BIOLOGIA PLANTARUM 64: 764-772, 2020 DOI: 10.32615/bp.2020.122

Ultraviolet-B radiation induces cell death in root tips and reprograms metabolism in *Arabidopsis*

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Abstract

Ultraviolet-B (UV-B) radiation inhibits root system growth, however, the influence of UV-B radiation on the regulation of root development remains unclear. Here, we investigated the effects of UV-B radiation on root growth and metabolism in *Arabidopsis* using physiological, pharmacological, and transcriptome approaches. Our previous study has demonstrated that UV-B radiation depresses auxin accumulation in roots by reducing auxin biosynthesis, transport, and response. In this study, we found that UV-B radiation inhibited primary root (PR) growth by inducing root tip cell death and thereby disrupting cell division and elongation in root tips. The destructed root structure and distorted auxin flow caused by UV-B-induced root tip cell death also led to a reduced auxin accumulation in roots. Supplementation with an auxin α-naphthylacetic acid alleviated UV-B-repressed PR growth and further supported a notion that auxin is involved in UV-B-repressed PR growth. The UV-B radiation downregulated the expression of genes encoding the enzymes or regulators of the biosyntheses and degradations of the structural constituents of cell wall and genes involved in wax, cutin, and suberin biosyntheses, thereby repressing root system growth and development. The UV-B radiation also markedly repressed photosynthesis-related gene expression in roots, a non-photosynthetic organ. Taken together, this study suggests that UV-B radiation affects root growth by inducing cell death in root tips and reprogramming metabolism in roots.

Additional key words: endogenous auxin flow, gene expression, α-naphthylacetic acid application, primary root growth.

Introduction

Ultraviolet (UV)-B radiation is detrimental to plant growth and development (Nawkar *et al.* 2013). In the past fifty years, a significant decrease in stratospheric ozone led to a continuous exposure of the earth to higher dosages of UV radiation (Solomon *et al.* 2008). Therefore, it is necessary to study, in detail, the molecular and physiological mechanisms of UV-disturbed plant growth responses. Previous studies helped our understanding of UV-B perceptions, signaling, and UV-B-induced DNA damage in plant cells (Lytvyn *et al.* 2010, Nawkar *et al.* 2013). UV-B-induced DNA damage, including the formation of abasic sites, the production of cyclobutane pyrimidine dimers (CPDs), and pyrimidine (6-4) pyrimidine photoproducts (6-4PP) by formation of covalent bonds between adjacent pyrimidine residues on the DNA strand, leads to deleterious mutation and even cell death in plants (Ulm *et al.* 2004, Fujimori *et al.* 2014, Lario *et al.* 2014).

The regulatory pathways that respond to UV radiation trigger the production of nitric oxide (NO) and reactive oxygen species (ROS), accompanied by the activation of repair mechanisms and antioxidant enzymes (Nawkar *et al.* 2013). High levels of UV radiation creates conditions similar to that of the oxidative stress response that results from ROS production (Mackerness *et al.* 1999, Jia *et al.* 2009). The ROS bursts lead to the opening of mitochondrial membrane permeability transition pore, and thereby result

Submitted 2 April 2020, *last revision* 27 July 2020, *accepted* 19 August 2020.
Abbreviations: ANAC032 - NAC domain containing protein 32; bZIP60 - basic region/leucine zipper motif 60; Col-0 - Columbia-0; CYCs - cell cycle regulators cyclins; DAPI - 4,6-diamidino-2-phenylindole; DEGs - differentially expressed genes; DIN2 - dark inducible 2; *GO - gene ontology*; IBS1 - BABA-induced sterility 1; MYB2 - myeloblastosis domain protein 2; NAA - α-naphthylacetic acid; PCD - programmed cell death; PI - propidium iodide; PR - primary root; ROS - reactive oxygen species; SRA - Short Read Archive; UV-B - ultraviolet-B; WOX - WUSCHEL-related homeobox.
Acknowledgements: The authors gratefully acknowledge the Central Laboratory of the Xishuangbanna Tropical Botanical Garden for providing research facilities. This work was supported by the National Key Research and Development Program of China (2016YFC0501901), the China National Natural Sciences Foundation (31772383), the Basic Research Program of Qinghai Province (2019-ZJ-7033), and the Qinghai innovation platform construction project: Qinghai Provincial Key Laboratory of Restoration Ecology of Cold Area (2017-ZJ-Y20).
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in the release of cytochrome *c* and the generation of more ROS, which leads to a feedback loop, amplifying the stress signal induced by the initial programmed cell death (PCD) (Reape and McCabe 2008).

