Received: 12 September 2022 | Revised: 3 December 2022 | Accepted: 6 December 2022

DOI: 10.1002/pld3.475

ORIGINAL RESEARCH

Plasticity of Arabidopsis rosette transcriptomes and photosynthetic responses in dynamic light conditions

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Funding information
National Science Foundation, Grant/Award Number: MCB-1515002

Abstract

With the high variability of natural growth environments, plants exhibit flexibility and resilience in regard to the strategies they employ to maintain overall fitness, including maximizing light use for photosynthesis, while simultaneously limiting light-associated damage. We measured distinct parameters of photosynthetic performance of *Arabidopsis thaliana* plants under dynamic light regimes. Plants were grown to maturity then subjected to the following 5-day (16 h light, 8 h dark) regime: Day 1 at constant light (CL) intensity during light period, representative of a common lab growth condition; Day 2 under sinusoidal variation in light intensity (SL) during the light period that is representative of changes occurring during a clear sunny day; Day 3 under fluctuating light (FL) intensity during the light period that simulates sudden changes that might occur with the movements of clouds in and out of the view of the sun; Day 4, repeat of CL; and Day 5, repeat of FL. We also examined the global transcriptome profile in these growth conditions based on obtaining RNA-sequencing (RNA-seq) data for whole plant rosettes. Our transcriptomic analyses indicated downregulation of photosystem I (PSI) and II (PSII) associated genes, which were correlated with elevated levels of photoinhibition as indicated by measurements of nonphotochemical quenching (NPQ), energy-dependent quenching (q_E), and inhibitory quenching (q_I) under both SL and FL conditions. Furthermore, our transcriptomic results indicated downregulation of tetrapyrrole biosynthesis associated genes, coupled with reduced levels of chlorophyll under both SL and FL compared with CL, as well as downregulation of photorespiration-associated genes under SL. We also noticed an enrichment of the stress response gene ontology (GO) terms for genes differentially regulated under FL when compared with SL. Collectively, our phenotypic and transcriptome analyses serve as useful resources for probing the underlying molecular mechanisms associated with plant acclimation to rapid light intensity changes in the natural environment.

KEYWORDS
fluctuating light, light acclimation, photoinhibition, photosynthesis, sinusoidal light, tetrapyrrole biosynthesis

1 | INTRODUCTION

Plants are sensitive to changes in the ambient environment, including light cues (e.g., predominant wavelengths, direction, or intensity). Given high variability of natural growth environments, the extent to which plants adapt to maximize light use for photosynthesis, while limiting light-associated damage, is critical and associated with overall plant fitness. Many studies assessing the acclimation response of plants to high light use constant high light conditions, whereas insights into natural mechanisms used by plants for persisting in nature may be advanced though analyses of plant growth and adaptation under dynamic conditions.

Light energy funneled into photosystem II (PSII) and photosystem I (PSI) fuels the primary reactions of photosynthesis, which generally move electrons from water at the donor side of PSII to ferredoxin and subsequently to NADPH at the acceptor side of PSI, through a series of electron carriers known as the photosynthetic electron transfer chain (pETC). Electron flux is coupled to the accumulation of protons in the thylakoid lumen forming a proton motive force (pmf) across the thylakoid membrane, which is used for driving ATP synthesis via the chloroplast ATP synthase. The ATP and NADPH generated by the "light reactions" provide chemical energy and reducing power primarily for photosynthetic CO_2 assimilation through the Calvin Benson Bassham Cycle, as well as for other metabolic pathways including photorespiration and nitrate reduction (Noctor & Foyer, 1998).

The light reactions involve formation of high energy redox intermediates capable of interacting with oxygen to form reactive oxygen species (ROS) such as singlet oxygen (Dogra & Kim, 2020) and superoxide (Allen et al., 2012), when the availability of absorbed light energy exceeds downstream demand for ATP and/or NADPH. For example, the formation of singlet oxygen is strongly linked to increased rates of PSII photoinhibition and is more likely to occur under fluctuating light (FL) (Davis et al., 2016). Accumulation of ROS intracellularly can lead to cellular damage, if unmitigated.

There are generally two different types of responses to dynamic light intensity. One set of responses is rapidly inducible, reversible and includes transient biological processes. Non-photochemical quenching (NPQ) encapsulates a number of mechanisms that actively quench, or appear to quench, absorbed light energy from PSII antenna. "Energy-dependent" quenching (q_E) depends on pH-dependent activation of violaxanthin de-epoxidase and protonation of the PsbS protein, resulting from the acidification of the lumen that accompanies formation of the light-induced ΔpH component of pmf (Ruban, 2016). "Inhibitory" quenching (q_I) is attributed to quenching by photoinhibited PSII centers, which accumulate when the rate of PSII photodamage exceeds the rate of repair (Murata et al., 2012; Tyystjärvi, 2013; Tyystjärvi et al., 2005). State transitions (q_T) can decrease PSII antenna size through reversible dissociation of antenna proteins from the complex. Triggered by the redox state of the plastoquinol pool, state transitions serve to rebalance the rates of energization between PSII and PSI (Taylor et al., 2019). More recently identified components of NPQ include q_Z (zeaxanthin-dependent quenching), which depends solely on the accumulation of zeaxanthin (Nilkens et al., 2010) and q_M, which is the intensity dependent movement or photorelocation of chloroplasts in response to blue light (Suetsugu & Wada, 2007).

The ΔpH component of *pmf* not only induces q_E but also decreases the rate of electron transfer to PSI through pH-dependent slowing of plastoquinol oxidation at the cytochrome b_6f complex as the lumen becomes more acidic (Nishio & Whitmarsh, 1993). Plants also initiate irreversible developmental responses to FL, including those that result in changes in the composition and accumulation of photosynthetic complexes and in the morphology of photosynthetic organs of plants (Murchie et al., 2005; Weston et al., 2000). One long-term acclimation to high light is a reduction in the formation of the semi-crystalline arrays of PSII complexes and PsbS protein accumulation (Kouřil et al., 2013). Leaf carotenoid content also increases under high-light and excess-light conditions (Bartoli et al., 2006; Demmig-Adams & Adams, 1992; Grace & Logan, 1996; Lichtenthaler, 2007; Matsubara et al., 2009). Other irreversible changes in response to variations in light intensity result in anatomical changes, such as formation of extra palisade cell layers in the primordia of young leaves as well as enlargement of palisade cell surfaces to alter CO_2 uptake by chloroplasts under high-light (Terashima et al., 2006).

