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ORIGINAL ARTICLE

A Chloroplast-targeted S1 RNA-binding Domain Protein Plays a Role in Arabidopsis Response to Diverse Abiotic Stresses

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Abstract Although accumulating evidence points to the essential roles of nucleus-encoded chloroplast S1 domain-containing proteins (SDPs) in chloroplast RNA metabolism and plant development, functions of chloroplast SDPs in abiotic stress responses are largely unknown. In this study, we investigated the role of a SDP (At1g12800) in Arabidopsis response to diverse abiotic stresses. Analysis of the *sdp* knockout mutant and complementation lines demonstrated that loss of SDP function results in decreased survival rate of Arabidopsis under salt, heat, UV, or freezing stress, but not under dehydration stress or ABA. In consistent with a previous report demonstrating that SDP is involved in chloroplast rRNA processing, translation in chloroplasts was impaired in the *sdp* mutant. Expression of several nuclear genes involved in stress response and adaptation was altered in the *sdp* mutant subjected to different abiotic stresses, suggesting that modulation of chloroplast translation affects the expression of nuclear genes under abiotic stresses. These data reveal that chloroplast-localized SDP plays an important role in abiotic stress response by modulating chloroplast translation and the expression of nuclear genes possibly via unidentified plastid-to-nucleus signaling.

Keywords: Abiotic stress, *Arabidopsis thaliana*, chloroplast, RNA metabolism, S1 domain protein.

Introduction

A chloroplast is an essential organelle for photosynthesis and plant survival. A recent study has demonstrated that photosynthesis is a physiological process responding to abiotic stresses (Biswal et al. 2011). Therefore, fine-tuned regulation of chloroplast biogenesis and photosynthesis is crucial for plant survival under adverse environmental conditions as well as under normal conditions. Many recent studies have shown that chloroplast biogenesis and function are regulated via posttranscriptional control of gene expression, including pre-mRNA processing, splicing of chloroplast introns, mRNA editing, translational control, and RNA decay (Nickelsen 2003; Marin-Navarro et al. 2007; del Campo 2009; Stern et al. 2010; Barkan 2011). The chloroplast genome encodes only 120-130 genes that are essential for chloroplast biogenesis and photosynthesis (Abdallah et al. 2000; Richly and Leister 2004). However, more than 3,000 proteins encoded by the nuclear genome are transported to the chloroplast and play important roles in organellar gene expression (Nott et al. 2006; Koussevitzky et al. 2007; Pesaresi et al. 2007). In particular, many RNA-binding proteins (RBPs), including RNA-recognition motif protein, RNA helicase, pentatricopeptide repeat protein, and S1 domain-containing protein (SDP), are transported to chloroplasts and are essential for chloroplast gene expression (Nickelsen 2003; Jacobs and Kück 2011; Barkan and Small 2014; Lee and Kang 2016; Nawaz and Kang 2017). As many nucleus-encoded proteins play essential roles for chloroplast gene expression, communications between the nucleus and chloroplasts through anterograde or retrograde signaling are crucial for the proper functions of both organelles (Nott et al. 2006; Pesaresi et al. 2007; Kakizaki et al. 2009; Terry and Smith 2013; Woodson et al. 2013; Chan et al. 2016; de Souza et al. 2017).

The S1 domain-containing protein is one of the nucleus-encoded chloroplast proteins. The structure and function of SDPs have first been demonstrated in *Escherichia coli,* which binds to RNAs (Draper et al. 1977) and is involved in translation and RNA decay (Aliprandi et al. 2008; Briani et

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al. 2008; Delvillani et al. 2011). In plants, the S1 domain is known as an RNA-binding module that plays a role in RNA degradation and polyadenylation, translation, and chloroplast gene expression in *Arabidopsis thaliana* and C4 plants (Chekanova et al. 2002; Yu et al. 2012; Bowman et al. 2013; Yu et al. 2018). A chloroplast-targeted ribosomal protein PSRP-7, which contains two S1 domains, functions in mRNA binding and translation control in *Chlamydomonas reinhardtii* (Yamaguchi et al. 2002; Beligni et al. 2004). A S1 domain-containing transcription-stimulating factor plays a role in the transcription of plastid genes and the biogenesis of *Nicotiana benthamiana* chloroplasts (Jeon et al. 2012). SRRP1, a chloroplast-localized protein harboring two S1 domains, was recently shown to play a role in cotyledon greening in ABA response by modulating the splicing of tRNA intron and rRNA processing in chloroplasts (Gu et al. 2015).

