have been shown to play crucial roles in biotic interactions, abiotic stress and development including seed germination and seedling growth in higher plants (Torres and Dangl, 2005; Sagi and Fluhr, 2006; Carter et al., 2007, Singh et al., 2014). Water stress treated roots showed higher NADPH oxidase activity in case of spectrophotometric as well as in gel assay (Das and Kar 2016).

A working model on apoplastic ROS burst leading to cell wall relaxation

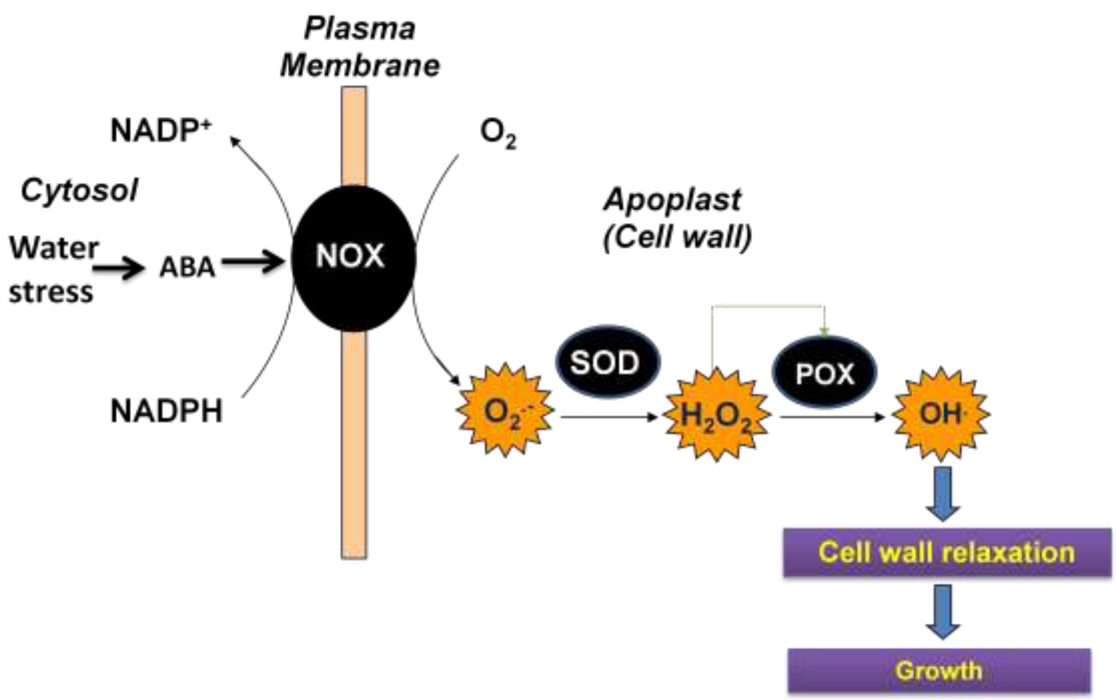

Figure 1:- Working model of apoplastic ROS during cell elongation growth of plants. PM-located NADPH oxidase (Rboh) generates $O_2^{\cdot -}$ that are converted to H_2O_2 either spontaneously or by the activity of apoplastic SOD (Cu–Zn SOD). Being relatively more stable, H_2O_2 can act as a signalling molecule or it converted via apoplastic peroxidase

(Prx) to hydroxyl radical ($OH^{\cdot}$). Hydroxyl radical ($OH^{\cdot}$) generation in apoplast resulting the breakdown of complex cell wall structure and related to cell loosening and cell extension growth.

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