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Review

Role of plant microRNAs and their corresponding pathways in fluctuating light conditions

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ABSTRACT

In recent years, it has been established that microRNAs (miRNAs) are critical for various plant physiological regulations in numerous species. Next-generation sequencing technologies have aided to our understandings related to the critical role of miRNAs during environmental stress conditions and plant development. Light influences not just miRNA accumulation but also their biological activities via regulating miRNA gene transcription, biosynthesis, and RNA-induced silencing complex (RISC) activity. Light-regulated routes, processes, and activities can all be affected by miRNAs. Here, we will explore how light affects miRNA gene expression and how conserved and novel miRNAs exhibit altered expression across different plant species in response to variable light quality. Here, we will mainly discuss recent advances in understanding how miRNAs are involved in photomorphogenesis, and photoperiod-dependent plant biological processes such as cell proliferation, metabolism, chlorophyll pigment synthesis and axillary bud growth. The review concludes by presenting future prospects via hoping that light-responsive miRNAs can be exploited in a better way to engineer economically important crops to ensure future food security.

1. Introduction

Plants require light in order to survive as it play vital role in photosynthesis [1]. Plant's architecture and development are influenced by what it learns about its neighbors by evaluating light quality and duration. Additionally, light cues provide information about the time of day and season [and the long and short days of spring and summer] [2]. In addition, light also provides circadian entrainment and contributes to the clock's rhythmicity. Biological processes will function properly when clocks are reset correctly, which will reflect in plant fitness [3].

The light signal provides important developmental cues alongside seasonal and positional cues. During photomorphogenesis, for instance, hypocotyl growth is inhibited as sprouting seedlings reach for light, encouraging roots to grow, cotyledons to open, and true leaves to appear [4]. Chloroplasts and chlorophyll accumulate in conjunction with these morphological changes leading toward initiating plant response to stress conditions created by light fluctuations (low light and high light) (Fig. 1). The light eventually regulates the flowering time [5]. Inflorescence meristem transition is triggered molecularly by the photoperiod (the length of daily light and dark periods). This occurs when specific transcription factors (TFs) accumulate such as MYB-like (CIRCADIAN CLOCK-ASSOCIATED 1 and LATE ELONGATED HYPOCOTYL), B-box zinc finger (CONSTANS) and TEMPRANILLO1/2 [6].

It's no wonder that light signals generate significant transcriptional modifications in transcripts in the presence of so many light-controlled and/or light-dependent activities [7]. Much research has focused on light's role in regulating protein-coding gene expression, but not nearly as much has been done on its role in non-protein-coding gene

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expression. Many critical reviews have explained the biogenesis of microRNAs (miRNAs) in plants [8–12]. During various plant development phases and plant response to environmental stresses, miRNAs exhibit accumulation at lower levels as compared to their target transcripts. Similarly, miRNAs play a vital function in light-dependent pathways (Table 1). In this review, we'll talk about how light affects miRNA expression, synthesis, processing, and function, as well as how they're involved in photomorphogenesis and photoapoptosis. Moreover, plant biological mechanisms that are photoperiod dependent, such as cell proliferation, metabolism, axillary bud growth and chlorophyll pigment production will also be described.

2. Role of plant miRNAs in fluctuating light conditions

Several mechanisms are involved to regulate light responsive miRNAs in plants: RISC (RNA-induced silencing complex) is a gene regulator that controls gene transcription and miRNA levels, as well as miRNA processing and function. miRNAs may be able to target genes encoding light signaling pathways and embedding components, which can then influence light-responsive processes, such as photomorphogenesis and photoperiod-dependent plant development. The recent developments in these fields of research have been discussed below.

2.1. Light mediated regulations of miRNA biogenesis, processing, and functions

miRNA gene expression that modulate miRNA levels and activity is not the only mechanism regulated by light. Light can be considered as a direct regulator of miRNA biogenesis through a direct connection with its regulators. i.e., family of RNA-binding proteins that participate in miRNA processing [13]. CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) regulates the amount of HYL1 (HYPONASTIC LEAVES1) ubiquitin-ligases degrade light signaling factors in *Arabidopsis*, such as photoreceptors [14]. A similar reduction in miRNA (miR157, miR158, miR164, miR166, miR172, miR173) levels was observed for *cop1* mutants in comparison to control plants, a finding that matched what was found for *hyl1* mutants. Analysis of the expression of HYL1 proteins showed that COP1 regulates its levels indirectly, rather than directly through ubiquitination. By combining autophagy and 26S proteasome inhibitors with protein synthesis blockers, it has been determined, that HYL1 is degraded by an unknown protease that removes the two RNA-binding domains, a vital component to miRNA processing. In the daytime, light regulates COP1 nucleocytoplasmic shuttling and, consequently, HYL1 accumulation results in the stabilization of COP1, which would in turn target the protease that would breakdown HYL1 [14].

It has recently been demonstrated that HYL1-CLEAVAGE SUBTILASE 1 (HCS1) is a cytoplasmic protein that is responsible for the destabilization of HYL1 [15]. In the absence of HCS1-function, HYL1 accumulates, disrupting miRNA biogenesis. In contrast, the presence of HCS1-function reduces HYL1. Consequently, researchers found that the *hyl1-K154A* mutant was insensitive to HCS1 proteolysis, confirming HCS1 as a crucial player in HYL1 proteostasis. The light/dark transition also influences the HCS1-activity that was suppressed by COP1-E3 ligase when exposed to light. COP1 blocks HYL1's access to HCS1's catalytic sites by interfering with its steric interaction with HCS1. Contrary to that, darkness unties HYL1-destabilization from nuclear COP1 relocation, which is associated with HCS1-activity. COP1-HYL1-HCS1 module may participate in two cellular pathways that are essential to cellular survival, biological miRNAs and light signaling [16]. There are several factors that regulate miRNA processing, which may explain why mature miRNAs become more abundant during the night, such as miR167/168, miR171/172, and miR397/398 [17].

