Arabidopsis Roots and Light – Complex Interactions

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Unlike the actively moving animals, plants actively change their body architecture via growth of their organs in responses to the environmental stresses. For example, changes of the *Arabidopsis thaliana* root apex zonation under phosphate (Pi) deficiency is considered for such an active response, including the inhibition of primary root (PR) elongation and increasing densities of lateral roots and root hairs (Abel, 2017). Current study modifies this hypothesis which is based on the transparent Petri-dish based culture method of young Arabidopsis seedlings causing illumination of roots (Zheng et al., 2019). These authors reported that the Pi-deficiency not only increases the malate secretion from Arabidopsis root apices via ALMT1 transporter, but also that the blue light triggers malate-mediated photo-Fenton reaction in the rhizosphere, increasing the ·OH radical levels. Importantly, the inhibition of primary root growth in Pi-deficiency occurs only in the Arabidopsis seedlings grown in transparent Petri-dishes due to blue light-triggered malate-mediated Fe redox cycle in the root apoplast (Zheng et al., 2019). This study not only provided a novel model to understand the Arabidopsis root apex responses to the Pi-deficiency, but also strongly warned us that too much light reaches the Arabidopsis roots grown within the transparent Petri-dishes. Illumination of roots causes stress not only to roots but also to the whole seedlings which modifies the root and plant physiology, and therefore, this issue cannot be ignored.

Root Senses Light Under the Soil Surface

Despite the fact that root is the underground plant organ, its ability to sense and react to light has been often ignored in routine laboratory works. The transparent Petri-dishes have been widely used, exposing the roots directly to light (Yokawa et al., 2011; Mo et al., 2015). Since the space below the soil surface is not in the complete darkness, and all known plant photoreceptors are expressed in root apex cells (Mo et al., 2015), it is obvious that light is important environmental factor for roots. Light can reach the root cells via two potential routes. It penetrates the soil for several centimeters deeply or is conducted by the vascular tissues (Mo et al., 2015). Several experimental systems with shaded roots were suggested to mimic a natural growth condition in order to improve the Petri-dish based Arabidopsis culture methods, and the differential gene expression pattern between lighted and shaded roots were compared (Rellán-Álvarez et al., 2015; Qu et al., 2017). The shading of Arabidopsis roots grown in Petri-dishes affects the expression pattern of main groups of plant photoreceptors in Arabidopsis roots (Qu et al., 2017). Altogether, light affects roots both via photoreceptor mediated signaling pathways (Mo et al., 2015) as well as via the non-enzymatic Fe redox cycle of the photo-Fenton reaction (Zheng et al., 2019).

Light and Phosphate Nutrient

Pi is a polyatomic ion which represents macro-nutrient element to plants. Pi deficiency inhibits growth of Arabidopsis primary roots grown on Petri-dishes, resulting in altered root architecture considered to be relevant for searching for the Pi. This phenomenon has been considered as an active process crucial for survival of plants under the Pi deficiency. Application of the darkened Petri-dishes (Xu et al., 2013) and the GLO-root system raised a critical question to this hypothesis. Importantly, when roots are kept in the darkness, seedlings of Arabidopsis do not show significantly differences their root architecture when grown on Pi-sufficient and Pi-deficient situations (Rellán-Álvarez, et al., 2015).

Currently, Liu and his colleagues provided evidences to understand the formation of

root architecture in Pi-deficiency with/without light illumination (Zheng et al., 2019). Under Pi-deficiency, the tonoplast-localized ALS3/STAR1 transporter complex inhibit the accumulation of the transcription factor STOP1 in nucleus, activating the ALMT1 to pump more malate into the rhizosphere (Zheng et al., 2019). Within the malate-rich environment, Fe^{3+} forms malate-Fe^{3+} complexes and the blue light triggers non-enzymatic photon-Fenton reaction to reduce the Fe^{3+} to Fe^{2+} and release the free radical, ·OH. As a signal molecule, ·OH modifies the root growth and alters the root development (Zheng et al., 2019). From this study, two aspects should be pointed out: 1) blue light modifies the root growth also via pathways not related to root apex expressed photoreceptors; 2) inhibition of the root growth is not always an active event, but a side-effects of blue light on roots evolutionarily optimized for darkness.

Light and Reactive Oxygen Species Control Root Growth and Development

Reactive oxygen species (ROS) play a crucial role as a signaling molecule for regulating root development, growth and tropisms in apex region. Since the nature of ROS is short-lived and highly reactive, root cells and tissues possess sophisticated system for controlling redox state. Yokawa et al. (2011) reported that 10 seconds of blue light illumination to Arabidopsis roots produce superoxide in the apices immediately. The oxidative burst caused by the sudden illumination increases root growth rate (Yokawa et al., 2011). Besides the visible wavelength, UV-B also promotes ROS production, and ROS changes the rate of endocytic vesicle recycling in the cells of root apex region (Yokawa et al., 2016). It indicates that light-induced ROS helps roots to grow faster or bend away from the light source (negative phototropism). The instant production of ROS is used as an alert signal in the case of root illumination rather than relative slow gene expression. It is because the exposure to light is a critical and dangerous situation for roots, and roots must take a speedy action against unfavorable situation. The new data of Zheng et al. (2019) reveal that ·OH production in illuminated root is generated via Fe redox cycle of the photo-Fenton reaction. The blue-light mediated ROS production in Arabidopsis root apex cells was shown to be mediated by cryptochrome 1 (CRY1) through the redox cycle of flavin (El-Esawi et al.,

2017). It is very interesting that blue light-induced ROS is produced through non-biological and non-enzymatic pathways based on the redox cycles of flavin and Fe contributing to root light responses (Fig. 1). However, to understand the exact mechanisms and pathways how ROS is generated by light will require further experimental investigations.

Future Perspectives

Roots, the underground organs of plants, can sense and react to the faint light penetrated the soil surface to modify its development and react to the changing environment properly. Direct and strong illumination on root raises unwanted physiological responses and chemical reactions in root cells and rhizosphere. Shaded Petri dishes (Xu et al., 2013) and the GLO-root system can provide a shaded root growth condition with a high resolution imaging platform for accurate analysis (Rellán-Álvarez et al., 2015). Simple methods with cheap equipment can also provide light gradient to mimic the underground world for roots (Qu et al., 2017). As seedlings with illuminated roots have lost their ROS homeostasis and show symptoms of stress, it is important to re-investigate interpretations of all previously published data obtained using the transparent Petri-dish system. For example, is the root growth inhibition reported for aluminium toxicity also related to blue light-induced ROS via Photo-Fenton reaction? For a better understanding of Arabidopsis roots and seedlings grown in the Petri-dish system, further experimental studies are needed. We need to re-investigate impacts of light on Arabidopsis roots related to stress-related photomorphogenesis based on both photoreceptor-mediated signaling pathways and the non-enzymatic photon-Fenton reaction processes; both mediated by ROS.

(1199 Words)

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Figure Legend

Figure 1

Schematic depiction of the non-enzymatic blue-light induced ROS in the cytosol via the flavin redox cycle (El-Esawi et al., 2017) and in the apoplast via the flavin redox

cycle of photon-Fenton reaction (Zheng et al., 2019).