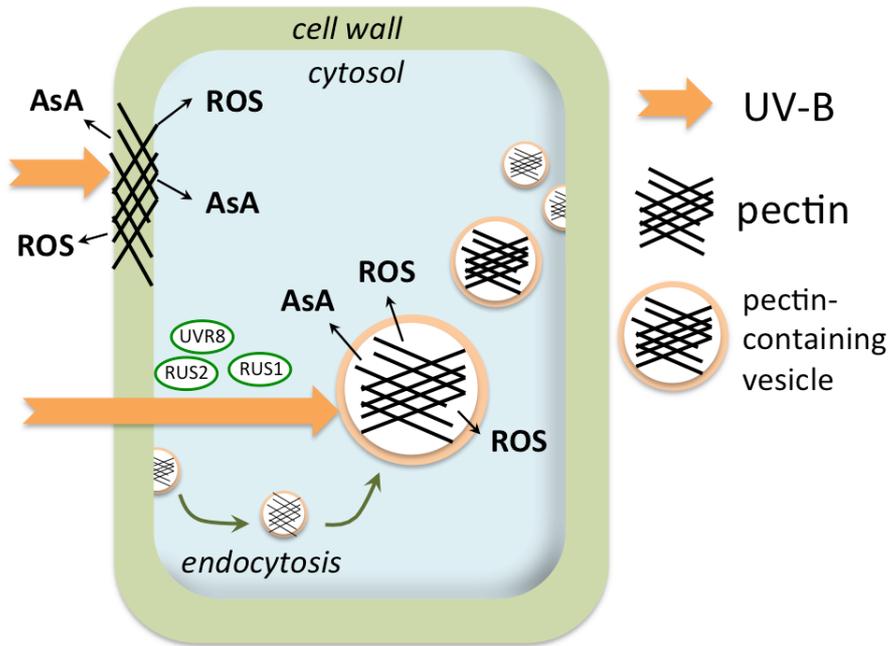


Graphical abstract



Possible role of internalized pectin as a redox regulator during UV-B response in cells of the root apex transition zone.

Mini-Review

Pectins, ROS Homeostasis and UV-B Responses in Plant Roots

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Abstract

Light from the sun contains far-red, visible and ultra violet (UV) wavelength regions. Almost all plant species have been evolved under the light environment. Interestingly, several photoreceptors, expressing both in shoots and roots, process the light information during the plant life cycle. Surprisingly, Arabidopsis root apices express besides the UVR8 UV-B receptor, also root-specific UV-B sensing proteins RUS1 and RUS2 linked to the polar cell-cell transport of auxin. In this mini-review, we focus on reactive oxygen species

(ROS) signaling and possible roles of pectins internalized via endocytic vesicle recycling system in the root-specific UV-B perception and ROS homeostasis.

1. Introduction

UV-B (280–315 nm) is short wavelength of light possessing high energy compared to visible region, which does harm directly to several important biomolecules of organisms. The ozone layer at an altitude of 20-30 km effectively absorbs the wavelength of some range of UV-B and whole UV-C rays. Since ozone and DNA molecule show almost same maximum of absorption, ozone layer functions as a natural sunshade to protect the life from hazardous sunray. While most of UV-B light is absorbed by ozone layer, some can penetrate through it, into the troposphere (Björn, 2008; Green, 1983). As reported by Kerr and McElroy (1993), ozone-depletion is becoming a serious problem causing the increase of solar UV-B levels reaching the ground. Almost all organisms on the ground have been affected by UV-B irradiation for a long time. Plants are no exception while they grow using the energy of sunshine. Until now, the light effect to plant aerial part has well documented in many papers (Vandenbussche et al., 2014). In this review, the effect of UV-B to plant root system will be discussed in terms of recently discovered light escape tropism of roots which is cooperatively triggered by reactive oxygen species (ROS), internalized cell wall pectin molecules via endocytic vesicle recycling, and polar transport of auxin.