The UV-B photoreceptor UVR8 signaling elicits NO generation in response to UV-B radiation (Krasylenko *et al.* 2012). UV-B radiation-induced NO also results in stomatal closure, limits water loss, and prevents cellular injury (Lytvyn *et al.* 2010, Krasylenko *et al.* 2012). Many studies have demonstrated that flavonoid pathway is also involved in the stress resistance to UV-B radiation in plants (Kootstra 1994, Karabourniotis *et al.* 1992, Santelia *et al.* 2008, Liu *et al.* 2012, Ma *et al.* 2016, Wan *et al.* 2018b). Flavonoids reduce UV-B radiation-induced lipid peroxidation and malondialdehyde (MDA) accumulation in plants, and thereby alleviating plant growth inhibition caused by UV-B radiation (Li *et al.* 1993, Chen *et al.* 2001, Lud *et al.* 2002, Winkel-Shirley 2002, Liu *et al.* 2012). In general, roots grow underground and are normally protected from UV-B exposure. However, the roots sometimes appear above ground due to earthquakes, animal behaviors, or strong wind (Yokawa *et al*. 2016, Wan *et al.* 2018b). The expression of *UVB-resistance 8* (*UVR8*) gene can be detected in roots, indicating that roots could sense UV-B radiation (Mo *et al*. 2015). However, the precise ways in which UV-B radiation modulates plant growth and root system architecture remains unclear.

Plant growth is regulated by root meristematic cell division potential and stem cell niche activity (Aida *et al.* 2004, Blilou *et al.* 2005, Grieneisen *et al.* 2007, Tian *et al.* 2014, Ji *et al.* 2015, Liu *et al.* 2016). The progression of mitosis of eukaryotic cells is modulated by conserved molecular mechanisms. The core cell cycle regulators cyclins (CYCs) play key roles in cell cycle progression through the form of cyclin-dependent kinase (CDK)/ CYC complexes (Wang *et al.* 2004, Wang and Yang 2007, Craddock *et al.* 2016). A total of 49 CYCs of 8 classes were identified in *Arabidopsis* genome, including CYCAs, CYCBs, CYCC, CYCDs, CYCH, CYCL, and CYCPs (Nafati *et al.* 2010, Craddock *et al.* 2016). Among these CYCs, A- and B-type CYCs regulate the cell cycle progression through the S-, G2- and early M-phase, while D-type CYCs regulate the cell cycle progression of G1/S phase transition (Nafati *et al.* 2010). The plant-specific homeobox transcription factor WUSCHEL-related homeobox (*WOX*) gene family plays vital roles in modulating plant growth and development by controlling stem cell activity in shoot/root apical meristem and cambium (Alvarez *et al.* 2018, Li *et al.* 2019).

Stem cell identity is maintained by root quiescent center (Scheres *et al.* 2007, Ji *et al.* 2015, Santuari *et al.* 2016). Maintaining a normal auxin gradient in the meristem is required for normal root growth (Galinha *et al.* 2007, Dinneny *et al.* 2008, Laskowski *et al.* 2008, Wang *et al*. 2009, Zhao *et al.* 2014). Our recent study found that UV-B reduces auxin accumulation in *Arabidopsis* seedlings by downregulating the expression of genes involved in auxin biosynthesis, including *abscisic acid aldehyde oxidase 3* (*AAO3*), *cytochrome* P_{450} (*CYP79B2*), *yucca 2* (*YUC2*), *YUC3,* and *YUC9* (Wan *et al.* 2018b). The UV-B radiation also reduces the abundance of *PIN-formed 2* (*PIN2*) and *auxin resistant 1* (*AUX1*) in root tips, and thereby repressing auxin transport in roots (Wan *et al.* 2018b). These results suggested that UV-B represses plant growth by disrupting auxin signaling. In this study, we investigated the effects of UV-B on primary root (PR) growth and the differentially expressed genes (DEGs) in UV-B-radiated roots.

Materials and methods

Plants and growth conditions: *Arabidopsis thaliana* L. Columbia-0 ecotype (Col-0) seeds were surface sterilized and then sown onto a 1/2 Murashige and Skoog agar medium (pH 5.75; *Sigma*, St. Louis, USA) with or without 10 nM naphthalene acetic acid (NAA). UV-B radiation was performed using a narrowband UV-B lamp (*TL 20W/01-RS* with a spectral peak at 311 nm; *Philips*, Eindhoven, The Netherlands) with a cellulose diacetate to block UV-C radiation as described previously (Wan *et al.* 2018b). Five-day-old *Arabidopsis* Col-0 seedlings were subjected to 20 W m^{-2} of UV-B for 2 - 10 min (2.4 - 12 kJ m^{-2}), and then the seedlings were transferred to normal growth conditions (a temperature of 22 °C, a 16-h photoperiod, an irradiance of 150 μmol m^{-2} s^{-1}, and a relative humidity of 60 - 70 %) for 5 d. The meristem zone length was measured as the distance between the quiescent center to the noticeably elongated cell (the cell length is two times larger than the minimum cell length in the cortex), and the cortical cell number in this region was also counted as described by Liu *et al.* (2013). The elongation zone length was measured as the distance between the first noticeably elongated cell to the first visible bulge (root hair emergence) (Wan *et al.* 2018a).