PIF4 (phytochrome-interacting factor 4), another protein involved in photomorphogenesis, also controls HYL1 protein levels in *Arabidopsis*

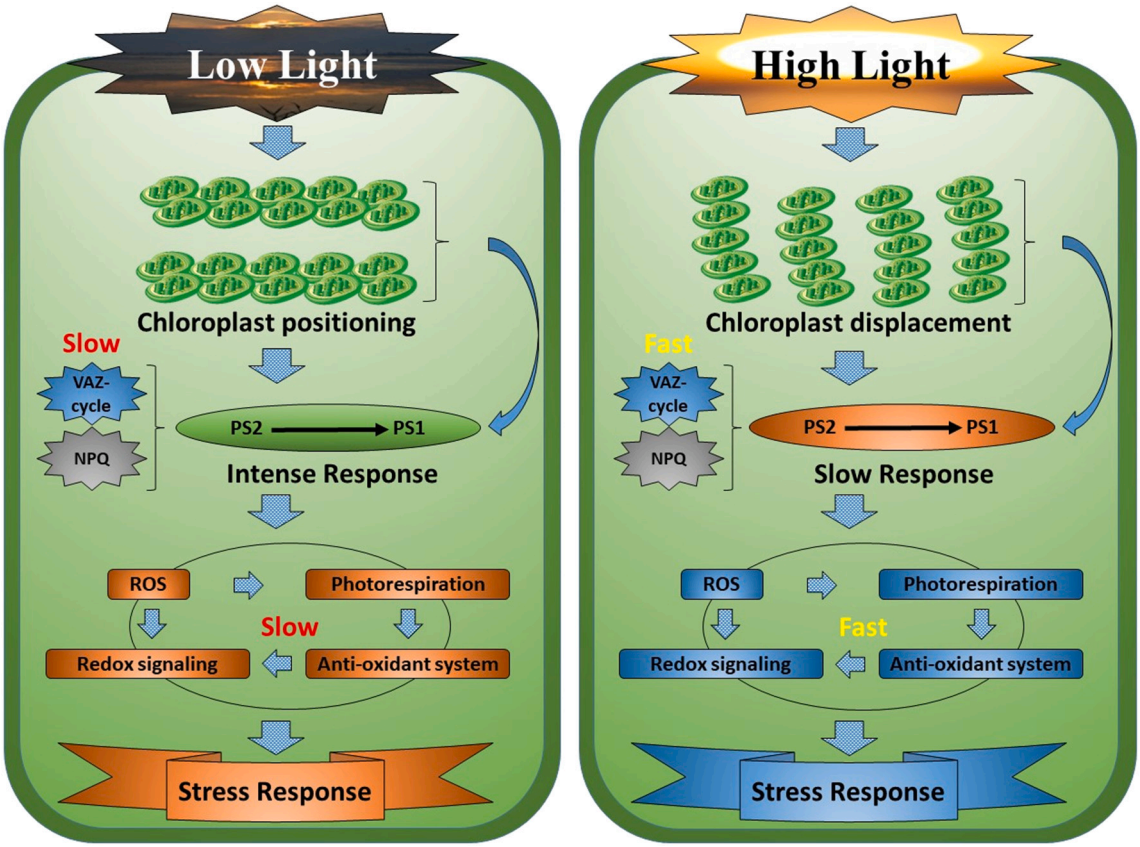

Fig. 1. Plant responses to fluctuating light (high-light and low-light) conditions.

Table 1
Light-responsive microRNA, their regulations and target functions in plants.

microRNAs	Target	Plant species	Regulations		References
			Up	Down	
miR148	PIFs	*Prunus persica*	■		[99]
miR156	SBP	*Zea mays*		■	[45]
	SPA1-RELATED 3	*Arabidopsis thaliana*		■	[100]
	SBP	*Populous tremula*	■		[44]
	DCLs, HYL1	*Arabidopsis thaliana*	■		[21]
	SPL	*Poplar spp.*		■	[75]
	Solyc01g080150.2	*Solanum lycopersicum*		■	[34]
miR157	SPLs	*Arabidopsis thaliana*	■		[100]
	HY5	*Eutrema salsugineum*		■	[19]
	DCLs, HYL1	*Arabidopsis thaliana*	■		[21]
	SPLs	*Arabidopsis thaliana*	■		[53]
miR159	MYBs	*Brassica rapa*	■		[40]
	PPR	*Populous tremula*		■	[44]
miR160	ARFs	*Populous tremula*	■		[44]
	HYL1	*Arabidopsis thaliana*		■	[18]
miR163	PXMT1	*Arabidopsis thaliana*	■		[100]
	DCLs, HYL1	*Arabidopsis thaliana*	■		[21]
	HY5	*Arabidopsis thaliana*	■		[36]
miR164	NAC	*Zea mays*	■		[45]
	NAC	*Populous tremula*	■		[44]
	DREB-like AP2 domain	*Arabidopsis thaliana*		■	[101]
	NAC	*Tradescantia spp.*	■		[102]
miR165	GRMZM Rolled Leaf 1	*Zea mays*	■		[45]
	PHYs	*Eutrema salsugineum*	■		[19]
miR166	GRMZM Rolled Leaf 1	*Zea mays*	■		[45]
	Homeodomain-leucinezipper protein	*Populous tremula*	■		[44]
	Methionine S-methyltransferase (SSM)	*Tradescantia spp.*	■		[102]
	PHYs	*Glycine max*	■		[25]
miR167	ARF	*Populous tremula*	■		[44]
	PHYs	*Glycine max*	■		[25]
	ARFs	*Arabidopsis thaliana*		■	[18]
	DCLs, HYL1	*Arabidopsis thaliana*	■		[21]
	Unkonwn	*Solanum lycopersicum*		■	[34]
miR168	AGO	*Populous tremula*	■		[44]
	PHYS	*Glycine max*	■		[25]
miR169	CCAAT-binding TF	*Populous tremula*		■	[44]
	NF-YA-10	*Arabidopsis thaliana*		■	[101]
	NF-YA (SubunitA3)	*Tradescantia spp.*	■		[102]
	Solyc06g068930.1	*Solanum lycopersicum*	■		[34]
	Lectin receptor kinase	*Arabidopsis thaliana*		■	[53]
miR171	SCLs	*Prunus persica*	■		[99]
	SCLs	*Zea mays*		■	[45]
	HY5	*Eutrema salsugineum*		■	[19]
miR172	AP2-like	*Zea mays*		■	[45]
	TATA-box	*Arabidopsis thaliana*		■	[101]
	Hydroxysteroid dehydrogenase 3	*Arabidopsis thaliana*		■	[53]
	BRI1 suppressor 1 (BSU1) like 1	*Tradescantia spp.*	■		[102]
miR191	Ubiquitin	*Brassica rapa*	■		[40]
miR319	DCL1	*Arabidopsis thaliana*		■	[18]
miR323	Unknown	*Brassica rapa*		■	[40]
miR390	Protein serine	*Populous tremula*		■	[44]
miR393	bHLH	*Populous tremula*		■	[44]
	Flavonoids	*Chrysanthemum morifolium*		■	[47]
miR394	Actin binding FH2 family protein	*Tradescantia spp.*	■		[102]