Plant responses to FL differ from those to either steady high-light or low-light conditions, depending on the light fluctuation amplitude, frequency, and duration (Schneider et al., 2019). For example, Arabidopsis plants grown under a diurnal photoperiod (12 h dark/12 h light) with low-light (50 μmol photons m^{-2} s^{-1}) and short (20-s) pulses of high-light (650 or 1250 μmol photons m^{-2} s^{-1}) for 7 days exhibited reductions in PSII, chlorophyll levels, and leaf growth; simultaneously, NPQ and ROS levels were upregulated (Alter et al., 2012). By comparison, Arabidopsis plants grown in low-light (100 μmol photons m^{-2} s^{-1}) after fluctuating treatment between 100 and 475 or between 100 and 810 μmol photons m^{-2} s^{-1} every 15 min, 1 h, or 3 h over 7 days exhibited an increase in the oxygen evolution capacity of PSII, indicating photosynthetic acclimation over days (Yin & Johnson, 2000).

In the last two decades, researchers were able to use global transcript profiling to explore the molecular mechanisms of specific pathways controlling plant responses to dynamic light environments (Ding et al., 2019; Schneider et al., 2019). In a transcriptome profiling study to identify differentially expressed genes (DEGs) under FL at distinct developmental stages in young and mature leaves between morning and the end of the day, Schneider et al. (2019) analyzed the

Arabidopsis transcriptome after transferring 4–5 week old plants from constant light (CL) to FL (i.e., 20-s pulses of ~1000 μmol photons m^{-2} s^{-1} every 5 min during the CL period at ~75 μmol photons m^{-2} s^{-1}) for 3 days. They reported global reprogramming of gene expression under FL, including differential expression of genes involved in photosynthesis, photoprotection, photorespiration, pigment and prenylquinone content, and vitamin metabolism. Here, we describe global transcriptome profiling based on RNAseq data of mature, whole plant rosettes exposed to short-term (~24 h) dynamic light conditions including three light regimes, commonly used CL followed by dark conditions, sinusoidal light (SL) representing a normal sunny day, and FL representing a cloudy day, as well as recovery conditions in CL after SL and FL. Our results indicated global downregulation of PSI and PSII genes with some exceptions of specific genes, as well as overall downregulation in tetrapyrrole biosynthesis genes, under both SL and FL compared to CL. In addition, genes involved in photorespiration and the Calvin cycle were downregulated under SL. Furthermore, we detected a misregulation of some stress response related genes in FL when compared with SL. Taken together with measurements of photosynthetic parameters, these analyses indicate distinct plant responses to SL or FL, compared with growth of plants in CL.

2 | MATERIAL AND METHODS

2.1 | Plant materials and growth conditions

Columbia-0 (Col-0) ecotype seeds were used as wild type (WT) and were stratified for 4 days before germination under white light (~100 μmol m^{-2} s^{-1}) with a long-day photoperiod (16 h light and 8 h dark cycle) at 22°C. After 16–18 days of growth, plants were transferred to DEPI chambers (Cruz et al., 2016) for further analyses.

2.2 | Chlorophyll fluorescence and photosynthetic parameter measurements

Chlorophyll fluorescence imaging was performed using the DEPI system, as previously described (Cruz et al., 2016). Plants were treated with three different light regimes for 5 days (R1–R5) under a 16 h light and 8 h dark cycle. Under the first light regime (R1), the plants were grown at CL intensity of 100 μmol m^{-2} s^{-1} during the light period. For the second light regime (R2), plants were treated with SL with a maximum light intensity of 500 μmol m^{-2} s^{-1} in the light phase. For the third light regime (R3), plants were grown under fluctuating sinusoidal light (FL) that layered an 8-min fluctuation of light intensity of 2000 μmol m^{-2} s^{-1} every 30 min over a sinusoidal pattern that peaked at a maximum intensity of 1000 μmol m^{-2} s^{-1}. For the fourth (R4) and fifth (R5) regimes, additional R1 and R3 treatments were reapplied, respectively. Image data were processed using Visual Phenomics software developed in-house, as described by Cruz et al. (2016), to yield images of F_0, F_M, F_S, F_M', and F_M" and subsequently to calculate values for ϕ_{II}, NPQ, q_E, and q_I (Baker & Oxborough, 2004). Heat maps of the photosynthetic parameters were generated using the OLIVER software package (https://caapp-msu.bitbucket.io/projects/oliver/) developed in-house using Eclipse IDE (https://www.eclipse.org/).

2.3 | RNA isolation and library preparation

Total RNA was extracted from quadruplicates of whole rosettes grown in the DEPI system at midday of R1, R2, and R3 using the OMEGA E.Z.N.A Plant RNA kit (catalog no. R6827) according to the manufacturer's protocol. Respective mRNA libraries were prepared with an Illumina TruSeq Stranded mRNA Library Preparation Kit (Cat. No. 20020595) using a Perkin Elmer Sciclone G3 robot following manufacturer's recommendations. Completed libraries were assessed for quality and quantified using a combination of Qubit dsDNA HS and Advanced Analytical Fragment Analyzer High Sensitivity DNA NGS assays. cDNA Libraries were quantified using the Kapa Biosystems Illumina Library Quantification qPCR kit. Each pool was loaded onto one lane of an Illumina HiSeq 4000 flow cell and sequenced in a 1 × 50bp single read format using HiSeq SBS reagents. Base calling was done by Illumina Real Time Analysis (RTA) v2.7.7, and output of RTA was demultiplexed and converted to FastQ format with Illumina Bcl2fastq v2.19.1.

2.4 | RNAseq data analysis

An initial quality check of the RNA reads was performed using FastQC (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). Trimmomatic v0.32 (Bolger et al., 2014) was used to filter the RNA reads to remove adaptors and low-quality reads. A sliding window method was used to scan the reads with 4-base wide and cut when the base quality was below a threshold of 2. The minimum read length cutoff was 36 bp. Data quality was explored after filtering with FastQC.

STAR/2.6.0c (Spliced Transcripts Alignment to a Reference, Dobin et al., 2013) was used to map the RNAseq reads to Tair10 genome with the default settings of the twopassMode Basic option with intron size 21–6000 nt. In all samples, >90% of the RNAseq reads were mapped to the reference genome. The number of sequenced reads, filtered reads, and mapping information are presented in Table S1.

2.5 | Differential expression and clustering analyses

The HTseq-count function in HTseq (High-Throughput sequencing) v0.6.1 (Anders et al., 2015) was used in the default mode and stranded = yes for generating read counts. HTseq-count output was fed into DESeq2 (Love et al., 2014) for differential expression analysis using the standard steps represented in DESeq function

(Love et al., 2017). A gene was considered differentially expressed if the adjusted p value < .05 and the log fold change > 1 and had a transcript per million (TPM) > 1 in at least one condition. The p value was adjusted with a q-value false discovery rate (FDR) (Benjamini & Hochberg, 1995). DEGs from all comparisons among R1, R2, and R3 were categorized into 6 gene sets: Set 1 included upregulated genes under SL and FL, Set 2 included downregulated genes under SL and FL, Set 3 represented upregulated genes under SL only, Set 4 included downregulated genes under SL only, Set 5 represented upregulated genes under FL only, and Set 6 included down-regulated genes under FL only (Data Set S1).