Although these previous studies emphasize the prominent roles of SDPs in chloroplast function and plant development, the roles of SDPs in stress responses are largely unknown. The Arabidopsis SDP (At1g12800) investigated in this study was previously shown to affect the processing of chloroplast rRNAs, chloroplast biogenesis, and photosynthesis, which is crucial for Arabidopsis growth under normal conditions (Han et al. 2015). In this study, we show that SDP is involved in Arabidopsis response to various abiotic stresses by modulating chloroplast translation and the expression of nuclear genes.

Results

SDP Affects the Response of Arabidopsis to Diverse Abiotic Stresses

To determine the role of SDP in abiotic stress responses, the

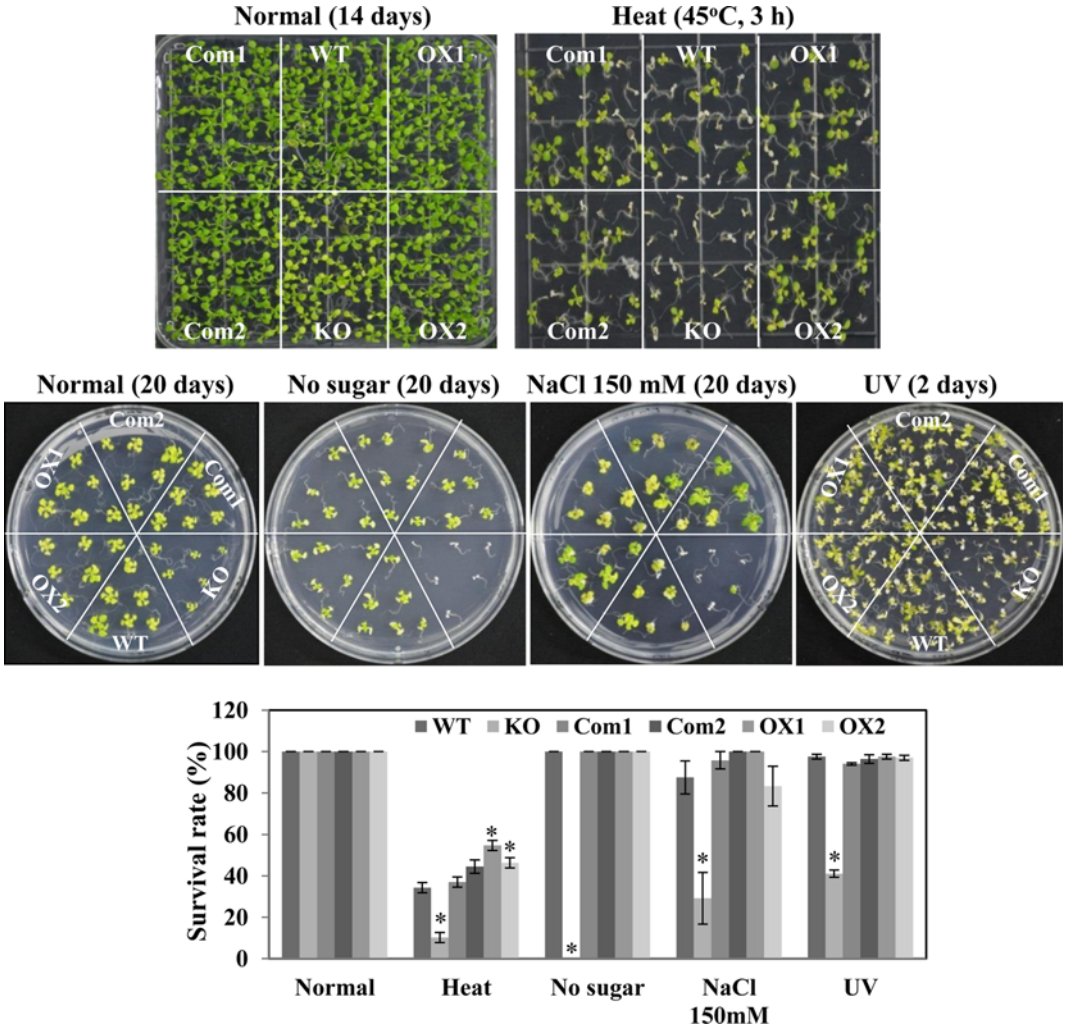

Fig. 1. SDP affects survival of Arabidopsis seedlings under various abiotic stresses. The wild-type (WT), *sdp* knockout mutant (KO), complementation lines (Com1 and Com2), and overexpression lines (OX1 and OX2) were grown on half-strength MS medium, subjected to heat stress (38°C pre-treatment for 2 h, 22°C for 2 h, and 45°C for 3 h), salt stress (150 mM NaCl), or UV stress, and the survival rate of seedlings was calculated at the indicated days. Data are the mean ± SE obtained from three biological replicates (n = 25 for heat stress, n = 20 for UV stress, and n = 6 for other stress), and asterisks above the columns indicate values that are statistically different from the WT values ($P \leq 0.05$).