	PHYs	*Glycine max*	■		[25]
	Galactose oxidase	*Arabidopsis thaliana*	■		[53]
	Solyc08g082260.1	*Solanum lycopersicum*		■	[34]
miR395	ATP sulfurylase	*Populous tremula*		■	[44]
	Ribonuclease III	*Prunus persica*		■	[99]
	PHYs	*Eutrema salsugineum*	■		[19]
miR396	GRFs	*Zea mays*		■	[45]
	PHYs	*Glycine max*	■		[25]
	E2Fe	*Arabidopsis thaliana*		■	[54]
	Glycolysis genes	*Chrysanthemum morifolium*		■	[47]
miR397	LAC	*Prunus persica*	■		[99]
	Glycolysis genes	*Chrysanthemum morifolium*	■		[47]
miR398	SOD	*Zea mays*	■		[45]
	Cu^{2+}/Zn^{2+} SOD	*Populous tremula*	■		[44]
	SPA1-RELATED 3	*Arabidopsis thaliana*	■		[100]
miR399	PHO2	*Prunus persica*		■	[99]
	PHO2	*Populous tremula*		■	[44]
	Sodium Bile acid symporter family	*Arabidopsis thaliana*		■	[53]
miR403	AGO2	*Arabidopsis thaliana*		■	[101]
miR406	DCLs, HYL1	*Arabidopsis thaliana*	■		[21]
miR408	Plastocyanin-like	*Populous tremula*	■		[44]
	PHYs	*Eutrema salsugineum*	■		[19]
	SPA1-RELATED 3	*Arabidopsis thaliana*		■	[100]
miR418	Ubiquitin	*Brassica rapa*	■		[40]
miR460	Ubiquitin	*Brassica rapa*	■		[40]
miR472	F-box protein	*Populous tremula*		■	[44]
miR529	Thioesterase-Like	*Zea mays*		■	[45]
	SBP-like	*Tradescantia spp.*		■	[102]
miR530	PHYs	*Glycine max*	■		[25]
miR824	AGAMOUS-LIKE16	*Arabidopsis thaliana*		■	[100]
miR827	GAG-motif	*Arabidopsis thaliana*	■		[101]
	HY5	*Eutrema salsugineum*		■	[19]
miR828	MYBs	*Vitis vinifera*	■		[71]
miR840	G-Box	*Arabidopsis thaliana*	■		[101]
miR842	SPXs	*Prunus persica*	■		[99]
miR850	G-Box	*Arabidopsis thaliana*	■		[101]
miR858	MYBs	*Vitis vinifera*	■		[71]
	MYBC1	*Actinidia arguta*		■	[73]
miR864	DARK INDUCIBLE 4	*Arabidopsis thaliana*		■	[53]
miR1309	ZFP	*Tradescantia spp.*	■		[102]
miR1507	PHYs	*Glycine max*	■		[25]
miR1508	PHYs	*Glycine max*	■		[25]
miR1509	PHYs	*Glycine max*	■		[25]
miR2218	PHYs	*Glycine max*	■		[25]
miR3627	Nucleic acid binding proteins	*Prunus persica*	■		[99]
miR5302	Solyc09g097880.2	*Solanum lycopersicum*		■	[34]
miR7122	Metal ion binding proteins	*Prunus persica*		■	[99]
miR8133	Metal ion binding proteins	*Prunus persica*		■	[99]
miR9472	Solyc06g050510.2	*Solanum lycopersicum*		■	[34]

Here:- *PIF (Phytochrome-interacting factor), SBP (SQUAMOSA PROMOTER BINDING PROTEIN), DCL (Dicer-Like), SPL (SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE), HY5 (ELONGATED HYPOCOTYL5), MYB (myeloblastosis), PPR (Pentatricopeptide repeat), ARF (Auxin Response Factor), PHY (Phytochrome), HYL1 (HYPONASTIC LEAVES1), PXMT1(Paraxanthine methyltransferase 1), NAC {NAM (no apical meristem, Petunia), ATAF1–2 (Arabidopsis thaliana activating factor), and CUC2 (cup-shaped cotyledon, Arabidopsis)}, AGO (Argonaute), NF-Y (Nuclear factor Y-sub unit A), SCL (SCARECROW-LIKE), AP2 (APETALA2), bHLH (basic helix-loop-helix), GRF (Growth response factors), LAC (LACCASE), SOD (Superoxide dismutase), ZFP (Zinc finger protein).*

