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Exposure to Low UV-B Dose Induces DNA Double-Strand Breaks Mediated Onset of Endoreduplication in *Vigna radiata* (L.) R. Wilczek Seedlings

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Multiple lines of evidence indicate that solar UV-B light acts as an important environmental signal in plants, regulating various cellular and metabolic activities, gene expression, growth and development. Here, we show that low levels of UV-B (4.0 kJ m^{-2}) significantly influence plant response during early seedling development in the tropical legume crop *Vigna radiata* (L.) R. Wilczek. Exposure to low doses of UV-B showed relatively less growth inhibition yet remarkably enhanced lateral root formation in seedlings. Both low and high (8.0 kJ m^{-2}) doses of UV-B treatment induced DNA double-strand breaks and activated the SOG1-related ATM-ATR-mediated DNA damage response pathway. These effects led to G2-M-phase arrest with a compromised expression of the key cell cycle regulators, including CDKB1;1, CDKB2;1 and CYCB1;1, respectively. However, along with these effects, imbibitional exposure of seeds to a low UV-B dose resulted in enhanced accumulation of FZR1/CCS52A, E2Fa and WEE1 kinase and prominent induction of endoreduplication in 7-day-old seedlings. Low dose of UV-B mediated phenotypical responses, while the onset of endoreduplication appeared to be regulated at least in part via UV-B induced reactive oxygen species accumulation. Transcriptome analyses further revealed a network of co-regulated genes associated with DNA repair, cell cycle regulation and oxidative stress response pathways that are activated upon exposure to low doses of UV-B.

Keywords: DNA double-strand breaks • DPI • Endoreduplication • ROS • UV-B • *Vigna radiata*

Introduction

Plants, being sessile in nature and with their obligatory dependence on sunlight for photosynthesis, cannot escape the damaging effects of solar UV-B light. Therefore, they have developed a sophisticated and highly regulated balance between optimal light capture and UV-B protection. Some plant species escape UV-B exposure by limiting their life span to the season or places where they perceive only low levels of UV-B, while others, including crops, grow during the summer months and experience a high incidence of solar UV-B light (Ulm and Jenkins 2015). In tropical climates, plants receive sunlight for longer duration, and the effects of UV-B radiation are greater under such conditions. Early studies in tropical crops, including *Oryza sativa* (Teramura and Sullivan 1994), *Vigna mungo* (Fukumoto and Mazza 2000), *Vigna radiata* (Amudha et al. 2005), *Glycine max* (Guruprasad et al. 2008) and *Triticum aestivum* (Kataria and Guruprasad 2014) have shown compromised growth and yield in response to exposure to ambient UV-B light. More recent studies in cucumber (*Cucumis sativus* L. cv. 'Hi Jack') have correlated the growth retardation effect with the regulatory mechanism associated with the acclimation processes of UV radiation (Qian et al. 2021). Other studies mainly in *Arabidopsis* and some other species indicated that two major mechanisms of UV-B mediated responses, including the accumulation of UV-B absorbing compounds and the DNA damage response, actually vary among various plant species. These factors eventually generate variations in UV-B response in plants (Hidema et al. 2007, Xu and Sullivan 2010). However, the variations in UV-B response in nonmodel crops and other field plant communities remain largely unexplored.

UV-B represents an energy-rich intrinsic component of solar radiation. It affects plant growth and development through diverse physiological and metabolic processes (Jenkins 2009). At high fluence rate, UV-B causes damage to the photosynthetic components (Correia et al. 1998), DNA (Schmitz-Hoerner and Weissenböck 2003), proteins and membranes (Bornman and Teramura 1993). The UV-B-induced photodimers (Taylor 2006), primarily cyclobutane pyrimidine dimers (CPDs) and pyrimidine-6,4-pyrimidinone dimers (6,4PPs) (Gill et al. 2015), create distortions in the DNA double-helical structure and eventually block transcription and replication (Britt 2004, Manova and Gruszka 2015). Furthermore, the inefficient repair

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ORIGINAL ARTICLE

The Negative Impact of Prolonged Desiccation on the Recovery of *Selaginella bryopteris*: Insights Into Autophagy and Cellular Protection Strategies

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Keywords: autophagy | cell death | cellular protection | desiccation tolerance | metabolomics | protein homeostasis | ROS | *Selaginella bryopteris* | transcriptome | WGCNA

ABSTRACT

Desiccation tolerance is a complex biological phenomenon that allows certain plants to survive extreme dehydration and revive upon rehydration. Although significant progress has been made in understanding the physiological and molecular mechanisms involved in desiccation tolerance, recovery mechanisms after prolonged desiccation periods are enigmatic. Combining physiological, biochemical, transcriptomic and metabolomic approaches, we investigated the role of prolonged desiccation on recovery of *Selaginella bryopteris*. Prolonged desiccation causes a decline in the antioxidant system, leading to accumulation of ROS that hinder recovery by inducing cellular damage. Transcriptome and WGCNA analysis revealed the significance of protective proteins, alternative respiration and protein homeostasis in cellular protection and recovery after short and long-term desiccation. Metabolomic analysis exhibited an increased accumulation of antioxidant compounds, which can be substituted for antioxidant enzymes to maintain cellular protection during prolonged desiccation. The significant role of autophagy and autophagic components was evaluated by H_2O_2 treatment and phylogenetic analysis of ATG4 and ATG8, which unveiled their substantial role in desiccation tolerance and remarkable conservation of the autophagy-related genes across plant species. Our data demonstrated that prolonged desiccation leads to ROS-induced cell death by extensive autophagy due to enormous loss of protective proteins, antioxidant enzymes and energy resources during desiccation.

1 | Introduction

Drought, a major threat to global food security, is considered a central environmental challenge for crop growth and productivity (Zhu 2002; Lobell, Schlenker, and Costa-Roberts 2011). Extreme drought damages plants by desiccating cells. Seeds and spores of most plants can withstand desiccation (Bewley 1979), while the vegetative tissues of most plants lack this feature (Dinakar and Bartels 2013). However, a limited group of plants, termed desiccation tolerant plants (hereafter DT plants), possess exceptional survival potential in the vegetative tissues against desiccation. DT plants are also known as 'resurrection plants' because of their ability to revive from a complete water loss or an air-dry state, upon re-watering. DT plants can survive dehydration by