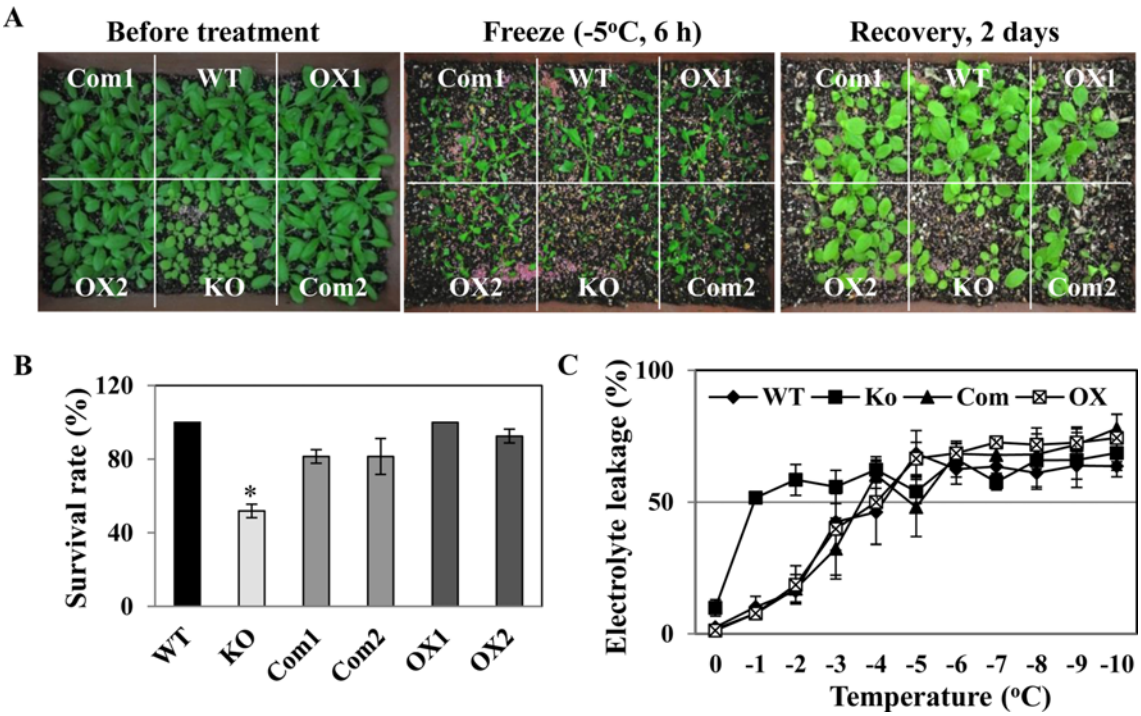

Fig. 2. SDP affects survival of Arabidopsis under freeze stress. (A) Photographs of 21-day-old the wild-type (WT), *sdp* knockout mutant (KO), complementation lines (Com1 and Com2), and overexpression lines (OX1 and OX2) before and after freeze stress treatment. (B) Survival rate and (C) electrolyte leakage of seedlings after freeze stress treatment. Data are the mean ± SE obtained from three biological replicates (n = 9), and asterisks above the columns indicate values that are statistically different from the WT values ($P \leq 0.05$).

growth of wild-type, loss-of-function *sdp* mutant, transgenic plants that overexpress SDP, and complementation lines was examined on MS medium or in soil upon various abiotic stress application. Because the seedling of the *sdp* mutant is smaller than that of wild type when grown under normal conditions (Fig. 1; Han et al. 2015), we evaluated the stress tolerance or sensitivity of the wild type and *sdp* mutant by measuring survival rates but not seedling growth upon each stress treatment. Notably, SDP affected differently the growth and survival of Arabidopsis under various abiotic stresses. When subjected to high temperature stress at 45°C for 3 h and subsequent recovery at normal temperatures, approximately 35% of the wild-type plants survived, whereas survival rates of the *sdp* mutant were approximately 10%. In comparison, the complementation lines and overexpression transgenic plants showed survival rates comparable with or a slightly higher than those of wild-type plants (Fig. 1; Fig. S1). When salt stress was imposed to the plants with 150 mM NaCl for 20 days, survival rates of wild-type plants were approximately 85%, whereas survival rates of