[18]. In red light (RL), HYL1 and DCL1 (Dicer-Like 1) are destabilized, while in the dark, they are stabilized by PIF4. There is no ubiquitin-proteasome pathway or transcriptional regulation involved in PIF4 mediated regulations of HYL1 and DCL1 that bind tightly to PIF4 and PHYB, two factors necessary for miRNA processing, leading one to wonder if these factors also contribute to light responses. Furthermore, under RL-, *dcl1* and *hyl1* mutant plants produce shorter hypocotyls than wild type (WT) plants suggesting that DCL1 and HYL1 are negatively involved in photomorphogenesis [18]. In addition, a recent research related to *Eutrema salsugineum* plants' photosynthetic adaptation to RL, looked into the expression of essential photoreceptor apoprotein genes, TFs, and associated *miRNA* genes involved in phytochrome (PHY) system control [19]. A significant increase in the expression of *PHYA*, *PHYB*, and *PHYC*, the TF gene *PIF4* and *PIF5, miR395, miR408*, and *miR165* transcripts, as well as decreased expression of the *PHYA*, *PHYB*, and *PHYC* transcripts was noted. The adaptation impact of photosynthetic apparatus to RL is linked to a rise in pigment content, such as total phenolic compounds and carotenoids. This is related to changes in the expression of *PHY* genes such *PHYA*, *PHYB*, and *PHYC*, as well as *PHY* gene signaling TFs (*PIF4, PIF5*, and *HY5*) and other *PHY* system genes [19].

Light signaling pathways also control HEN1, which is a factor in miRNA processing. Induction of *HEN1* expression by light is caused by the inter-linked actions of HY5 and its respective homolog (HYH) [20]. In the case of HEN1, repression of key TFs involved in photomorphogenesis is the reason for its role as a negative regulator of photomorphogenesis [20,21].

miRNA activity toward its targets can be affected by the de-etiolation process [22]. Although light exposure had no effect on the levels of most miRNAs, it did have an effect on the activity of their targets. With the exception of miR163, the levels of most miRNAs did not change throughout the light transition. According to the analysis, de-etiolation did not correlate with degradation signatures, indicating an increased level of degradation activity for miR156/157 and miR396 [22]. Despite

the finding, that miR168 modulates RISC activity during exposure to light, the mechanisms by which it regulates Argonaute 1 (AGO1) levels have yet to be elucidated. Originally discovered as a light-stabilized suppressor of miRNA biogenesis, Forkhead-associated domain 2 (FHA2) has recently been identified [23]. In the presence of FHA2 deficiency, mature miRNAs were increased accompanied by a diminution of pri-miRNAs and target RNAs. The FHA2 protein forms a complex with the DCL1, HYL1, and SE (SERRATE) microprocessors, suppressing the processing of pri-miRNAs. According to the researchers, FHA2 enhances HYL1 binding while suppressing DCL1-PAZ-RNase-RNA-binding domains (DCL1-PRR) binding to miRNAs. FHA2, on the other hand, does not bind to these RNAs directly. Furthermore, it was discovered that the FHA2 protein is unstable in the dark, but becomes stable when de-etiolated and exposed to light. After prolonged light deprivation, de-etiolated seedlings exhibited reduction in survival rates due to FHA2 disruption mediated defects in light-triggered miRNA expression [23]. These results indicated that FHA2 suppresses miRNA synthesis during de-etiolation by facilitating its light-stabilized function.

It is interesting to note that another study suggests AGO1 can regulate adventitious rooting and hypocotyl length in response to light. The PHYA-dependent light signal transduction pathway is impaired in *Arabidopsis ago1* mutants, probably due to hypersensitivity to light [24]. Additionally, an *ago1–27* mutant of *Arabidopsis* was incompetent in de-etiolation under far-RL, indicating that AGO1 is essential for photomorphogenesis [25]. As AGO1 is a necessary component of RISC, it is likely that miRNA plays a role in far-RL responses. The highly conserved CCR4-NOT complex is an essential component of a novel signaling pathway downstream of PHYA [26]. When bound to NOT1, the scaffold protein of the complex, NOT9B, an *Arabidopsis* homolog of human CNOT9, functions as a negative regulator of PHYA-specific light signaling. CCR4-NOT signaling may be mediated by light-activated PHYA by displacing NOT9B from NOT1. The development of alternative splicing (AS) events regulated by PHYA has been found to require NOT9B. Moreover, association with nuclear localized AGO1 suggests PHYA-mediated gene regulation might involve NOT9B and CCR4-NOT [26]. Hernando et al. [27] observed that the miRNAs and their target genes are involved in AS under altering light conditions. Researchers explained that in *Physcomitrella patens*, RL or blue light (BL) are vital for inducing the intron retention in DCL, C-terminal domain phosphatase-like 1, SE and HEN1. Moreover, it has been demonstrated that different light types have different intragenic effects on AS via regulating the miRNAs and corresponding machinery e.g., RL affects DAWDLE but not HYL1 [28,29], however, BL shows its considerable impact on AS of HYL1 [27]. Hernando et al. [27] further explained that different types of light have the ability to produce alternative isoforms of same gene. e.g., RL helps to retain the second intron while BL causes the retention of the first intron. However, both these light wavelengths make the HEN1 non-functional as RL results in disruption of methyltransferase while BL helps in production of truncated proteins. Also the RL causes the donor AS in DCL, while BL helps in acceptor AS in the transcripts [27]. In conclusion, we believe that certain light responses are controlled by several components of the miRNA machinery. The biogenesis pathway controls the expression of miRNA genes, their accumulation, and their activity through the regulation of miRNA gene expression.

2.2. Light dependent changes in miRNA levels

In addition to light, photoperiod, and the circadian clock (CC), there are a number of factors that influence miRNA gene expression. Light regulates the expression of these genes because they contain light-responsive elements (red, blue, far-red, UV-A, and UV-B), that are discussed below.

2.2.1. Light regulation and miRNA levels

The identification of miRNA families has been done by a variety of screening approaches, leading to extensive lists of light-responsive miRNAs. *phyB* mutants were found to have 135 significantly different miRNAs, including 97 upregulated and 38 downregulated miRNAs in comparison to WT rice (*Oryza sativa*) plants. Several miRNAs were identified in the miRNA transcriptome, including miR156, miR166, miR170, and miR410. Although this study did not look at the miR172 family, which responded to PHYB in rice as per previous study [30], however according to another report, the particular miRNA was found responsive to PHYB in potato [31]. Plant species may use different mechanisms for regulating their miRNAs through PHYB. *PhyB* mutants and WT rice have different miRNA expression profiles that target different rice genes. In a degradome analysis, it was discovered that 32 differently expressed miRNAs targeted 70 rice genes between the WT and the *phyB* mutants [31]. PHYB-mediated light signaling may be regulated by miRNA target genes, since a significant percentage of them (42 %) contain TFs. The authors identified several TFs that participate in *Arabidopsis* responsive for light signaling. There is notable similarity between miRNA targets and the *TANDEM ZINC KNUCKLE PROTEIN (TZP)* gene, the circadian-regulated BL-dependent growth gene in *Arabidopsis* [32].