2. Plant roots express all photoreceptors and use them to control their behavior

To date, *Arabidopsis* has been reported to express 14 photoreceptors including several

phytochromes, cryptochromes and phototropins. Interestingly, all these photoreceptors are found not only in aerial part of plants but also in roots (Briggs, 2012). In addition, UV RESISTANCE LOCUS 8 (UVR8) protein was discovered to act as a UV-B specific receptive protein. Intriguingly, UVR8 is expressed not only in leaf and stem, but also in root apices (Rizzini et al., 2011). Arabidopsis roots express besides the UVR8 UV-B receptor also root-specific UV-B sensing proteins RUS1 and RUS2 (Tong et al., 2008; Leasure et al., 2009). All these indicate that root system possesses the physiological ability to respond to broad light wavelengths, intensities and directions; allowing roots use light for fine control of their behavior (Mullen et al., 2002; Pedmale and Liscum, 2007; Laxmi et al., 2008; Burbach et al., 2012; Kutschera and Briggs, 2012; Wan et al., 2012). Roots, in contrast to photosynthetic organs, grow naturally underground in darkness. It has been reported that Arabidopsis roots grow quicker when illuminated (Laxmi et al., 2008; Daychok et al., 2011; Yokawa et al., 2011; Xu et al., 2013). This root behavior, closely associated with generation of ROS, is evolutionarily optimized to seek for dark conditions and can be considered as a light-escape phototropism of roots (Yokawa et al., 2011, 2013; Burbach et al., 2012).

3. UV-B induced ROS production in plant cell

Excess levels of light induce harmful effects to certain critical biomolecules in plants. For instance, cyclobutane pyrimidine dimer is immediately formed after DNA molecules absorb UV-B energy, which leads to mutation or cell death, unless it is correctly repaired by certain enzymes such as photolyases (Garinis et al., 2005). Lipids and proteins are also

damaged by UV-B irradiation directly (Kramer et al., 1991; Caldwell, 1993). Moreover, UV-B light causes the generation of ROS in plant cells. At the modest concentration, it is well known to play an important role as signaling molecule in plant cells. However, excess of ROS production may damage cell components resulting in apoptosis. UV-B-induced ROS-production alters the pattern of gene expression such as anti-oxidative enzymes (Egert and Tevini, 2003) and pathogenesis-related gene PR-1 (Green and Fluhr, 1995). In addition, it also promotes the biosynthesis of natural sunscreens such as flavonoids or anthocyanins (Landry et al., 1995; Reddy et al., 1994; Schenke et al., 2011). Upon plant cells are UV-B irradiated, the activity of NADPH oxidase, SOD (superoxide dismutase) and peroxidase are enhanced whereas catalase activity is decreased (Rao et al., 1996). Multiple sources of UV-B-induced ROS have been proposed such as peroxidase and several other unknown factors produce ROS (Egert and Tevini, 2003; A-H-Mackerness et al., 2001; Yannarelli et al., 2006). Thylakoid membrane was proposed to act as a source of free radicals (mainly hydroxyl radical) generated via the cleavage of hydrogen peroxide (H₂O₂) receiving the energy of UV-B directly (Hideg and Vass, 1996).

We have previously reported that Arabidopsis root apex cells generate burst of ROS when roots are illuminated with visible light, resulting in the significant promotion of root growth (Yokawa et al., 2011; Xu et al., 2013; Yokawa et al., 2013). Thus, ROS species generated by UV-B may also play an important role in the root escape tropism from light environment. However, it is not fully known so far which mechanisms are behind the generation of UV-B induced ROS and which signaling cascades connect the perception of UV-B with these

root growth responses. Generally, root growth and tropism are modulated by auxin distribution and contents. One possible effect of light on root growth might be linked to auxin and its photodegradation, as endogenous auxin levels are close to the saturation level with respect of root growth (Leasure et al., 2013). On the other hands, it was also proposed that auxin biosynthesis by illumination of plant cells (Koshiha et al., 1993; Yokawa et al., 2014).