the *sdp* mutant were approximately 25%, and the complementation and overexpression lines showed survival rates similar to those of wild-type plants (Fig. 1). When subjected to UV stress for 2 days, all of the wild-type, complementation lines, and overexpression transgenic plants survived, whereas only 40% of the *sdp* mutant survived (Fig. 1).

We next investigated the response of the wild-type and mutant plants to freeze stress (-5°C). Evidently, the *sdp* mutant displayed a much severe damage than the wild type under freeze stress (Fig. 2A). The survival rate of the *sdp* mutant decreased down to approximately 50% of the wild-type level (Fig. 2B), and the *sdp* leaves resulted in significantly higher electrolyte leakage than the wild-type and complementation line leaves upon freeze treatment (Fig. 2C). These results suggest a positive role of SDP in Arabidopsis tolerance against freeze stress. However, all genotypes showed a similar survival rate when subjected to dehydration stress or ABA (Fig. S2; Fig. S3). It is evident that SDP is involved in Arabidopsis response to heat, salt, UV, and freeze stress but not to dehydration stress and ABA.

Translation in Chloroplasts Is Impaired in the *sdp* Mutant

Given that SDP is localized in chloroplasts and impacts the processing of chloroplast rRNAs (Han et al. 2015), it is likely that SDP influences translation in chloroplasts. We tested this possibility by examining the response of the *sdp* mutant to spectinomycin that specifically inhibits translation in chloroplasts. Spectinomycine interrupts translation in bacteria by binding to the 30S subunit of the bacterial ribosome (Vazquez 1974) and is commonly used to analyze the translation efficiency in chloroplasts (Wang et al. 2016).

