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Control of root growth and development by reactive oxygen species

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Reactive oxygen species (ROS) are relatively simple molecules that exist within cells growing in aerobic conditions. ROS were originally associated with oxidative stress and seen as highly reactive molecules that are injurious to many cell components. More recently, however, the function of ROS as signal molecules in many plant cellular processes has become more evident. One of the most important functions of ROS is their role as a plant growth regulator. For example, ROS are key molecules in regulating plant root development, and as such, are comparable to plant hormones. In this review, the molecular mechanisms of ROS that are mainly associated with plant root growth are discussed. The molecular links between root growth regulation by ROS and other signals will also be briefly discussed.

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Introduction

Roots are important plant organs not only for structurally supporting the plant within the soil, but also for the uptake of nutrients and water; in addition to sensing and responding to changes in the immediate environment. The growth of plant roots depends on maintaining a balance between cell proliferation and differentiation at the root tip [1]. Plant roots can be roughly divided into three regions along their longitudinal axis; a meristematic zone, a elongation zone, and a maturation zone. In the meristematic zone, cells exhibit a high rate of cell division, but undergo little elongation. In the elongation zone, cell proliferation ceases and cells elongate and begin to differentiate [2]. The maturation zone is characterized by cells that have completed elongation and are strongly committed to differentiation, including root hair development, which are tip growth cellular structures of epidermis cells, and vascular tissue formation [3,4]. Even more, lateral roots, which are newly formed organ in the maturation zone of primary root, play a key role for providing branched root architecture [5].

Root development is determined by the balance of activity within these three zones. Therefore, studies examining the molecular and biochemical components that regulate this balance are crucial for understanding plant root development and growth. While decades of research have led to the identification of plant hormones that play an essential role in root development [6–9], more recent studies have demonstrated role of plant hormones in regulating plant root growth by acting as signal molecules. ROS have been found to be especially important for maintaining the balance between cell proliferation and differentiation. Significant evidence has accumulated supporting the premise that ROS can act as signaling molecules serving a functional role similar to hormones. The present review focuses mainly on the role of ROS as regulators of plant root development, which includes primary and lateral root development, as well as root hair differentiation.

ROS production and usage in plant root cells

ROS, such as superoxide, hydrogen peroxide, and hydroxyl radicals, are continuously produced in aerobic organisms during respiration [10]. Due to the highly reactive nature of ROS, they can be very injurious to plant cells, damaging DNA, lipids, and proteins. Thus, they can cause cells, and whole plants, to die if the levels of ROS are sufficiently high. Due to the potentially harmful nature of ROS, plants have evolved elaborate systems for detoxifying ROS [11].

Even though ROS are potentially harmful, they do accumulate in root cells even under normal growth conditions [12], and in fact are needed for root growth and development. One of the important roles of ROS in root development is their function in modifying cell walls [13,14]. ROS are produced in plant roots by the activity of enzymes located on the plasma membrane, NADPH oxidases that are also called as Respiratory Burst Oxidase Homologs (RBOHs) in plant, and by the process of respiration in mitochondria and plastids [15–17]. Oxygen

(O_2) is reduced by NADPH oxidase to superoxide (O_2^-). Since the catalytic domain of NADPH oxidase is directed towards the apoplast, the superoxide is released into the apoplastic space [15]. This superoxide is then dismutated into H_2O_2 and O_2 spontaneously or enzymatically by the catalytic activity of superoxide dismutase (SOD) [18], apoplastic oxalate oxidase [19], diamine oxidase [20], or peroxidase [21]. H_2O_2 generated in the apoplastic region is degraded by the enzymatic activity of class III peroxidases, which are also secreted into the apoplast [21].