2.6 | Gene ontology (GO) enrichment analysis

GO analyses were conducted by Panther classification system using the PANTHER Enrichment analysis (Released 20200728), with annotation version GO Ontology database (10.5281/zenodo.4033054) against GO biological process complete annotation data set. The results were statistically analyzed using Fisher's Exact test, and for correction, we used the calculation of FDR.

3 | RESULTS

3.1 | Photosynthetic measurements under dynamic light treatments

To investigate possible global transcriptome differences in response to dynamic light environments, we used the DEPI system (Cruz et al., 2016) to grow Arabidopsis in simulated natural light environments. We measured PSII quantum efficiency (ϕ_{II}) and dissipative NPQ of absorbed light energy, including additional components of NPQ including the more rapidly relaxing component q_E and more slowly relaxing q_I, which is associated with the photoinhibition of PSII. In general, the photosynthetic measurements indicated that ϕ_{II} decreases with increasing light intensity during R2 (SL) and R3 (FL). This behavior is hysteretic (where ϕ_{II} values collected at the end of the day tend to be lower than values collected earlier in the day at a matching intensity), which implies that R2 and R3 lead to net accumulation of photodamage. This assumption is supported by the generally lower values for ϕ_{II} under CL observed after dynamic light treatments (R4) relative to the control day (R1). However, the higher values for ϕ_{II} during R5 compared with corresponding time points during R3 are consistent with an acclimation response allowing photosynthetic electron flux to operate at higher efficiency under FL (Kono & Terashima, 2014).

In a corresponding manner, NPQ, q_E, and q_I levels increased with increased light intensity during R2 and R3, with similar hysteretic behavior (but with quenching higher at the end of the day relative to the beginning). More notably, the higher q_I observed during R3 and the beginning of R4 further support the idea that residual photodamage accumulates over R2 (SL) and R3 (FL) (Figure 1). As a first approach for identifying components potentially involved in acclimation of photosynthesis in response to SL and FL, plants grown under identical conditions as those that were used for photosynthetic measurements were used for mRNA extraction and analyses of DEGs under CL, SL, and FL conditions. We specifically discuss DEGs that may be associated with the observed changes in photosynthetic parameters in response to growth of plants under dynamic conditions, noting that our FL conditions sequentially follow the SL exposure.

3.2 | Identification of DEGs

We used CL growth (R1) as a baseline for the level of gene expression in order to identify effects of the SL growth (R2) and our FL growth (R3) treatments (Figure 2a). Our results indicated a total of 2336 DEGs under SL, including 1433 upregulated and 903 downregulated genes. By comparison, we identified a total of 1761 DEGs in response to FL, including 1007 upregulated and 754 downregulated genes. There were 1212 genes common to SL and FL conditions (Figure 2b).

We categorized the DEGs into seven categories: Set 1 included 689 upregulated DEGs under SL and FL, Set 2 included 522 downregulated DEGs under SL and FL, Set 3 included 744 upregulated DEGs under SL only, Set 4 included 380 downregulated DEGs under SL only, Set 5 included 317 upregulated DEGs under FL only, Set 6 included 232 downregulated genes under FL only, and Set 7 included one hypothetical protein-encoding gene (*AT5G60260*) that was downregulated under SL and upregulated under FL (Figure 2b).

3.3 | GO enrichment analyses and classification of DEGs

Following the identification and categorization of DEGs, we performed GO enrichment analyses. The GO analyses identified a list of enriched pathways as indicated in Data Set S2. In assessing enrichments in particular growth conditions, 122 GO terms were significantly enriched under SL, and 86 were enriched under FL. There were 66 GO terms enriched under both SL and FL; thus, 57 GO terms were enriched only under SL, and 20 GO terms were significantly enriched only under FL. Among the pathways enriched under SL and FL, three photosynthesis and light harvesting reaction pathways were significantly downregulated under both SL and FL conditions. The most enriched biological process based on GO terms according to the TAIR10 slim GO list was determined for SL (Figure 3a) and FL (Figure 3b). GO-enrichment analysis indicated that GO terms that include response to abiotic stimulus, response to radiation, response to light stimulus, and photosynthesis were significantly enriched under SL and FL. However, GO terms for protein import into mitochondrial, protein targeting to mitochondria, protein localization to the mitochondrion, and mitochondrial transport were enriched under SL only. By comparison, GO terms for the response to oxidative stress, response to heat, and generation of precursor metabolites and energy were only enriched under FL.