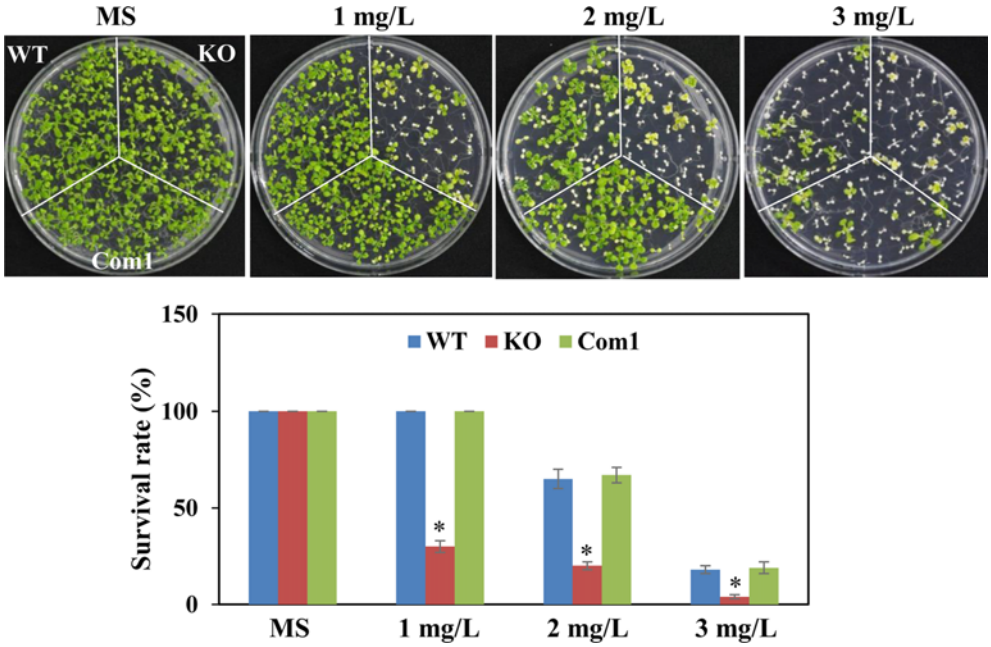

Fig. 3. SDP affects survival of Arabidopsis seedlings in the present of spectinomycin. The wild-type (WT), *sdp* knockout mutant (KO), and a complementation line (Com1) were grown on half-strength MS medium supplemented with different concentrations of spectinomycin, and survival rate of seedlings was calculated 14 days after germination. Data are the mean ± SE obtained from three biological replicates (n = 48), and asterisks above the columns indicate values that are statistically different from the WT values ($P \leq 0.05$).

When the seeds were sown, germinated, and further grown on MS medium supplemented with spectinomycin at concentrations of 1-3 mg L^{-1}, the *sdp* mutant exhibited yellowish leaves and survived significantly lower than wild-type plants (Fig. 3). By contrast, the complementation line maintained green leaves and survival rates similar to wild-type plants (Fig. 3). These results suggest that translation in chloroplasts is defective in the *sdp* mutant under normal growth conditions, which results in dysfunction of chloroplasts and yellowish leaves and retarded growth of the *sdp* mutant (Fig. 1; Han et al. 2015).

SDP Influences the Expression of Stress-Responsive Nuclear Genes

To get clues on how SDP affects Arabidopsis response to diverse abiotic stresses, expression levels of several stress-responsive genes, which are known to be involved in stress response or adaptation process, was analyzed in the wild type and *sdp* mutant plants subjected to different abiotic stresses. Interestingly, several heat stress-responsive genes were marginally up-regulated in the *sdp* mutant compared with wild type under heat stress. Up-regulated genes include heat shock transcription factor (HSF) *HsfA1a, HsfA2, HsfA7a, HsfB1* and *HsfB2a*, as well as heat shock protein (HSP) HSP90-*3, HSP90-5* and *HSP70B* (Fig. 4). However, transcript levels of other *Hsfs* and *HSPs*, including *HsfA3, HsfA6a, HsfA8, HsfA9, HsfB3, HsfB4, HSP90-1, HSP90-2, HSP90-4*