Detection of reactive oxygen species and nitric oxide in root tips: Endogenous ROS and NO production was monitored using a ROS fluorescence probe 2',7'-dichlorofluorescin diacetate (DCF DA) (*Beyotime*, Shanghai, China) and an NO-specific fluorescence probe 4,5-diaminofluorescein-2 diacetate (DAF-2 DA, *Beyotime*) (Xu *et al.* 2010). After UV-B treatment for 3.6 kJ m^{-2}, the seedlings were cultured for 15, 30, 60, 120, or 240 min under normal growth conditions, and then the fluorescences of ROS and NO were detected. The fluorescences were examined using a confocal laser scanning microscope (*LSM710*, *Zeiss*, Jena, Germany; excitation/emission wavelengths: 488/530 nm for ROS and 490/515 nm for NO).

Detection of root tip cell death: UV-B-induced cell death in roots was first detected using propidium iodide (PI) staining as described previously (Xu *et al.* 2010). After UV-B treatment for 3.6 kJ m^{-2}, the seedlings were cultured for 2 h, and then the fluorescence of PI and 4,6-diamidino -2-phenylindole (DAPI) were detected. Briefly, after the roots were immersed in PI dye (*Beyotime*, 3 mg dm^{-3}) for 1 min, the roots were washed with distilled water and then were observed using a fluorescence microscope (*Axioskop*, *Zeiss,* Jena, Germany; an excitation wavelength of 546

nm). For DAPI staining, the roots were incubated with DAPI dye (*Sigma*, 1 mg dm^{-3}) for 10 min, and then washed with distilled water. The roots were observed using a fluorescence microscope with UV radiation filter (Xu *et al.* 2010). The PI and DAPI staining was repeated three times independently.

Transcriptome data analysis: *MapMan* (http://mapman.gabipd.org), *Clustering* (http://www.omicshare.com/tools/Home/Soft/trend) and *Gene ontology* (*GO*) enrichment (http://www.omicshare.com/tools/Home/Soft/gogsea) analyses were used to analyze the root transcriptome data (log2 fold change ≥ 1, FDR ≤ 0.01) [National Center for Biotechnology Information's Short Read Archive (*NCBI SRA*) under accession No SRP094914, Wan *et al.* 2018b].

Statistical analysis: The experiments were repeated three times and the measurements were performed on three biological replicates with three technical repetitions and 12 plants were used per treatment. The statistical analysis of the differences was carried out by Student's *t*-test or *ANOVA* using the Statistic package for social science.

Results and discussion

Ultraviolet-B radiation significantly inhibited PR growth in a dosage-dependent manner. As shown in Fig. 1*A*, the PR growth was inhibited by 21.5, 20, 53.2, and 70 % when the seedlings were irradiated with UV-B of 3.6, 6, 9.6, and 12 kJ m^{-2}, respectively. We found that the effect of 12 kJ m^{-2} is the most significant, and this dose can inhibit root growth in a short time, and does not affect seedlings survival. Two major factors affect PR growth: cell division and cell elongation in root tips (Sabatini *et al.* 1999, Baluška *et al.* 2010, Zheng *et al.* 2011, Ji *et al.* 2015, Liu *et al.* 2015). Previously, Wan *et al*. (2018a) have demonstrated that the UV-B photosensitive part can be located at roots, and UV-B photoreceptor UVR8 is also expressed in roots. Furthermore, the expression of photosynthesis-related genes has been changed, but its biological significance is still unclear. To further investigate the inhibitory effects of UV-B radiation on PR growth in detail, we measured the meristem cell number and the length of meristem and elongation zones in UV-B-radiated roots (González-García *et al.* 2011, Li *et al.* 2015). As shown in Fig. 1, UV-B