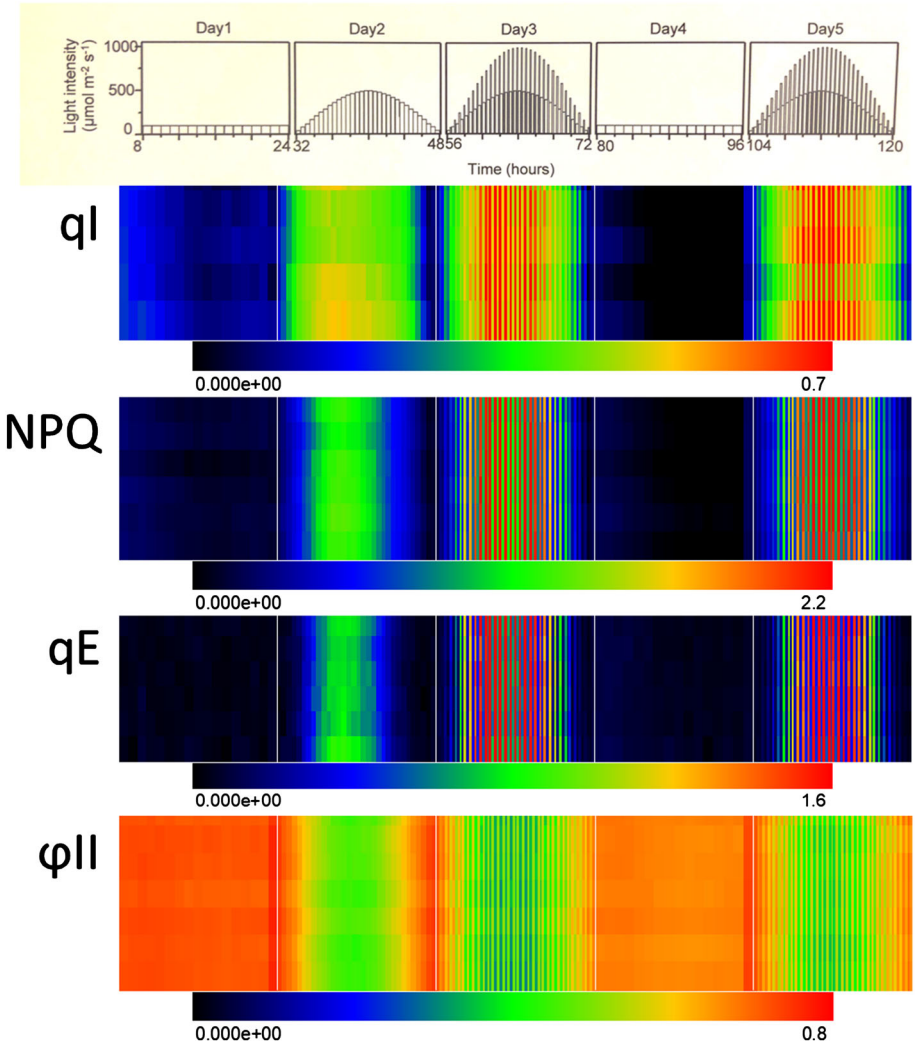

FIGURE 1 Heat maps of averaged data for photosynthetic parameters over the course of a 5-day DEPI chamber experiment. Shown are data for the q_I response or the onset of photoinhibition or chloroplast movements by the slow relaxation of non-photochemical quenching (NPQ); NPQ, or the dissipative non-photochemical quenching of absorbed light energy as heat; the qE response, or the measurement of the activation of the photoprotective mechanisms; and ϕ_{II}, or photosystem II (PSII) quantum efficiency. Each row in the heatmap represents one plant. Intensity settings are shown below the heat maps with color scaling showing the range in values from 0 (low) to 0.7 for q_I, 2.2 for NPQ, 1.6 for q_E and 0.8 for ϕ_{II}. $n = 26$ plants.

3.4 | Transcriptome changes in response to SL or FL light indicate plant resilience to stress

3.4.1 | Effect of changes in light regime on the photosynthetic and light reaction-related transcripts

The light conditions of any natural environment are responsible for major shifts in a plant's global transcriptome to ensure optimal plant survival. The transcriptome data and GO analyses indicated significant downregulation of genes encoding eight PSI and three PSII related proteins, as well as the electron transport protein plastocyanin 1 (PETE1) (Pesaresi et al., 2009) indicating a possible decrease in electron flux capacity (Data Set S3). Prior analyses demonstrated a decrease of PSI-related proteins in proteome analyses with Arabidopsis (Chen et al., 2022). In addition, genes that encode photosynthesis antenna proteins including light-harvesting chlorophyll protein complexes (LHCs) are mostly downregulated in SL and FL conditions indicating a decrease in light absorption compared to the CL condition (Figure 4); this decrease could explain the increased ϕ_{II} levels and decreased NPQ, q_I, and q_E. Only LHCB7 is overexpressed in both SL and FL (Figure 4b). Of note, *lhcb7* mutants show decreased light-saturated photosynthesis rates and diminished irradiance threshold for the activation of NPQ (Peterson & Schultes, 2014), and *LHCB7* was upregulated in prior analyses of leaves in FL (Schneider et al., 2019). Furthermore, under FL condition, the gene encoding the PSII core protein Psb28 is significantly upregulated (Data Set S2, Figure 4a). This specific protein plays a role in the recovery of PSII at high temperatures in the cyanobacterium *Synechocystis* (Sakata et al., 2013), although a role for Psb28 in plants remains to be definitively confirmed. *PSB28* is known to be highly expressed in green leaves of Arabidopsis (Winter et al., 2007), as well as regulated by phytochrome signaling via phytochrome-interacting factor 3 (PIF3) (Al-Sady et al., 2008; Monte et al., 2007). *PSB28* also is induced by high light in rice (Jung et al., 2008). The observed upregulation of *PSB28* in FL may indicate an organismal attempt to facilitate the repair of PSII under these conditions.

Among genes that are most upregulated under SL and FL conditions is *GLUCOSE-6-IPHOSPHATE/PHOSPHATE TRANSLOCATOR 2* (*GPT2*) (Data Set S1), which encodes a protein that regulates the dynamic acclimation of photosynthetic capacity in response to high light (Athanasiou et al., 2010). GPT2 is responsible for transferring glucose 6-phosphate between plastid and cytosol (Niewiadomski

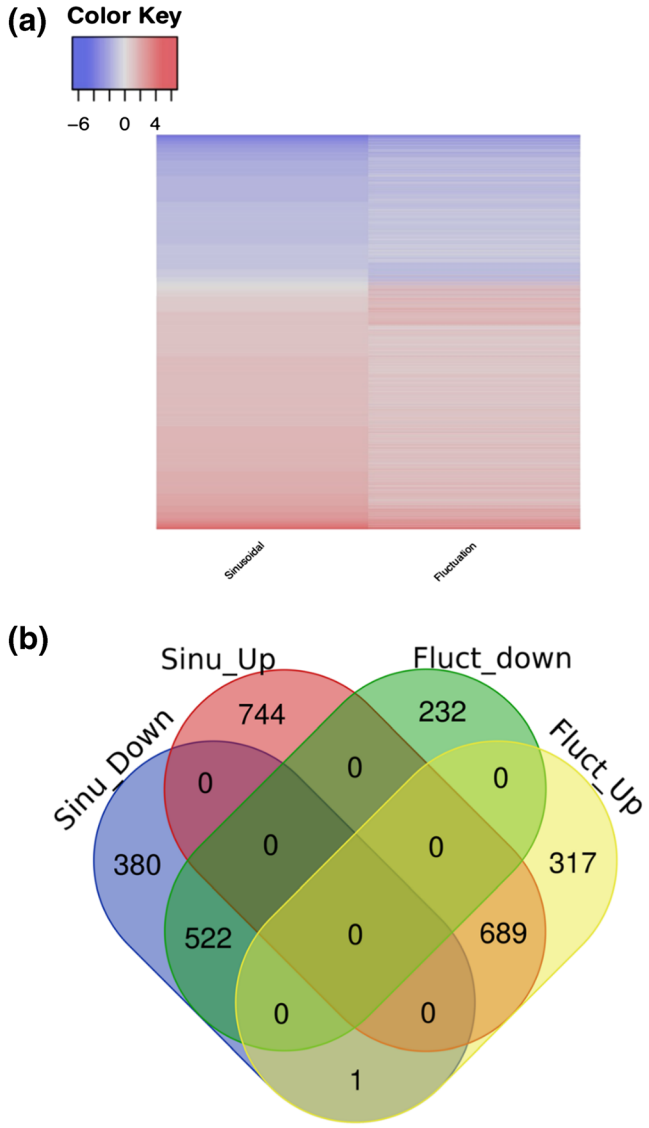

FIGURE 2 Comparison of transcriptomic responses in *Arabidopsis thaliana* rosettes under sinusoidal light (SL) and fluctuating light (FL) conditions. (a) Heat map highlighting the comparative transcriptomic responses in SL and FL with a gene considered differentially expressed if the adjusted *p* value < .05 and the log fold change > 1, and there was a transcript per million (TPM) > 1 in at least one condition. Colors and scale represent the $\log^2$ fold change. (b) Venn diagram illustrating the overlaps of differentially expressed (DE) genes under SL ad FL conditions

et al., 2005). Previously, Kunz et al. (2010) reported that *GPT2* expression positively correlates with decreased carbon metabolism during the light–dark cycle. Also, an increase in photosynthesis due to an increase in light irradiance leads to increased *GPT2* transcript levels (Athanasiou et al., 2010; Weise et al., 2019). We observed an increase in *GPT2* mRNA levels at high light conditions in both SL and FL. However, the ϕ_{II} photosynthetic measurement was decreased. This distinction may be due to the high light intensity level in our experiment that was higher than those used in prior experiments (Athanasiou et al., 2010; Weise et al., 2019). The upregulation of *GPT2* under SL and FL in our experiments may indicate a cellular response of attempting to adjust photosynthetic levels in dynamic conditions.