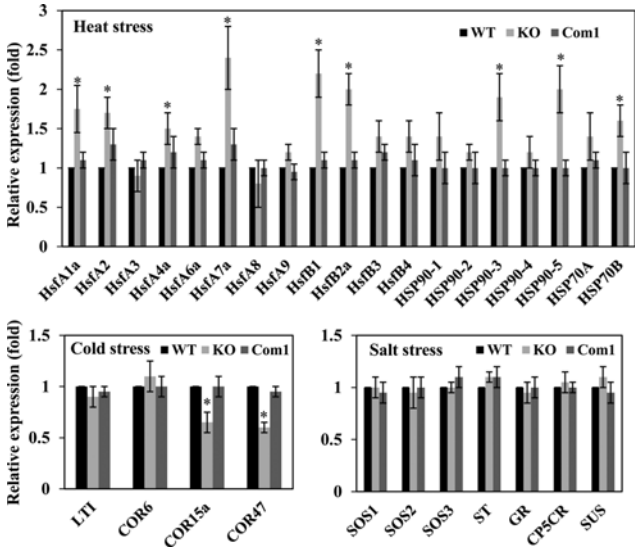

Fig. 4. Transcript levels of stress-responsive genes in the *sdp* mutant upon stress treatment. Total RNA was extracted from the wild-type (WT), *sdp* knockout mutant (KO), and a complementation line (Com1) subjected to heat, cold, or salt stress as described in Fig. 1 and 2, and relative expression levels of each gene between the mutant and wild type were determined by real-time RT-PCR. Data are the mean ± SE obtained from three biological replicates, and asterisks above the columns indicate values that are statistically different from the WT values ($P \leq 0.05$).

and *HSP70A*, were not altered in the *sdp* mutant compared with wild type (Fig. 4). When subjected to cold stress, the levels of cold stress-responsive genes such as *COR15a* and

COR47 were down-regulated, whereas expression levels of *LTI* and *COR6* were not changed in the *sdp* mutant compared with wild type (Fig. 4). Notably, transcript levels of the genes involved in salt stress response and adaptation, including *SOS1, SOS2, SOS3, ST, GR, CP5CR* and *SUS* were not altered in the *sdp* mutant compared with wild type (Fig. 4). These results suggest that malfunction of SDP directly affects translation of chloroplast transcripts and chloroplast biogenesis, which in turn indirectly influences the expression of a subset of nuclear genes during stress adaptation process.

Discussion

This study shows that the chloroplast SDP functions as an organellar component in Arabidopsis response to diverse abiotic stresses. The *sdp* mutant was sensitive to heat, salt, UV, cold, or freeze stress but not to dehydration stress or ABA (Fig. 1; Fig. 2; Fig. S1; Fig. S2; Fig. S3), suggesting that SDP affects positively Arabidopsis response to diverse stresses such as heat, salt, UV, cold, or freeze stress. Photosynthesis in chloroplasts is a physiological process responding to abiotic stresses (Biswal et al. 2011), and the biogenesis and photosynthetic activity of chloroplasts are important for plant survival under stress conditions as well as under normal conditions. Our previous report demonstrated that, as a chloroplast-transported ribosomal protein, SDP influences the processing of chloroplast rRNAs. Northern blotting and polysome loading analyses of chloroplast rRNAs revealed that the processing of chloroplast 16S, 23S, 4.5S, and 5S rRNAs is impaired in the *sdp* mutant (Han et al. 2015). Improper chloroplast rRNA processing in the *sdp* mutant was further supported by current data showing a much poorer growth of the *sdp* mutant than wild type upon spectinomycin application (Fig. 3), which is probably due to impairment of protein biosynthesis in chloroplasts. It remains to be determined whether levels of chloroplast proteins are altered in the *sdp* mutant. These results highlight that SDP is an essential component in rRNA processing and concomitant translation in chloroplasts, which influences photosynthetic activity and plant growth under both favorable and unfavorable conditions. The essential role of SDP in photosynthesis was clearly supported from the finding that the *sdp* mutant could not survive on sucrose-deficient medium (Fig. 1; Han et al. 2015). The importance of chloroplast RNA metabolism in stress response has been demonstrated in several previous studies; a DEAD-box RNA helicase AtRH3 (Gu et al. 2014), a S1 domain-containing protein (Gu et al. 2015), and a chloroplast RNA splicing and ribosome maturation protein CRM (Lee et al. 2014), which are involved in intron splicing or rRNA processing in chloroplasts, were shown to play as an important cellular factor in stress responses. Clearly, regulation of RNA metabolism in chloroplasts is an essential cellular process crucial for plant response to diverse abiotic stresses.