Additionally, light seems to directly influence miRNA abundance. miRNA sequencing study suggested that seedling apical hook miRNA levels change after far-RL treatment of soybean (*Glycine* max) grown under dark conditions. More than 10 miRNAs showed different responses to far-RL in soybean seedlings, with most of them showing an upregulation in response to far-RL [25]. Thus, light may increase the levels of miRNAs in the apical hook, thereby preventing the transcription of target genes that repress the opening of cotyledons. A few years ago, the level of miRNA and mRNA expression was measured in dark-treated and RL leaves and detached tuber skin [33]. In leaves, most of the novel and known miRNAs were upregulated, while the majority were downregulated in tuber skin. The novel miR55 and members of the miR399 family reacted to light in opposite ways, upregulating in leaf cells and downregulating in tuber skin cells [33].

A study of *Arabidopsis* provided further evidence that RL influences miRNA levels. Based on the identification of the differentially expressed miRNAs in RL versus darkness [18]. This effect may be mediated at least in part by PIF4, a TF that negatively regulates PHYB-mediated RL signaling. A *pif4*-mutant showed altered levels of miRNAs with RL-responsiveness. The binding of PIF4 to the promoters of several of these genes enhanced the expression of several miRNAs (miR156, miR157, miR160, miR165, miR166, miR167, miR170, miR171, and miR394), whereas miR172 and miR319 were inhibited [18]. Similarly, it was reported that PIF4 was also involved in miRNA processing in addition to transcriptional regulation of *miR* genes. On the other hand, 108 known and 141 projected new miRNAs were discovered in samples from tomato leaves treated with various light qualities. When compared to the control, the BL therapy resulted in differential expression of 15 known and five newly predicted miRNAs [34].

ELONGATED HYPOCOTYL 5 (HY5) is a critical regulator of photomorphogenesis. In *Arabidopsis*, it modulates the expression of miRNAs such as miR156d, miR402 and miR408 by acting downstream of several photoreceptors [35]. By using small RNA (sRNA) sequencing, researchers found that *Arabidopsis* seedlings exhibited significant increase in miR163 expression in response to light [36]. HY5 functions genetically downstream of the light-induced response of miR163. One G/C-hybrid element is located near the transcription start site, is vital in miR163 expression alterations particularly when light is applied to the promoter. HY5 shows its direct binding with the G/C-hybrid elements of the miR163 promoter with unequal affinity. Overexpression of miR163 decreased primary root elongation but not lateral root development in *hy5* mutant seedlings, while overexpression of miR163 target *PXMT1* repaired the deficits in primary root elongation. These findings describe a novel mechanism by which miR163 and *PXMT1* regulate root photomorphogenesis post-transcriptionally [36].

Day length can affect miRNA accumulation as well as light exposure.

According to Li et al. [37], soybean miRNA levels were regulated by day length, based on high-throughput sequence (HTS) analysis. The day-length-responsiveness of miRNAs was found to exist in 37 families in seedlings grown under long days (LDs) and short days (SDs). Four miR156 target genes were downregulated under LD conditions, while five miR156 family members were induced [37]. The difference in miR156 levels between SD and LD, which are higher under LD, could explain why SD induces soybean flowering. Repression of 11 anticipated targets from the APETALA2 (AP2)-like family was coordinated under SD circumstances, but expression of the miR172 family was increased. Moreover, it was observed that conserved miRNAs, including miR159, miR166/167, miR319, miR395/396, and miR408, were also photoperiod-dependently regulated [37].

Light is the input that confers the CC's entrainment in the simplified model. Like light, plants' internal clock also regulates gene expression, especially at times of transition between darkness and light [38]. An interesting finding is that the CC affects both protein-coding and non-coding transcripts [39]. By comparing mature and pri-miRNA transcript levels over two consecutive days, Siré et al. [17] found that they were circadianly influenced by light/dark cycles or constant lighting conditions. Researchers found that light/dark cycle-controlles the expression of miR167, miR168, miR171, and miR398. A phase delay, rather than an antiphasic expression, accompanies some miRNAs' wave pattern rather than their target expressions. Similarly, the miR171/*SCARECROW-LIKE 6 (SCL6)* and miR398/*Cu/Zn SUPEROXIDE DISMUTASE 2 (SOD2-CSD2)* pair results in reduced gene expression as levels of miRNA rise. However, in the case of miR168/*AGO1* and miR167/*AUXIN RESPONSE FACTOR 6 (ARF6)*, it was found that miRNAs can function as feedback loops by regulating their targets [17]. It became apparent during testing of these modules under free-running conditions that there was no clear oscillation, indicating that these miRNAs are probably light dependent.

2.2.2. *UV-responsive miRNAs*

To better understand how UV-A and UV-B radiation effects miRNA accumulation and their target genes, various screening methodologies have been devised. Researchers devised a solution to differentiate between conserved and novel miRNAs in the seedlings of *Brassica rapa* exposed to UV-A and BL [40]. After BL and UV-A exposure, the expression levels of miR156/157 were moderately reduced, which correlated with an increase in their targets, *SPL9* and *SPL15*, that encode TFs critical to the development of plants, including the juvenile-to-adult transition and flowering, as well as secondary metabolism, including anthocyanin biosynthesis (Fig. 2) [40]. The *miR156* gene and *SPLs* regulate feedback loops in *Arabidopsis*. miR156 levels decrease in aging plants, which results in an increase in *SPLs* (especially *SPL9*) inhibiting biosynthesis of anthocyanins [41]. Furthermore, it has been postulated that BL and UV-A light activate numerous miR156/157 related genes involved in light signaling, some of which boost anthocyanin production before balancing anthocyanin metabolism via a regulatory feedback loop [40].