EXORDIUM-LIKE1 (*EXL1*) was also highly upregulated under both SL and FL conditions (Data Set S1). *EXL1* was previously reported to be upregulated under extended night, sugar starvation, and anoxia stress, all conditions that result in low carbon availability, suggesting that responses to carbon and light availability are controlled by EXL1 (Schröder et al., 2011).

High light intensity stimulates anthocyanin production in many plant species (Maier & Hoecker, 2015). These pigments assist in the photoprotection process in Arabidopsis leaves by decreasing the capacity for light capture, which increases ϕ_{II} and decreases NPQ (Gould et al., 2018). Our results indicated upregulation of most of the anthocyanin biosynthesis related genes under both SL and FL (Data Set S4).

We noticed a strong upregulation of the *PRODUCTION OF ANTHOCYANIN PIGMENT 1 & 2* (*PAP1* and *PAP2*) genes under SL and FL (Data Set S4 and Figure S2). *PAP1* has previously been reported to be positively regulated by HY5, as *PAP1* transcript levels were reduced under far-red and blue light conditions in *hy5* mutant lines (Das et al., 2011; Shin et al., 2013). Cominelli et al. (2008) reported an increased accumulation of anthocyanins in *PAP1* and *PAP2* overexpressed Arabidopsis lines. Our results suggest that increased *HY5* transcript levels may be correlated with upregulation of *PAP1* level, which could lead to elevated anthocyanin biosynthesis under SL and FL.

3.4.2 | Effect of changes in light regime on photoreceptor-related transcripts

Genes encoding some of the major photoreceptors are misregulated with a change of light intensity (Data Set S2). Our results indicated downregulation of *PHYA* under SL, with a slight decrease under FL as well. By contrast, *PHYB* was upregulated in response to FL and to a lesser degree under SL. PhyB is known to regulate photosynthetic processes (Kreslavski et al., 2015; Rao et al., 2011; Schittenhelm et al., 2004; Thiele et al., 1999). Organismal changes induced by *PHYB* upregulation could include increasing sink capacity and altering leaf morphology, which, in turn, could explain some of the observed effects on ϕ_{II} and quenching.

In Arabidopsis plants, phyB activity results in increased chlorophyll and carotenoid levels, as well as smaller but thicker leaves, increased stomatal density, and higher stomatal conductance that would increase CO_2 uptake and availability. In regard to the latter, an increase in CO_2 assimilatory capacity increases ϕ_{II} and decreases feedback regulation of NPQ (Talbott et al., 2003) and supports higher photosynthetic rates (Boccalandro et al., 2009; González et al., 2012). Similar results were observed when the Arabidopsis *PHYB* gene was introduced into potato plants (Kreslavski et al., 2015; Schittenhelm et al., 2004; Thiele et al., 1999). Transgenic *PHYB* potato lines also exhibited higher photoinhibition resistance than WT (Kreslavski

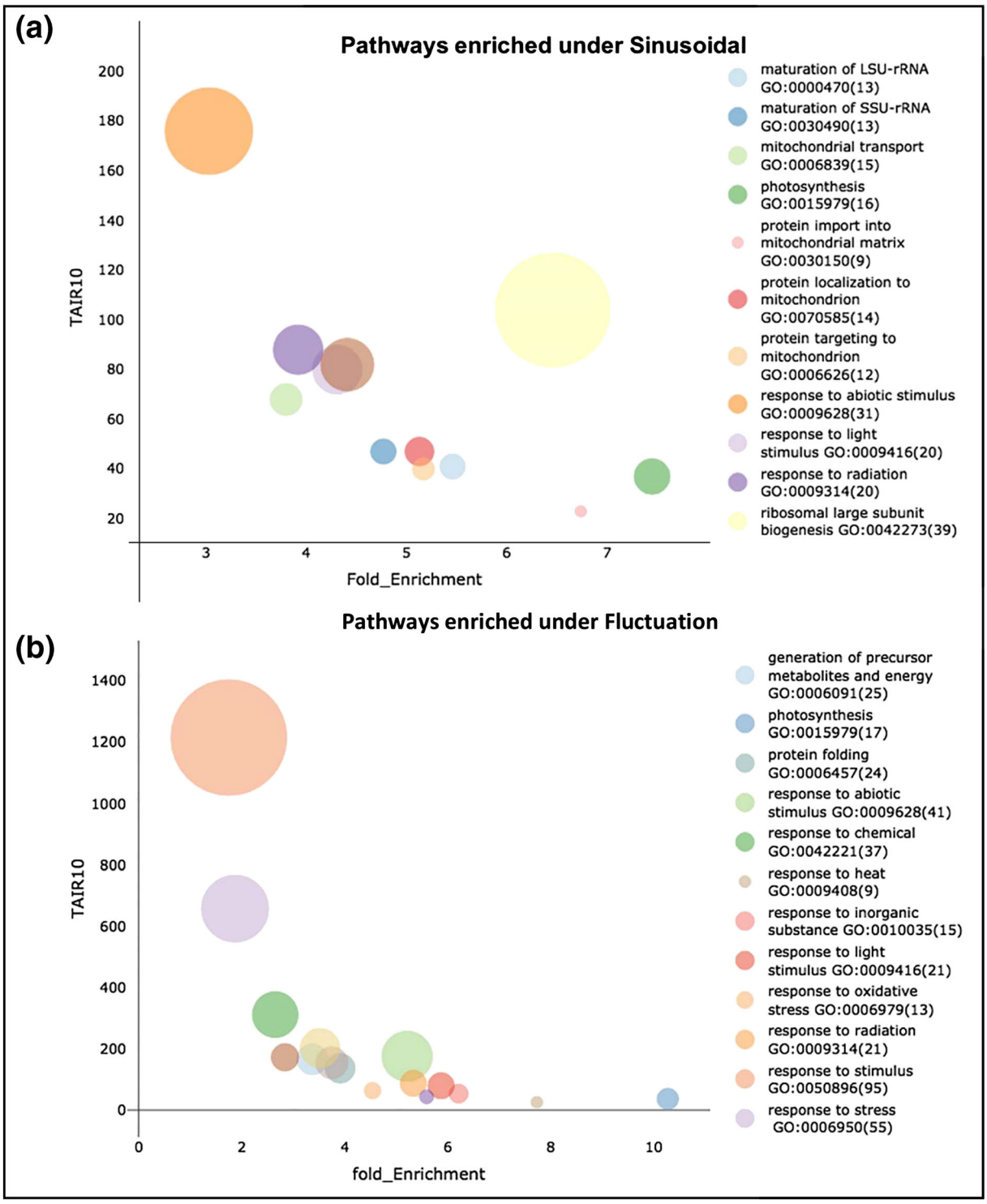

FIGURE 3 Gene ontology (GO) distribution of differentially expressed transcripts in Arabidopsis rosettes. (a) Sinusoidal light (SL) and (B) fluctuating light (FL). The results are summarized based on the most enriched biological processes in the TAIR10-Slim GO terms list.