It is important to understand how SDP affects Arabidopsis response to diverse abiotic stresses. Our RT-PCR analyses showed that the levels of *COR15a* and *COR47* were down-regulated in the *sdp* mutant compared with wild type under cold stress (Fig. 4). Because COR15a and COR47 are known to be involved in cold tolerance in plants (Chinnusamy et al. 2007; Zhao et al. 2015), the results suggest that the cold-sensitive phenotype of the *sdp* mutant is due to, at least in part, lower expression levels of these cold stress-responsive genes. Interestingly, several heat shock transcription factors and heat shock proteins such as *HsfA1a, HsfA2, HsfA7a, HsfB1, HsfB2a, HSP90-3, HSP90-5* and *HSP70B*, whose expression is modulated by heat stress and are involved in heat stress response (von Koskull-Döring et al. 2007; Ohama et al. 2017), were marginally up-regulated in the *sdp* mutant upon heat treatment (Fig. 4). HsfA1s are master regulators in heat stress response and directly regulate the expression of many heat stress-responsive transcription factors, including HsfA2, HsfA7a, and HsfBs (Ohama et al. 2017). It is unclear at present how these HSFs and HSPs are up-regulated, although not significant, in the heat-sensitive *sdp* mutant under heat stress. It appears that SDP affects the expression of nuclear genes differently under cold or heat stress conditions. It remains to be determined the physiological relevance of the modulation of these nuclear genes during the stress response of the *sdp* mutant. In this regard, it would be interesting to probe how the chloroplast SDP influences nuclear gene expression. Accumulating data have suggested that communications between chloroplasts and the nucleus are essential for fine-tuned regulation of organellar gene expression (Mochizuki et al. 2001; Larkin et al. 2003; Kakizaki et al. 2009; Terry and Smith 2013; Woodson et al. 2013), during which diverse molecules or ions, including ROS, Ca^{2+}, and Mg-proto IX, serve as signal molecules for retrograde signaling (Surpin et al. 2002; Nott et al. 2006; Pesaresi et al. 2007; Singh et al. 2015; Maruta et al. 2016). It would be worthy to determine whether any chloroplast-derived signal molecules such as ROS, Ca^{2+}, or cellular metabolites function in nuclear gene regulation in the *sdp* mutant. Because chloroplast dysfunction can indirectly influence the levels of nuclear gene transcripts, it is also possible that changes in the levels of nuclear genes observed in the *sdp* mutant were due to the general disruption of chloroplast function. It remains to be determined whether the changes in the levels of nuclear genes in the *sdp* mutant resulted from direct plastid-to-nucleus signaling or indirect effects due to disruption of chloroplast function.

In conclusion, this study points to the importance of chloroplast SDP in plant response to different abiotic stresses

through the modulation of nuclear gene expression. Considering the essential roles of organellar RBPs in RNA metabolism and plant survival under harsh environmental conditions, functions of as-yet uncharacterized organellar RBPs need to be determined. In particular, it would be worthy to determine whether any molecules or compounds generated in chloroplasts are transmitted to the nucleus and regulate nuclear gene expression during stress response. More studies are needed to identify the potential plastid-to-nucleus signal molecules and to determine the importance of communications between chloroplasts and the nucleus during stress adaptation in plants.

Materials and Methods

Plant Materials and Growth Conditions

All *A. thaliana* used in this study was Col-0 ecotype. The *sdp* knockout mutant (SALK_032069), complementation lines that express full-length SDP in the *sdp* mutant background, and SDP-overexpressing transgenic plants were generated and described in the previous report (Han et al., 2015). Seeds were sown on Murashige and Skoog (MS) medium containing 1% sucrose or in pots containing a mixture of peat moss, vermiculite, and perlite (3:1:1, v/v/v). Seeds were stratified at 4°C for 3 days in the dark before transferring to a growth room maintained at 23±2°C and 65% relative humidity with 16 h light (approximately 100 mE m^{-2} sec^{-1}).