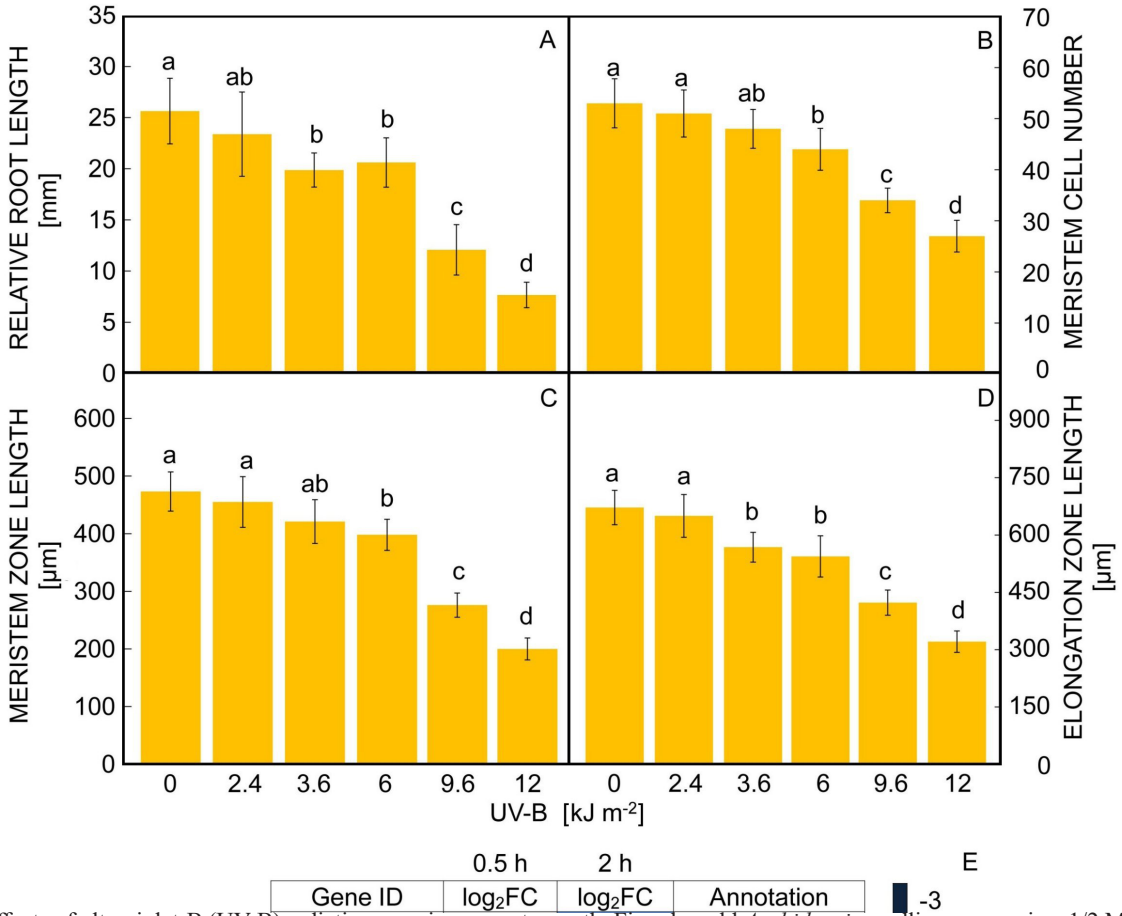

Fig. 1. Effects of ultraviolet-B (UV-B) radiation on primary root growth. Five-day-old *Arabidopsis* seedlings grown in a 1/2 Murashige and Skoog medium were subjected to UV-B of 2.4 - 12 kJ m^{-2} and then were transferred to normal conditions. Primary root length (*A*), meristem cell number (*B*), meristem zone length (*C*), and elongation zone length (*D*) were measured after 5 d. Means ± SEs, $n = 3$ (12 plants/treatment/repeat); different letters indicate significantly different values ($P < 0.05$). *E* - heat maps indicating log_2 fold changes in expressions of genes involved in cell cycle and stem cell development according to the transcriptome data (see Table 1 Suppl. for the detailed gene expression).