et al., 2015). In our study, we detected elevated photoinhibition (measured by ϕ_{II}) and lower chlorophyll content associated with a slight increase in *PHYB* transcript levels under SL and FL. Similar to PHYA, CRY1 is downregulated in SL (Data Set S1). Previously, Kleine et al. (2007) and Shaikhali et al. (2012) demonstrated a photoprotective role of Cry1 under short-term high light stress of 1000 µmol m^{-2} s^{-1} for 3 h, conditions distinct from the high light conditions used here for SL and FL. Moreover, it has been reported that Cry1 is known to play a role in regulating the redox equilibrium of electron transport chain when plants are under high light stress (Walters et al., 1999). Also, Weston et al. (2000) reported that Cry1 has a significant role of regulating LHCB as well as the chlorophyll a/b ratio. Furthermore,

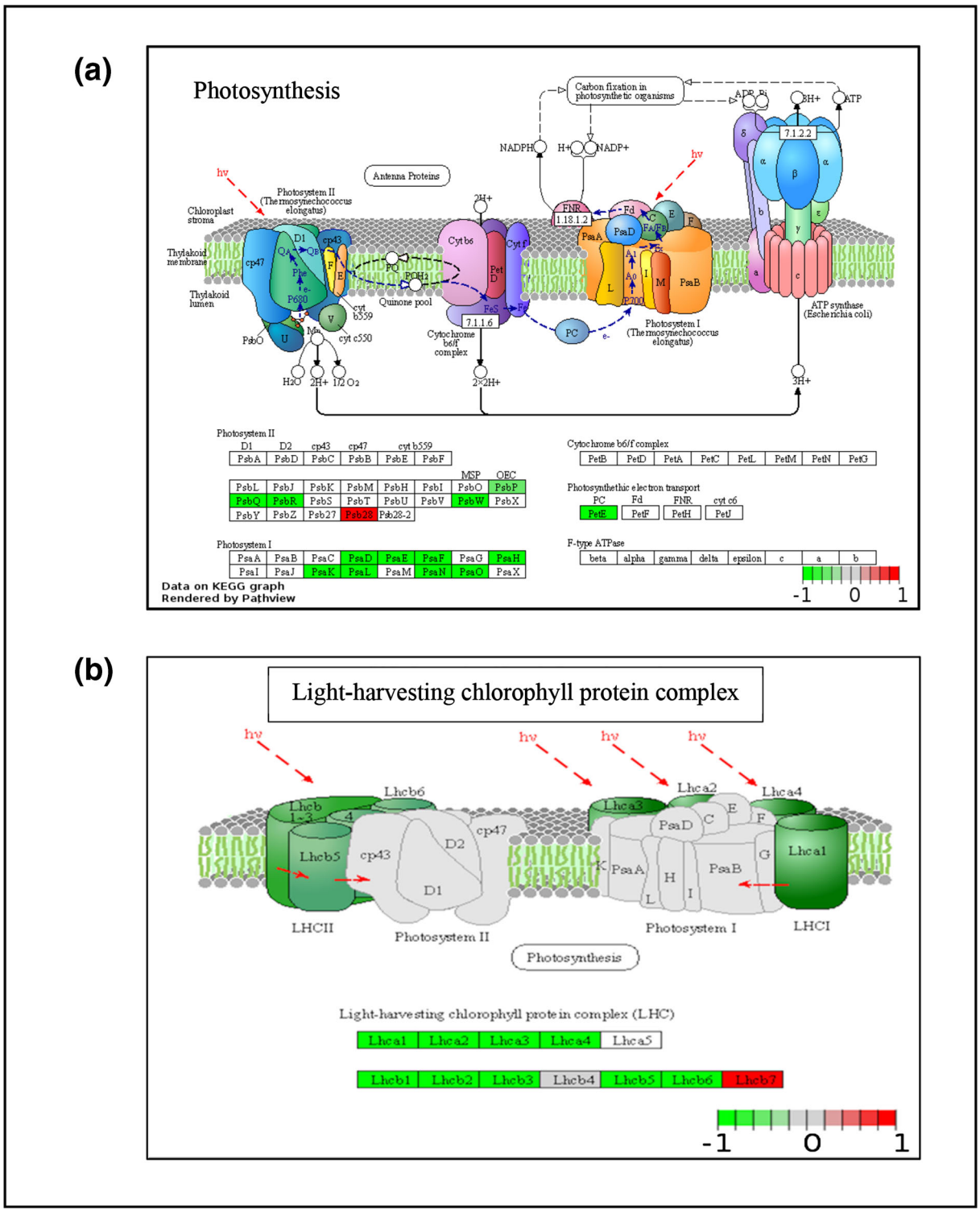

FIGURE 4 Schematic diagram illustrating the molecular changes in the (a) photosynthesis components and (b) antenna proteins under sinusoidal light (SL) and fluctuating light (FL). The image was produced using Pathview (https://pathview.uncc.edu; Luo et al., 2017).

Cry1 has been reported to have a role in ROS production by regulating the several Arabidopsis genes that encode the salt tolerance zinc finger (ZAT10), ascorbate peroxidase 2 (APX2), sigma factor binding protein 1 (SIB1), ethylene responsive element binding factor 4 (ERF4), and NAD(P)H dehydrogenase B2 (NDB2) sis at transcription level (Consentino et al., 2015; Danon et al., 2006; El-Esawi et al., 2017 and Kleine et al., 2007). Our results indicated an overexpression of *ZAT10*, *ERF4*, and *NDB2* under both SL and FL; however, *SIB1* was upregulated only under SL, suggesting that Cry1 might negatively regulate ROS levels under high light stress. Furthermore, we noticed a

significantly altered-regulation for some stress-related genes, such as Glutatione peroxidase7 (*GPX7*), which is known to play a role in regulating the plant's response to photooxidative stress (Chang et al., 2009). *GPX7* was upregulated under SL and FL.