Abiotic Stress Treatment

Germination percentage and survival rates of the plants were evaluated on MS medium or in soil under various abiotic stresses as described previously with some modifications (Jung et al. 2013; Xu et al. 2014; Gu et al. 2014). For the analysis of salt or dehydration stress tolerance, seeds were sown on half-strength MS medium supplemented with 200 mM NaCl or 350 mM mannitol. For the analysis of heat stress tolerance, the seedlings grown for three days and three weeks on MS medium and in soil, respectively, were first acclimated at 38°C for 1 h and maintained at 22°C for 2 h. The seedlings were then subjected to heat stress at 45°C for 3-9 h, and survival rates were measured by incubating the seedlings further at normal temperatures for 3-10 days. For UV-B treatment, the seedlings were grown for seven days under normal conditions and then incubated in a growth chamber equipped with white light and G15T8E UV-B tubes (Sankyo Denki, Japan) at the intensity of 3.0 W m^{-2} for 2 days. Survival rates were measured by incubating the seedlings further at normal light conditions for 7 days. For spectinomycin treatment, seeds were sown and grown on MS medium supplemented with 1-3 mg L^{-1} of spectinomycin. For the analysis of freeze tolerance, the seedlings were grown for 3 weeks at normal temperatures, placed at 4°C for 1 day, and then treated freeze stress at -1°C for 1 day or at -5°C for 6 h. After freeze shock, plants were kept immediately at 4°C for 1 day in the dark, and survival rates were measured by incubating the seedlings further at normal temperatures for 3 days.

Electrolyte Leakage Measurement

Membrane damage of plants was evaluated by measuring electrolyte leakages of the leaves essentially as described previously (Kim et al. 2008). Briefly, leaves from 2-week-old seedlings were placed in 100 μL deionized water and kept at 0°C for 1 h. The temperature of the solution containing the leaves was decreased to -10°C at a rate of 1°C per 30 min. The sample was taken out at intervals, and the whole solution was mixed with 20 mL deionized water. The conductivity of the solution with the leaves was measured using a conductivity meter (Cole-Parmer Instrument Co., Vernon Hills, IL, USA). The samples were then autoclaved to measure the total conductivity of each sample. Percent electrolyte leakage was calculated as the ratio of conductivity before and after autoclaving the solution with the leaves.

RNA Extraction and Quantitative Real-time RT-PCR

Total RNA was isolated from frozen leaves using an RNA extraction kit (GeneAll Biotechnology Co. Ltd, Seoul, Korea), and any contaminating DNA was removed with RNase-free DNase I (Promega, Madison, WI, USA). The purity and concentration of the RNA was quantified using a NanoDrop spectrophotometer (Thermo Scientific, Wilmington, DE, USA). Quantitative real-time RT-PCR was conducted essentially as described previously (Choi et al. 2015; Kim et al. 2017). Briefly, 100 ng RNA was amplified using a Rotor-Gene Q cycling system (Qiagen, Valencia, CA, USA) and SYBR Green RT-PCR kit (Qiagen). The specific primers amplifying each gene were designed using a GeneRunner program (http://www.generunner.net) and are listed in Table S1.

Acknowledgements

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Author's Contributions

HK and SND designed the experiment. SND; SJP, and JHH performed the experiments and analyzed the data; HK and SND wrote the manuscript. All the authors agreed on the contents of the paper and post no conflicting interest.

Supporting Information

Fig. S1. SDP affects survival of Arabidopsis seedling under heat stress.
Fig. S2. SDP does not affect Arabidopsis seedling growth under dehydration stress.
Fig. S3. SDP does not affect Arabidopsis seedling growth in the presence of ABA.
Table S1. Gene-specific primer pairs used in RT-PCR experiments.

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