Like UV-A radiation, UV-B has a negative impact on plant development, metabolism, and physiology [42]. Using a computational approach, researchers have demonstrated that UV-B light controls 11 different miRNA families i.e., miR156/157, miR159/319, miR160, miR165/166, miR167, miR169, miR170/171, miR172, miR393, miR398 and miR401 [43]. Many studies have shown that UV-B affects the expression of miRNA in *Populus tremula* despite not having been tested in *Arabidopsis thaliana, Zea mays, Triticum aestivum* and

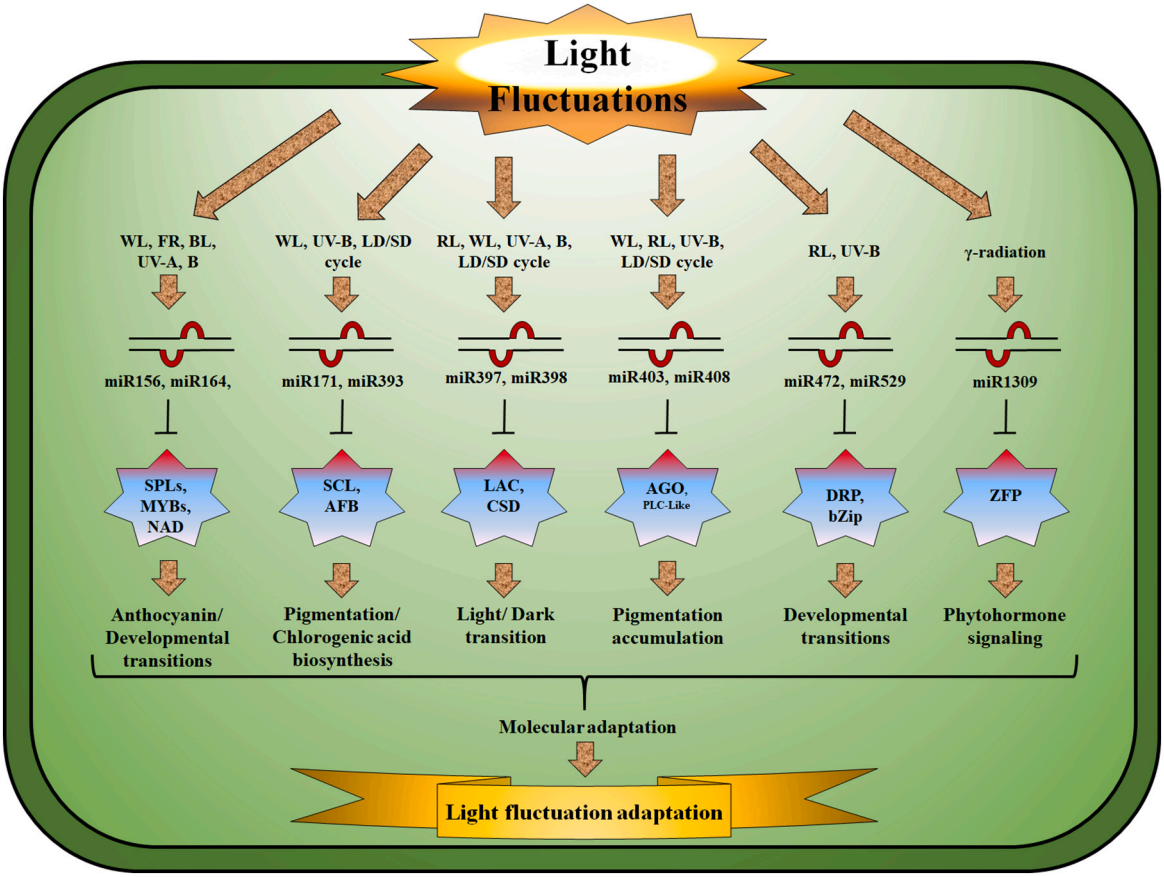

Fig. 2. Plant miRNA, their genetic targets and corresponding functions during fluctuating light conditions. Here, WL (White light), RL (Red light), FR (Far-red light), LD/SD (Long days/Short days) cycle, UV-A, B (Ultraviolet- A, B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Chrysanthemum morifolium [44–47]. According to Jia et al. [44], in response to UV-B light stress in *P. tremula*, miRNA levels increased in eight families (miR156, miR160, miR165, miR166, miR168, miR169, miR398, miR408) and decreased in seven families (miR159, miR167, miR390, miR393, miR395, miR399, miR472). There were seven (miR159, miR164, miR165, miR166, miR398, miR444, miR1427) upregulated miRNA families and ten (miR156, miR171, miR172, miR395, miR396, miR399, miR529, miR896, miR903, miR1858a) downregulated miRNA families in *Z. mays* [45]. *T. aestivum* plants treated with UV-B upregulated three known miRNAs (miR159, miR167, miR171) and downregulate three others (miR156, miR164, miR395), in addition to one novel miRNA (miR6000), which is induced briefly by UV-B and is subsequently deregulated [46]. There were 13 UV-B specific miRNA families (miR156/157, miR159, miR160, miR164, miR165/166, miR167, miR169, miR170/171, miR172, miR393, miR395 miR398, miR399) analyzed in this study, including some conserved miRNAs. A total of 245 miRNA families representing 42 classical groups were identified in *Chrysanthemum*. When exposed to UV-B light, 137 miRNAs, including 71 known and 67 novel miRNAs, showed differential expression [47]. For 85 novel and 80 known miRNAs, there were about 1800 projected target genes involved in various biological processes. Three glycolysis-related genes, glucan endo-1,3-beta-D-glucosidase, glyceraldehyde 3-phosphate dehydrogenase, and pyruvate kinase, might be targets of miR396, 5p-294,053, and miR397, respectively [47].