Early Light Induced Proteins 1 and 2-encoding genes (*ELIP1* and *ELIP2*) exhibit elevated transcript levels under high light stress (Huang et al., 2019) and FL (Schneider et al., 2019). Hutin et al. (2003) indicated that ELIPs exhibit photoprotection by stabilization of pigment-binding proteins during light stress or by binding to chlorophylls released during turnover of those proteins. Both ELIP1 and ELIP2 transiently bind to released chls to prevent the formation of free radicals and to initiate a photoprotection role under high light stress conditions (Adamska, 2001; Montané & Kloppstech, 2000). Both *ELIP1* and *ELIP2* were upregulated under SL and FL, with higher levels observed under FL, perhaps suggesting a role for these proteins in the regulating NPQ levels under SL and FL.

3.4.3 | Expression of genes involved in hormone signaling pathways is modulated in response to dynamic light

Many hormonal pathways are involved in mediating light-dependent changes to dynamic light conditions, including modulation of photosynthetic efficiency and photoprotection (Lau & Deng, 2010; Neff et al., 2006; Wang et al., 2019). The change in light intensity under SL and FL relative to CL conditions resulted in mis-regulation of some of the major hormone signaling pathways, including jasmonic acid (JA), gibberellic acid (GA), cytokinin, and auxins (Data Set S4 and Figure S1).

JA is required for plant acclimation to a change in light intensity (Balfagón et al., 2019); it is also known to be part of the stress response. Sirhindi et al. (2020) link JA to improved recovery of PSII (i.e., repair cycle) in response to stress. Our results indicated mis-regulation of a number of JA-related genes (Data Set S4 and Figure S1B). Allene oxide cyclase 3 (*AOC3*) and Lipoxygenase 3 (*LOX3*) genes play important roles in the JA biosynthesis pathway (McGrath et al., 2005; Gollan et al., 2017, and Zhang et al., 2020) and are upregulated under SL and FL, with higher transcription levels under SL (Data Set S1 and Data Set S4).

In addition, GA is known to increase the photosynthetic rate and chlorophyll levels, and, thus, it may also regulate the sink–source relationship of photosynthetic products (Wen et al., 2018). A number of gibberellin-regulated genes were misregulated in our analyses; particularly, genes encoding gibberellin-regulated proteins exhibited decreased transcript levels in response to a change in light intensity (Data Sets S1 and S4 and Figure S1C). Furthermore, GA2-oxidases of classes I, II, and III are known to regulate the deactivation of bioactive GAs (Li et al., 2019). These genes encode proteins whose activity are correlated with the regulating the rate of photosynthesis activity. For example, Biemelt et al. (2004) and Zhou et al. (2011) reported an increase of CO_2 uptake in GA_2 overexpressed plants in tobacco and *Brassica napa*, respectively. Our results indicated that they were all upregulated aligned with the decreased level of ϕ_{II} under both SL and FL.

Cytokinins are linked to protection of photosynthetic complexes and pigments particularly under stress conditions (Chernyad'ev, I. I., 2009). Some cytokinin biosynthesis genes were upregulated under both SL and FL (Data Set S4 and Figure S1F). Genes impacted included those encoding zeatin-O-glycosyltransferases (UGT73C1 and UGT73C3), which encode enzymes that glycosylate brassinosteroids and cytokinin in *A. thaliana* (Hou et al., 2004; Husar et al., 2011). Our results showed that *UGT73C1* and *UGT73C3* were upregulated more under FL compared to SL (Data Sets S1 and S4).

Related to the regulation of photosynthetic process and anthocyanin synthesis, we were able to detect downregulation of 7 members of auxin-associated B-box protein family-encoding genes (*BBX* genes) under SL and FL (Figure 5). Prior downregulation of *BBX17* under FL was reported (Schneider et al., 2019). Of note, four members of the *BBX* family were overexpressed under both SL and FL. BBXs directly and indirectly regulate anthocyanin biosynthesis genes (Gangappa & Botto, 2014). These factors also play a role in additional hormone pathways, including brassinosteroid (Wei et al., 2016), GA (Wang et al., 2011), and ABA signaling pathways (Xu et al., 2014).

3.4.4 | FL promotes expression of genes associated with stress response pathways in Arabidopsis rosettes

To highlight the difference between plant responses to SL and FL conditions, we compared transcript levels from R3 and R2 in whole Arabidopsis rosettes that average distinct changes that may be seen in individual leaves of distinct developmental stages. Our data indicated 448 DEGs (Data Set S5). We performed pathway enrichment analysis with this set of DEGs, and the results indicated enrichment of stress response GO-terms including response to oxidative stress, heat, and osmotic stress. Notably, a group of genes encoding members of the family of heat shock proteins (HSPs) was among the most highy expressed group of genes under FL (R3). These genes included *HSP17.4*, *HSP17.6A*, *HSP17.6II*, *HSP17.6B*, *HSP70*, and *HSP81.1*, which were previously reported to have an important role in mediating plant responses to light-dependent priming of thermotolerance (Kim et al., 2021, Roeber et al., 2021, Han et al., 2019a, Han et al., 2019b, and others).

Another important group of genes among those most downregulated under FL compared with SL are the APETALA2/ETHYLENE RESPONSIVE FACTOR (AP2/ERF) family transcription factors (AP2/ERFs), such as *ERF018*, *CBF1*, *CBF3*, *ERF105*, *ERF104*, *ERF103*, *ERF05*, *ERF06*, *ERF11*, *RAP2.9*, *ERF1*, *ERF2*, *ERF54*, and *CYTOKININ RESPONSE FACTOR 2* (*CRF2*). The AP2/ERFs are involved in plant responses to various abiotic stresses (Licausi et al., 2013; Xie et al., 2019). For example, CYTOKININ RESPONSE FACTORS (CRFs) are induced by different abiotic stresses to regulate osmotic positively and freezing tolerance (Rashotte et al., 2006; Rashotte & Goertzen, 2010); in addition, the ERF-VII subfamily in Arabidopsis and rice play