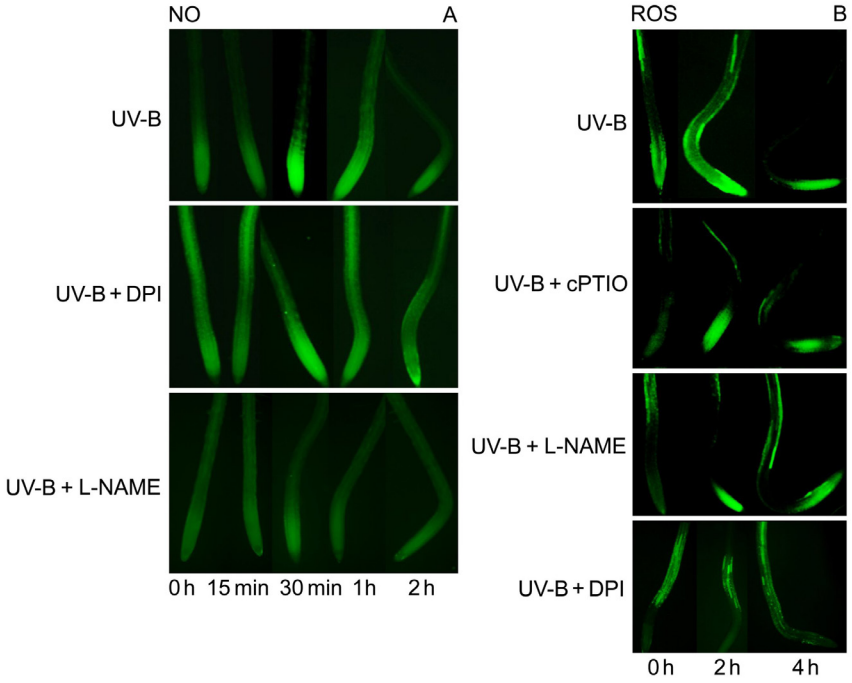

Fig. 2. *A* - detection of NO production in ultraviolet-B (UV-B)-treated *Arabidopsis thaliana* roots with or without 1 μM diphenyleneiodonium chloride (DPI) and 100 μM NG-nitro-L-arginine methyl ester (L-NAME) by an NO-specific fluorescence probe 4,5-diaminofluorescein-2 diacetate (DAF-2 DA). *B* - detection of reactive oxygen species (ROS) production in UV-B-treated *Arabidopsis thaliana* roots with or without 200 μM 2-phenyl-4,4,5,5-tetramethylimidazoline-1-oxyl 3-oxide (cPTIO) or 100 μM L-NAME, and 1 μM DPI by a ROS-specific fluorescent probe 2',7'-dichlorofluorescin diacetate (DCF-DA).

radiation decreases the meristem cell number (Fig. 1*B*), and the length of both meristem and elongation zones (Fig. 1*C*,*D*) with the increase of radiation doses.

To further confirm the results, we investigated the differentially expressed genes (DEGs) (log_2 fold change > 1, FDR ≤ 0.01) by analyzing the transcriptome data of UV-B-treated Col-0 roots (*NCBI SRA*) under accession No. SRP094914 (Wan *et al.* 2018a). After irradiating with UV-B of 3.6 kJ m^{-2}, the seedlings were transferred to normal conditions for 0.5 or 2 h. The expression of stem cell development-related gene *WUSCHEL-related homeobox4* (*WOX4*) was markedly downregulated at 0.5 and 2 h after transfer, and the expression of three core cell cycle genes, *CYCLIN D1,1* (*CYCD1,1*), *CYCLIN P3,1* (*CYCP3,1*) and *impaired in BABA-induced sterility 1* (*IBS1*), were also markedly downregulated at 2 h after transfer (Fig. 1*E*, Table 1 Suppl.). *WOX4* modulates procambium differentiation in plants (Nic-Can *et al.* 2013). *CYCD1,1* is one of core cell cycle regulators that modulates the G1/S phase transition of the cell cycle (Nafati *et al.* 2010). *IBS1* is a core cell cycle gene encoding a cyclin-dependent kinase-like protein (Chen *et al.* 2010, Shamloo-Dashtpagerdi *et al.* 2015). These results indicated that UV-B radiation represses cell division in meristem zones by disrupting the expression of genes involved in meristematic cell division and stem cell activity in root tips, and thereby inhibiting PR growth.

Both nitric oxide (NO) accumulation and reactive oxygen species (ROS) burst can repress PR growth by inducing cell death in roots (Xu *et al.* 2010). We thus examined the content of ROS and NO induced in UV-B-treated Col-0 roots. As shown in Fig. 2*A,B*, UV-B radiation induces an increase in ROS and NO fluorescence, especially in root meristem zone. Supplementing the UV-B-treated roots with the ROS scavenger diphenyleneiodonium chloride (DPI) significantly inhibits ROS accumulation in roots, however, it has no effect on NO content (Fig. 2*A*). Similarly, supplementation with either the NO synthase (NOS) inhibitor NG-nitro-L-arginine methyl ester (L-NAME) or the NO scavenger carboxy-2-phenyl-4,4,5,5-tetramethylimidazoline-1-oxyl 3-oxide (cPTIO) significantly inhibit NO accumulation in roots, whereas it fails to alter ROS production compared with UV-B treatment alone (Fig. 2*B*). These data suggest that the UV-B-induced accumulation of NO and ROS might be mutually independent in the roots.