The miRNAs regulated by UV-B share their targets with TFs, auxin signaling components, and other stress-responsive factors [45]. In most cases, it is observed that UV-B affects miRNAs inversely in relation to their target transcripts [46]. The genes that are vital in the biosynthesis of chlorogenic acids and flavonoids have been outlined as potential targets of miR4367, 3p-40,855, mIR393b, and 3p-114,893 in *Chrysanthemum*, indicating that UV-B radiation contributes to bioactive ingredient accumulation [47]. It was found that short-term UV-B radiation inhibited the synthesis of several miRNAs which are involved in flavonoids biosynthesis, including 3p-114,893 and miR4367, thus suggesting that the contribution of UV-B to flavonoids accumulation depends on its dose [47].

It was found that RLD1 (Rollled Leaf 1) was decreased significantly along with a significant increase in the *miR165/166* gene in maize [45]. It has been suggested that miR165/166 contributes to the adaxial side of leaf primordia being delineated by homeodomain-leucine zipper III (HD-ZIP III) transcription. This suggests that this miRNA is essential for arching [48]. In aspens and wheat, miR395 is downregulated along with sulphate uptake responsible genes, which encodes enzymes to assimilate inorganic sulfates [44,46]. In spite of the negative correlation between miR395 and APS, overexpression of miR395 affects *Arabidopsis* responses to abiotic stress conditions by decreasing APS transcript levels [49], again linking UV-B-regulated miRNAs to stress responses. Furthermore, Ragupathy et al. [50] utilized HTS and identified more than 230 known miRNAs in *T. aestivum* via exposing to heat, UV and light wavelengths. Authors observed that UV treatment resulted in downregulation of 55 % of miRNAs including most commonly known miR156, miR398 and miR528 that play vital role in plant signaling and flowering [50]. Researchers found a similar correlation between downregulation of miR164 and enhanced levels of its stress-responsive target transcripts in UV-B-treated maize leaves [45]. Similarly, downregulation of the miR171, miR172, miR156, and miR529 has been observed when miRNAs targeting crucial developmental transitional genes are exposed to UV-B light [51]. Due to UV-B exposure, plants may delay certain developmental transitions through miRNA-mediated responses, allowing them to repair UV-induced damage or adapt to adverse conditions.

2.3. miRNAs accumulation in high light conditions

In a global analysis of the reports so far available (Fig. 2), light-regulated miRNAs are affected under diverse light conditions (Table 1). It has been shown that at least five of these genes, including miRNAs (miR156/miR157, miR159/miR319, miR164, miR165/miR166, miR167, miR170/miR171, miR172, miR395, miR398 and miR399) are activated by high light conditions, providing evidence that these genes may control light responses (Table 1). In addition, light may have an effect on miRNA processing and its activities. Plant species can also be negatively affected by high levels of light wavelengths. The authors utilized stem-loop RT-qPCR samples to identify novel miRNAs in Ma-bamboo (*Dendrocalamus latiflorus*) plants subjected to white light (WL), high light, or dark conditions. The most abundant miRNA family was miR168, followed by miR156/miR157, miR535/miR635/miR636, and miR165/miR166/miR167. The plants' unique flowering cycle probably prevented the detection of miR172 [52]. Moreover, a very recent study have shown that three new miRNA families (miR447, miR861 and miR863) were induced in *A. thaliana* during high light conditions. Additionally, the authors revealed that miR399a was consistently upregulated [53].

2.4. miRNA mediated light regulations of different plant biological processes

2.4.1. miRNA mediated light regulations of cell proliferation

A number of plant species have been affected by UV-B radiation [42]. Solar UV-B light stimulates *Arabidopsis* miR396 levels and represses the *GROWTH REGULATORY FACTORS; GRF1, GRF2* and *GRF3* [54,55], resulting in a reduction in cell proliferation in leaves. miR396 inhibits the expression of *GRF3* and *GRF2*, but this is not the case when miR396-resistant forms are expressed. Thus, *GRFs* appear to be a critical mediator of the UV-B induced leaf growth phenotype. It seems that UV-B light also works by other ways rather than miR396 in downregulating GRF3. A mitogen-activated protein kinase implicated in UV-B stress responses, MPK3, is also required for miR396 to inhibit leaf cell proliferation under UV-B radiation conditions [55]. Increasing *GRF* expression when miR396 is inhibited has the opposite effect in UV-treated maize leaves [45]. The differing developmental stages between *Arabidopsis* and maize may have contributed to miR396's involvement in UV-B-dependent responses, though more research is needed on this aspect.

2.4.2. miRNAs mediated light regulation of plant metabolism

Plant metabolism is modulated by light-governed miRNAs through the methylation of signaling molecules (such as hormones), which promoted nutrient allocation and boosted pigment synthesis [56]. There have been recent findings that in *Arabidopsis*, both miR163 and pri-miR163 were significantly induced by light [57]. Additionally, miR163 can target *PXMT1* which encodes a gene associated with methylation of hormones, such as 1,7-paraxanthine methyltransferase. In contrast to light inducing pri-miR163 activation and inhibiting *PXMT1* expression, in the absence of light, pri-miR163 cannot mature or process [57]. miR163 accumulation in roots enhances root length through *PXMT1*, particularly in the elongation/differentiation zone. miR163/*PXMT1* appears to regulate germination as well as seedling emergence and de-etiolation during the early stages of plant growth. To fully comprehend miR163's role in this process, however, a more comprehensive functional characterization of *PXMT1* is required [57].