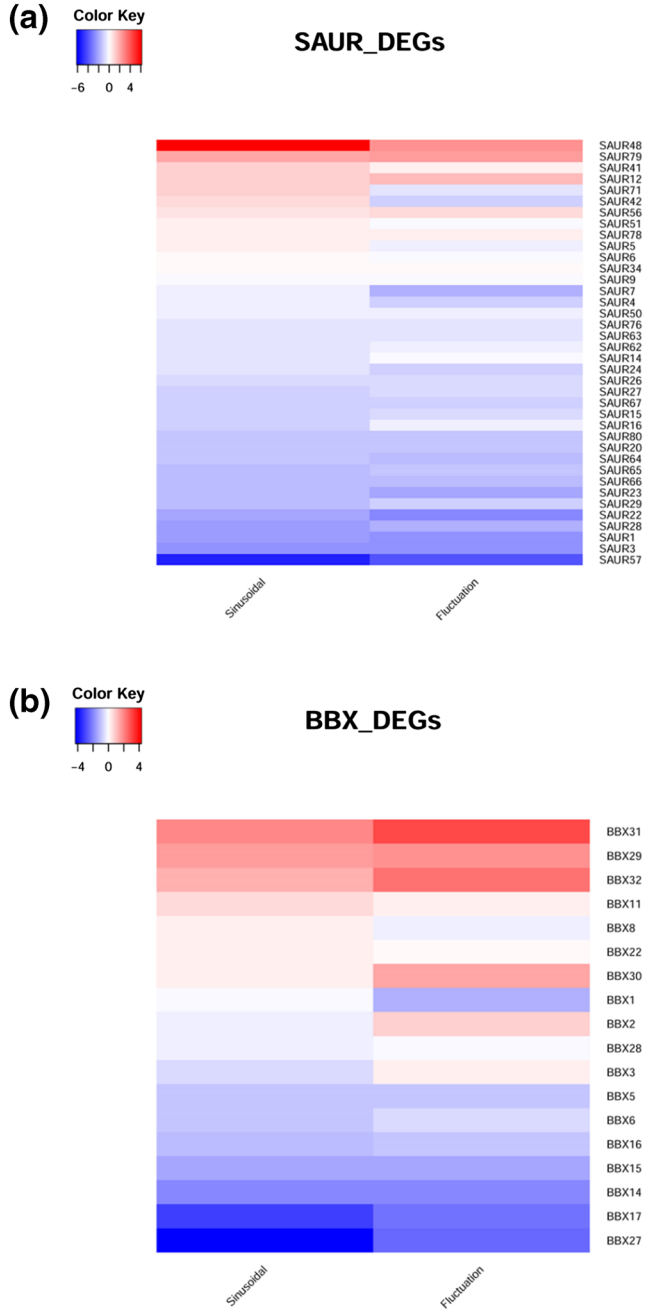

FIGURE 5 Heat map showing the differentially expressed genes (DEGs) of two gene families. (a) *SAUR* gene family involved in the auxin biosynthesis pathway, and (b) *BBX* gene family involved in the anthocyanin biosynthesis pathway. (Colors and scale representing the $\log^2$ fold change.)

significant roles in flooding and low oxygen (hypoxia) (Bailey-Serres et al., 2012; Bui et al., 2015; Gibbs et al., 2015). Additionally, RESPIRATORY BURST OXIDASE HOMOLOG D (RbohD), an NADPH oxidase, generates ROS (Yao et al., 2017). It is important to note that AP2/ERF is overexpressed in FL compared with CL but downregulated when compared with SL, and that can be due to the accumulation effect of damage due to high light exposure during the SL treatment.

4 | CONCLUSIONS

Light is one of the most critical environmental factors that affect major pathways in plants, and any change in light intensity may lead to significant changes in key biological processes. Those changes can be reversible (Johnson et al., 2011; Yamori & Shikanai, 2016) or irreversible (Anderson et al., 1998). Here, we presented the responses of plant rosettes at the transcriptomic level to sinusoidal and subsequent FL, as well as the effects of the change of light regimes on the photosynthetic capacity of plants. Our analyses of plant rosettes average changes in transcript levels at the individual leaf level that likely exhibits distinct responses based on spatial and developmental differences.

We detected a downregulation of genes encoding key factors important for major photosynthesis, light-harvesting, and light reaction pathways in rosettes, as well as pathways associated with upregulation of flavonoids, specifically anthocyanin biosynthesis and metabolism, under both SL and FL conditions (Data Set S4). Furthermore, our photosynthetic measurement results indicated that SL and FL are associated with a lower ϕ_{II} and elevated NPQ, q_E and q_I levels (Figure 1). Mattila et al. (2018) reported that when chlorophyll is decreased during senescence, flavonoid and anthocyanin levels are increased. Relatedly, flavonoids, especially anthocyanins, do not absorb visible light and can serve to block light absorption (Solovchenko & Merzlyak, 2008); thus, regulation of genes related to flavonoid biosynthesis and metabolism may be a part of regulating the photoprotection process to protect leaves from the excess light exposure.

Our results indicate a major reduction in transcripts for some hormone signaling pathways, especially aspects of the auxin-mediated signaling pathway associated with anthocyanin accumulation (Figure S2). We also noticed elevated transcripts associated with the JA stimulus pathway under SL only. Suzuki et al. (2015) reported that 12% of early accumulated transcripts under light stress were JA response transcripts.

In our experiments, the illumination of SL and FL treatments was performed in sequence; thus, the observed plant responses are likely to reflect both immediate and cumulative effects of individual light conditions. Notedly, our transcriptome data analyses (Data Set S5) indicated that rosette responses to FL differ from the response to SL; our data show enrichment of genes for a number of abiotic stress pathways under FL. The expression levels of genes encoding key transcription factors families were altered under FL comparing with SL, including HSP-encoding genes that play essential roles in plant responses to excess light (Han et al., 2019a; Han et al., 2019b; Kim et al., 2021; Roeber et al., 2021) and AP2/ERF-encoding genes, which are considered key regulators of several abiotic stresses and that respond to multiple hormones (Chandler, 2018; Dietz et al., 2010; Mizoi et al., 2012).

Taken together, our data provide global transcriptome profiles under three different light regimes. In order to fully understand plant responses to dynamic light, it will be important to consider other levels of regulation including post-trancriptional, translational, and

post-translational regulations, inclusive of proteomic and metabolomic regulation. The wide range of changes in transcript levels in rosettes associated with the major central pathways for under SL and FL regimes suggests that the dynamicity of the natural light environment should be considered in a wide range of plant research and opens the door for future questions about the regulation of gene expression at transcriptional and post-transcriptional levels.

ACKNOWLEGMENTS

We thank Professor David Kramer and Dr. Jeffery Cruz from the MSU-DOE Plant Research Laboratory at Michigan State University for their assistance with the DEPI system, analyzing the DEPI data, and fruitful discussions throughout the experiments. Furthermore, we would like to thank the Genomic Core Facility at MSU for performing the RNAseq and the High-Performance Computing Center (HPCC) at MSU for providing the computing capacity to analyze the RNAseq data. We also thank the anonymous reviewers for their helpful feedback. The National Science Foundation supported this research (grant no. MCB-1515002 to B.L.M.).

AUTHOR CONTRIBUTIONS

H.F.A. designed the research, performed research, analyzed data, and wrote the paper; B.L.M. designed the research, analyzed data, and edited the paper.

CONFLICT OF INTEREST

The authors did not report any conflict of interest.

DATA AVAILABILITY STATEMENT

The data for this study are available online at the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) repository. (BioProject ID: PRJNA912091).

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SUPPORTING INFORMATION

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How to cite this article: Alameldin, H. F., & Montgomery, B. L. (2023). Plasticity of Arabidopsis rosette transcriptomes and photosynthetic responses in dynamic light conditions. *Plant Direct*, *7*(1), e475. https://doi.org/10.1002/pld3.475