Peroxidases facilitate the conversion of H_2O_2 into H_2O and O_2. During this process, an electron is also produced which is utilized in entire plant cells for the modification of both primary and secondary cell walls [22••]. The modification process involves the transfer of the electron to monolignol molecules in cells within the maturation zone, where monolignol serves as a substrate for the formation of the polymer, lignin. Once activated by the addition of the electron, monolignol can then initiate the lignin polymerization process, which is then deposited in the secondary cell wall of plant cells during its formation [23]. The presence of lignin in the secondary cell walls provides significant mechanical strength especially in the vascular cells [24]. In addition, the activity of NADPH oxidase, peroxidase, and other enzymes, which catalyze ROS, play a crucial role in the formation of the casparian strip; which is a lignin based diffusion barrier present in the endodermis in plant root cells [25]. For specifying the casparian strip formation in the endodermis, casparian strip domain proteins (CASPs), which express specifically in the endodermis, guide these enzymes localized in the plasma membrane in a region of endodermal cell walls [25,26].

ROS production and metabolic cycles are tightly linked to ROS signaling. In the subsequent section of the review, the role of ROS signaling in root development will be discussed.

ROS affects cell division in the root apical meristem

In addition to the direct role that ROS plays in modifying the structure of cell walls, it also plays a role in determining the size of the meristimatic zone by regulating the cell cycle. In this regard, ROS has already been established as a cell cycle regulator in animal cells [27]. Regarding its role in plants, exogenous H_2O_2 treatment has been shown to repress the expression of cell cycle-related genes and reduce the meristem size of the root [28].

DNA damage arrests cell proliferation and, the linkage between ROS accumulation and DNA damage is also reported [29,30]. Recently Chen and Umeda reported that H_2O_2 was accumulated in the elongation zone of roots treated with the DNA double strand break (DSB) inducer, zeocin. A *sog1* mutant, *SOG1* is a major transcription factor that is induced in response to DSB [31], exhibited insensitivity to zeocin treatment and did not accumulate H_2O_2. SOG1 was found to directly regulate the expression of *FMO1*, which encodes a flavin-containing monooxygenase that oxidizes molecular oxygen. *fmo1* mutants exhibited insensitivity to zeocin treatment relative to root growth [32••]. These results strongly indicate that ROS homeostasis plays a key role in controlling the size of the root meristematic zone under DNA stresses.

H_2O_2 also affects the cortex proliferation, which is an inner cell type of the root [33]. SPINDLY (SPY), which is an O-linked N-acetyl glucosamine transferase [34] plays a key role for cortex proliferation by regulating cellular redox homeostasis. This study indicates H_2O_2 has an important function for cell proliferation in the cortex.

The redox status also regulates the maintenance of the plant root meristem. Because of highly reactive potential of ROS, accumulated ROS oxidize proteins, chemicals, metabolites, and etc. in a cell. For preventing this oxidative damage, adjusting the redox balance in a cell by using small antioxidant molecules, such as glutathione and thioredoxines (TRXs) [35,36] are important for considering ROS effect.

Plants with mutation in the *ROOT MERISTEM LESS1* (*RML1*) gene, which encodes a glutathione biosynthesis gene, are inhibited in the formation of an active root meristem [37]. Researchers demonstrated that the level of glutathione was important in regulating the G1 to S cell cycle transition [37]. Glutathione reductase (GR), that catalyzing the reduction of oxidized glutathione, is also important for regulating the root apical meristem maintenance. The Arabidopsis has two GR genes, GR1 [38] and GR2. Although complete loss of function mutant of GR2 is embryo lethal [39], a weak allele of GR2 mutant, miao, shows strong growth defect of root meristem [40]. And regulation of root apical meristem maintenance by the glutathione has some relation to a plant hormone, auxin (see later for further details in the cross talk section).

In addition to glutathione, TRXs also involve in regulating root meristem size. TRX reductase mutants (*ntrA* and *ntrB*) exhibit a small meristem phenotype [41,42]. Collectively, these findings strongly indicate that cellular redox regulation plays a crucial role in maintaining meristem activity.

ROS regulates the transition from cell proliferation to cell differentiation

ROS homeostasis at the root tip also plays an important role in controlling the transition of cells from a zone of cell division to a zone of cell elongation and differentiation. Superoxide accumulates in the meristematic zone, while H_2O_2 accumulates in the elongation zone [12]. Once this