To further study the physiological basis of UV-B radiation-mediated PR growth inhibition, we next examined whether UV-B radiation-mediated PR growth inhibition is caused by cell death in roots. For this purpose, we first investigated the degree of cell death in roots using propidium iodide (PI) staining. PI is a nucleic acid dye that only can penetrate into dead or dying cells (Xu *et al.* 2010). UV-B radiation induces significant cell death in roots, especially in the meristem zones (Fig. 3*A*). The result was further confirmed by 4,6-diamidino-2-phenylindole (DAPI) staining. DAPI staining can detect the degree of the internucleosomal DNA fragmentation and the chromatin condensation caused by programmed cell death (PCD) (Chen *et al.* 1997). As shown in Fig. 3*A*, only weak DAPI-positive nuclei were detected in the untreated control roots, whereas the strong DAPI fluorescence signals were

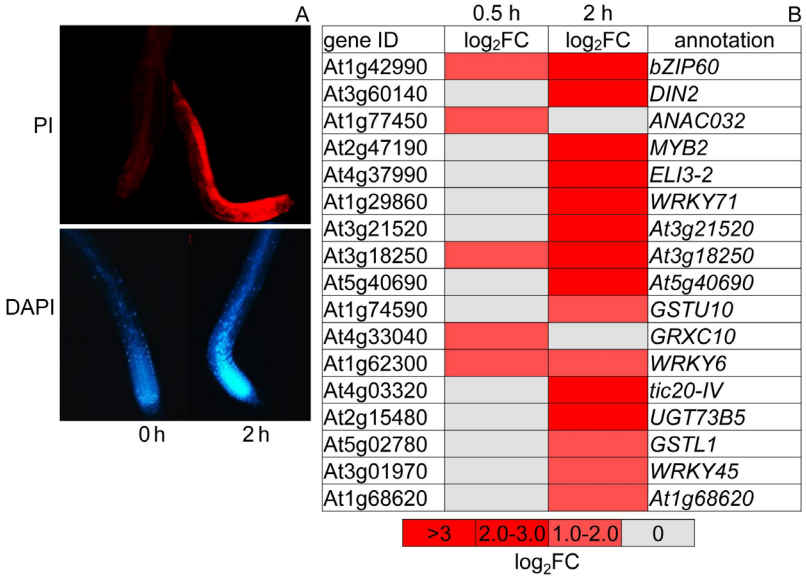

Fig. 3. Ultraviolet-B (UV-B) radiation induced cell death in root tips. *A* - images of staining with propidium iodide (PI) and 4-diamidino-2-phenylindole (DAPI) in UV-B-treated *Arabidopsis thaliana* roots. *B* - heat maps indicating $\log_2$ fold changes in expressions of genes encoding enzymes or regulators of cell death and senescence processes according to the transcriptome data (see Table 2 Suppl. for the detailed gene expression).

detected in UV-B-treated roots from the meristem zone to the elongation zone. These results are consistent with the previous report that exposure to UV-B causes PCD in BY-2 tobacco cells (Lytvyn *et al.* 2010). These results indicated that UV-B radiation induces DNA damage and cell death in the root tips, especially in the meristem zones.

To further elucidate UV-B-mediated cell death in roots, we investigated the DEGs in UV-B-treated roots (Wan *et al.* 2018a). We found that many genes involved in cell death and senescence processes were markedly upregulated in UV-B-treated roots ($\log_2$ fold change > 1, FDR ≤ 0.01) (Fig. 3*B*, Table 2 Suppl.), such as three WRKY family genes *WRKY6*, *WRKY45*, and *WRKY71*, *NAC domain containing protein 32* (*ANAC032*), *basic region/leucine zipper motif 60* (*bZIP60*), *dark inducible 2* (*DIN2*), *myeloblastosis domain protein 2* (*MYB2*), *etc*. Many studies have demonstrated that the plant specific WRKY transcription factors modulate plant senescence (Eulgem *et al.* 2000, Robatzek and Somssich 2001, 2002, Miao *et al.* 2004). Our previous studies indicated that overexpression of *ANAC032* induces H_2O_2 accumulation and age-dependent and stress-induced leaf senescence (Mahmood *et al.* 2016a,b, Sun *et al.* 2019). The *bZIP60* transcription factor is involved in endoplasmic reticulum stress-induced cell death in plants (Reis and Fontes 2012). The *DIN2* encodes a β-glucosidase protein that modulates senescence and necrosis caused by drought, dark, and sugar starvation (Fernández-Calvino *et al.* 2016). The *MYB domain protein 2* (*MYB2*) regulates senescence by inhibiting cytokinin signaling pathway (Guo and Gan 2011). Taken together, these transcriptome data further confirmed that UV-B radiation induces DNA damage and cell death in the roots.