4. Possible role of pectin endocytosis in UV-B responses

Polygalacturonic acid and galacturonic acid were reported to generate superoxide upon the UV-B irradiation in the presence of hydrogen peroxide. Superoxide anion radical was observed *in vitro* by using isolated cell wall from *Pisum sativum* leaves with electron paramagnetic resonance method (Pristov et al., 2013). In root cells, pectin is major component of polygalacturonic acid cell wall pectin cross-linked with boron and calcium has been shown to be internalized and transported by endocytosis (Baluška et al., 2002). For root tropisms, endocytic vesicle recycling is critical process, especially active in the root apex transition zone, which is located in-between the apical meristem and basal elongation zone (Baluška et al., 2010; Baluška and Mancuso, 2013). During tropic movements, rate of endocytic recycling is increased in order to re-localize many proteins allowing transport of critical biomolecules such as auxin. As the Figure 1 shows, internalized endosomal cell wall pectin is likely to affect cellular redox balance as it produces superoxide under UV-B stress as previously shown (Pristov et al., 2013). Furthermore, D-galacturonic acid released by the degraded cell wall is known to be

reutilized not only for newly forming cell wall, but also as a substrate of L-ascorbic acid biosynthesis (Valpuesta and Botella, 2004). L-ascorbic acid is well known as a reducing agent controlling cellular redox homeostasis via glutathione-ascorbate cycle (Foyer and Noctor, 2011). It is reasonable to expect importance of cross-linked cell wall pectins for ROS homeostasis because UV-B easily breakdown cell wall components and this might act as a cue for the ascorbate biogenesis at irradiated organ sides in order to recover the cellular redox balance. Of course, internalized cell wall pectin within endocytic vesicles and endosomes might also be a potential source for the L-ascorbate synthesis (Figure 1). Finally, similarly as in animal cells, also plant cell endosomes emerge to be enriched with ROS generating NADPH oxidases (Leshem et al., 2007; Takeda et al., 2008; Hao et al., 2014). Interestingly, salt stress is increasing *Arabidopsis thaliana* respiratory burst oxidase homolog D (RbohD) endocytosis. RbohD is one of NADPH oxidases functioning as ROS-generating membrane-associated enzyme (Hao et al., 2014) as well as ROS-enriched endosomes (Leshem et al., 2007) in root apex cells of *Arabidopsis*.

Pectins are well known to act as a source for methane emissions due to UV-B irradiation (McLeod et al., 2008; Bruhn et al., 2009, 2011; Messenger et al., 2009). Importantly, Messenger et al. (2009) demonstrated that UV irradiation of tryptophan and pectin is involved in methane formation from pectin, indicating that tryptophan might function as a photosensitizer generating radical species from UV-B exposed pectin molecules at the physiological conditions (Messenger et al., 2009). Taken together, the biological function of internalized pectin recycled via endocytic vesicle recycling can be proposed to act as a

movable source of ROS as well as of antioxidants and/or signaling molecules in response to the UV-B challenge. Interestingly in this respect, the root apex transition zone might be very responsive to UV-B due to the high rate of pectin recycling found precisely in this root apex region (Baluška et al., 2002; 2010; Baluška and Mancuso, 2013). In this zone, the UV-B sensing proteins RUS1 and RUS2 are expressed (Tong et al., 2008; Leasure et al., 2009) and, importantly, are controlling the polar auxin transport (Ge et al., 2010; Yu et al., 2013). This cell-to-cell auxin transport is based on the endocytic vesicle recycling and shows peak activities in the transition zone (Mancuso et al., 2005, 2007; Baluška et al., 2010; Baluška and Mancuso, 2013). Interestingly, exogenous vitamin B6 can rescue the UV-B inhibited root growth of *rus1* and *rus2* mutant lines due to its enhancing effects on the light-mediated auxin degradation (Leasure et al., 2009, 2013).

5. Evolution of land plant roots under UV-B environment

In this review, we have been discussing several physiological matters of roots responding to UV-B. An evolutionary question is raised: why are plant roots so sensitive for the light environments? Some cracks in the soil surface can appear anytime, allowing light to penetrate into soil. Roots may be easily exposed to light when it is heavy rains, drought condition, earthquakes, and so on. On the other hand, it is also important to accelerate the root growth rate of radicle immediately after the seed germination in order to reach the underground environment. It is obvious that roots have to be in the soil in order to fix the plant body properly and to take-up water and mineral nutrition. Therefore, this importance of the light escape behaviour of roots could be the reason why they evolved these abilities

to recognize sensitively the light sources and to accomplish the light escape. However, the mystery why roots have also the root-specific UV-B sensing mechanisms is still awaiting explanation.

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Figure Legend

Figure 1

Possible role of pectin as a redox regulator during UV-B response in cells of the root
apex transition zone. AsA indicates ascorbic acid, for other details see the text.

Figure 1