Auxin plays an important role in modulating PR growth and development (Jiang *et al.* 2003, Zhao *et al.* 2014). Our recent study has demonstrated that UV-B radiation represses auxin accumulation in roots by reducing auxin biosynthesis, transport, and response (Wan *et al.* 2018a). The above results indicated that UV-B radiation induces cell death in root tips (Fig. 3). UV-B-induced cell death in root tips can cause the destruction of root cell structure, and thereby disturbing normal auxin flow in root tips. To further confirm the role of auxin in UV-B-mediated root growth, we examined the effect of exogenous auxin NAA on the root elongation. Addition of NAA alleviates the PR growth inhibition caused by UV-B radiation (Fig. 4*A*,*B*). These results further confirmed the role of auxin in UV-B-mediated PR growth inhibition. Collectively, these results indicated that UV-B induces root tip cell death, and thereby disrupting root meristematic cell division and cell elongation. Meanwhile, the destructed root structure and distorted auxin flow caused by UV-B-induced root tip cell death also lead to reduced auxin accumulation in root tips, and finally resulting in PR growth inhibition (Fig. 4*C*). Gopalan (2008) reported that an immunity associated plant cell death can be reversed by auxin. The burst of ROS caused by UV-B is also the defense mechanism of oxidation system. In addition, there were studies proving that auxin plays a role in plant tolerance to arsenite-induced oxidative stress (Krishnamurthy and Rathinasabapathi 2013), so we speculated that auxin can alleviate cell death caused by oxidative damage.

To gain broader insight into UV-B-mediated plant growth, we performed an in-depth investigation of the DEGs ($\log_2$ fold change > 1, FDR ≤ 0.01) by analyzing the transcriptome data of UV-B-treated Col-0 plants (Wan *et al.* 2018a) using *Clustering* trend analysis (http://www.omicshare.com/tools/Home/Soft/trend). The DEGs are sorted into three clusters of similarly regulated genes ($P \leq 0.05$), in which enriched *GO* categories (http://www.

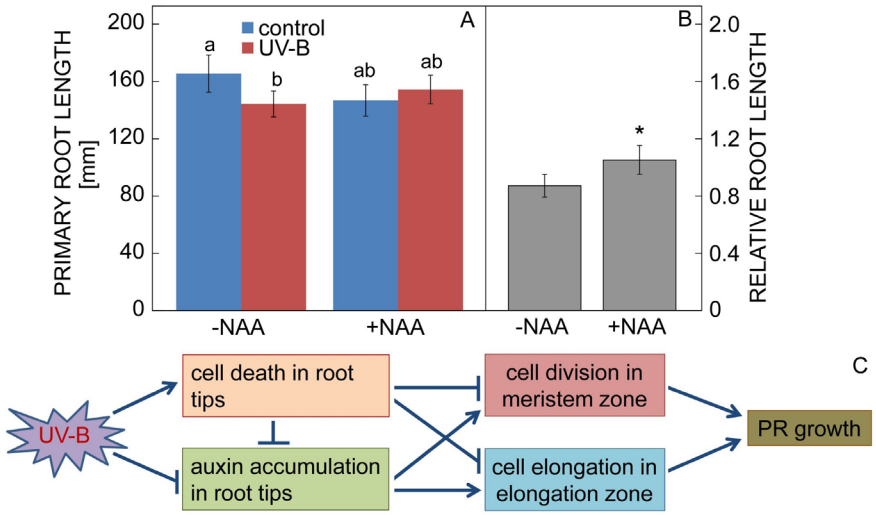

Fig. 4. Involvement of auxin in ultraviolet-B (UV-B)-repressed primary root (PR) growth. Primary root length (*A*) and relative root length (*B*) of UV-B-treated *Arabidopsis thaliana* seedlings with or without (10 nM) α-naphthylacetic acid (NAA) presented as relative to nonirradiated control values obtained using *Arabidopsis thaliana* seedlings. Means ± SEs, $n = 3$ (12 plants/treatment/repeat); *different letters* indicate significantly different values (Tukey's test, $P < 0.05$), *asterisks* indicate a significant difference from the control (Student's *t*-test, $P < 0.05$). *C* - a proposed model of UV-B radiation-mediated PR growth inhibition.

omicshare.com/tools/Home/Soft/gogsea) are identified (Q-value ≤ 0.001) (Fig. 1 Suppl., Table 3 Suppl.). Under UV-B radiation, the *GO* categories that are related to the photosynthesis and ion transport are markedly downregulated in cluster 1 (C1) and C2. By contrast, *GO* categories that are related to the response to hypoxia whose expression are upregulated after 2 h of UV-B radiation were specifically enriched in C3. These data implied that UV-B radiation modulates root responses to hypoxia stress and need to be elucidated further.

We then analyzed the DEGs involved in the biochemical or physiological processes using *MapMan* (http://mapman.gabipd.org). We found that the genes involved in the biosynthesis and metabolism of cell wall, lipids, glucosinolates, and terpenoids are universally downregulated in UV-B-irradiated plants (Figs. 2 Suppl., 3 Suppl., Table 4 Suppl.) indicating that UV-B radiation reprogrammed carbon metabolism and secondary metabolism in plants. Cell wall metabolism plays critical roles in modulating root growth (Keller and Lamb 1989, Showalter 1993, Hall and Cannon 2002). The cell elongation rate is closely related to the biosynthesis and degradation of the structural constituents of cell wall (Dexter 1987, Keller and Lamb 1989). In addition to cell wall metabolism, a lot of genes involved in the biosynthesis of wax, cutin, and suberin that are categorized into 'lipid metabolism' also play important roles in regulating root system architecture, such as *eceriferums* (*CERs*), *glycerol-3-phosphate acyltransferases* (*GPATs*), *3-ketoacyl-CoA synthases* (*KCSs*), *etc*. (Table 4 Suppl.). Barberon *et al.* (2016) found that the suberization of the roots regulates the plasticity of root endodermis. Berhin *et al.* (2019) found that the root cap cuticle also contributes to root growth. These data suggested that UV-B-mediated metabolism reprogramming affects root system growth and development.

Second, from the metabolism overview and photosynthesis pathways, we noted that a number of genes involved in light reaction, Calvin cycle, photorespiration, and tetrapyrrole biosynthesis are downregulated by UV-B radiation, by contrast, genes involved in mitochondrial electron transport are markedly upregulated in the roots of UV-B-radiated plants (Figs. 2 Suppl., 4 Suppl.). Tetrapyrroles serve as cofactors for essential proteins involved in photosynthesis and respiration. Tetrapyrrolic metabolites also act as signaling molecules that coordinate cell organelle functions (Zhang *et al.* 2014). These data indicated that UV-B radiation repressed photosynthesis, whereas it promoted mitochondrial respiration. The complexes I and III of mitochondrial electronic transport chain are one of the major sites for ROS production in plants. UV-B radiation induces ROS accumulation in plants (Ulm *et al.* 2004, Lytvyn *et al.* 2010, Nawkar *et al.* 2013). As an adaptive feedback regulation mechanism, the upregulation of mitochondrial electron transport-related gene expression might maintain redox homeostasis in plant cells.

UV-B radiation resulted in a significant reduction of photosynthesis-related gene expression in roots, a non-photosynthetic organ. Several studies have demonstrated that the changes in photosynthetic gene expression in roots affect root physiology (Kobayashi *et al.* 2013, Kang *et al.* 2014). Suppression of photosynthetic gene expression in roots is an adaptation regulation mechanism for plant growth under inorganic phosphate deficiency (Kang *et al.* 2014). However, the biological mechanisms of suppression of photosynthetic gene expression in roots remain unclear. The elevated expression of photosynthesis-related genes in roots increases CO_2 fixation and improves carbon utilization in plants (Kobayashi *et al.* 2013). In support of this result, we found that many of genes involved in Calvin cycle and the biosynthesis and catabolism of starch and

sucrose were generally downregulated in UV-B-treated roots. However, how the photosynthesis-related gene expression in roots regulates carbon utilization requires further elucidation.

Conclusions

Previous studies have shown that UV-B induced root bending (Wan *et al.* 2018a), however, the molecular mechanisms underlying UV-B-modulated root growth have not been investigated. In this study, we found that UV-B inhibited PR growth by inducing cell death in roots through the production of ROS and NO, and thereby decreasing root cell division and cell elongation. UV-B radiation-induced cell death also led to the destruction of root cell structure and subsequent distortion of auxin flow and reduced auxin accumulation in root tips, and thereby inhibiting PR growth. We also revealed that UV-B radiation-reprogrammed metabolism in *Arabidopsis* roots was associated with the reduction in PR growth. These findings are helpful for our understanding on UV-B-modulated plant growth through regulation of metabolism pathways in plants.

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