It is important for plant metabolism to allocate nutrients properly, particularly those that are cofactors and are present in different proteins. Copper (Cu), for instance, is an integral element of photosynthesis, the defense against ROS (reactive oxygen species), as well as a component of many other biochemical reactions, and the perception of ethylene [58]. For photosynthesis to be efficient and better plant growth, Cu homeostasis must be maintained [59]. The SPL7 is responsible for this. It functions as a Cu sensor, monitoring Cu levels and adjusting target gene expression accordingly. Transcriptional regulators, SPL7 and HY5 appear to be directly involved in genetic expression regulations [60]. Based on chromatin immunoprecipitation and RNA sequencing, researchers found a similarity between SPL7 and HY5. miR408 is a

common target of SPL7 and HY5, with SPL7 being the predominant TF controlling the gene's expression, thus confirming the similarity as evident by the previous studies explaining the role of HY5 in regulating the genetic expression [35]. Even so, Cu deficiency and high lighting allowed for miR408 accumulation when HY5/SPL7 coordinated regulation was active. *Hy5-Spl7* double mutants exhibited phenotypes showing miR408 silencing that were correlated with miR408 constitutive expression, indicating that miR408 plays an important role in the SPL7/HY5 network. Also, miR408 targets, *LACCASE12 (LAC12)* and *LAC13*, were found to be differentially regulated by the SPL7/HY5/miR408 module. This signaling network contributes to the modulation of Cu homeostasis, thus promoting efficient photosynthetic rates in plants [61].

2.4.3. miRNAs mediated light regulations of pigment synthesis

It has been shown that flavonoids protect plants against environmental stresses, and that their molecular diversity contributes to plant growth and development [62]. As an example, anthocyanins offer UV protection as well as attracting pollinators to plants (Fig. 2) [63]. MYB-like 2 and SPL9 regulate anthocyanin biosynthesis negatively in *Arabidopsis*. A small number of miR156 targets, including SPL9, repress the biosynthesis of anthocyanin in *Arabidopsis* [41,64]. When *Pyrus pyrifolia* fruits are bagged and exposed to light, anthocyanin is accumulated in their peel resulting in red coloration [65,66]. Anthocyanin accumulation in pears after bagging treatments may be influenced by miR156 and SPLs (Fig. 2). In peel, two pear *Pp-miR156* genes were found to have light-responsive elements in the promoters of bagged pear fruits. miR156 levels increased as a result of bag removal, but *Pp-SPL* transcripts decreased. In addition, anthocyanin biosynthesis genes were upregulated, followed by the upregulation of homologs of TFs involved in anthocyanin biosynthesis [65,66]. These results suggest that light-induced anthocyanin biosynthesis may be facilitated by miR156/*PpSPL* module in bagging-treated pear fruits.

Using HTS of sRNA libraries, Qu et al. [67] determined whether re-exposure to sunlight after fruit bagging affected the expression of miRNAs in apple peels. Comparing the bagged to the un-bagged group, there was a significant reduction in miRNA expression in the bagged group. Based on these findings, it was proposed that apple peel possesses a pool of miRNAs regulated by light that may modulate anthocyanin production. Additionally, miR858 targets specific reverse TFs to positively influence anthocyanin biosynthesis in sweet potato, litchi, tomato and grapes [68–71]. Moreover, the expression of miR156, miR828, and miR858 changed upon debagging in apple peels, suggesting that they play a role in anthocyanin synthesis [67,72]. Interestingly, miR156 was only correlated with anthocyanin in *Malus domestica* while miR5072 was correlated with it only in *M. pumila* [67,72]. This suggests that certain miRNA families control specific responses to light, including pigment accumulation to protect against light damage. Moreover, miR858 regulates anthocyanin biosynthesis positively [73]. HY5 is essential for HY5-dependent miR858a in *Arabidopsis* [74] and Kiwi fruit (*Actinidia arguta*) [73] and miR156 expression in popular [75]. The miR156 and miR858 molecules that promote anthocyanin biosynthesis seem to contradict *hen1* mutants with reduced mature miRNA levels, which accumulate high levels of anthocyanin [20].

Plants transmit energy to the atmosphere through chlorophyll pigments that absorb light. In addition to affecting plant growth and development, this fundamental process also contributes to ROS production by plants [76]. In light of the fact that precursors of chlorophyll biosynthesis are also sources of ROS, tight regulation of this pathway is of paramount importance. *HAM (HAIRY MERISTEM)* or *LOST MERISTEMS (LOM)* are TFs targeted by miR171 and its targeted *SCL* genes [77]. miR171-targeted *SCL* in *Arabidopsis* upregulates protochlorophyllide oxidoreductase, which is necessary for chlorophyll biosynthesis. Furthermore, miR171c-overexpressing plants, *scl6-scl22-scl27* triple mutants and plants expressing the miR171c-resistant form of SCL27 exhibited reduction in chlorophyll and protochlorophyllide oxidoreductase (POR) levels. Furthermore, mutants of *miR171c-OX* and SCLs with downregulated *POR-C* expression have reduced chlorophyll content, suggesting that both miR171c and SCLs have a role in chlorophyll regulation. By binding directly to its promoter, SCL27 represses *POR-C* expression [77]. Furthermore, miR171-SCL also modulates chlorophyll biosynthesis in the presence of gibberellin particularly, when DELLA proteins and *POR-C* expression are regulated by light. Because of this interaction between SCL27 and DELLA, SCL27 is unable to bind with specific *POR-C* promoter [77]. All of these findings suggest that miRNAs are involved in diverse light-regulated processes. Besides targeting the light-signaling pathways, miRNAs can also modulate the photoperiod pathway, with consequent effects on photomorphogenesis or flowering timing.

2.4.4. miRNA mediated light regulations of photomorphogenesis

miR156/157 family is a prominent light-responsive miRNAs group (Table 1). HY5 and TCP (TEOSINTE BRANCHED1, CYCLOIDEA, and PCF), encoded by miR157d and miR319, bind to and degrade respective TFs, which control photomorphogenesis in *Arabidopsis* [20]. The accumulation of HEN1 in de-elimination seedlings increased miR157d and miR319 expressions, causing both miR157d and miR319 induction and stabilization [22]. The expression of *HEN1* is induced by HY5 under light-dependent conditions. Therefore, miR157 signals the negative feedback regulatory loop between HEN1 and HY5, because miR157 targets HY5 transcripts for degradation. It is likely that the increase in miR157d is the cause of the light-hypersensitive phenotype in a *hen1* mutant [20]. *HY5* expression was knocked down by miR157 constitutive expression, leading to seedlings that exhibited a light hyposensitivity phenotype. It is possible, that light-hypersensitivity exhibited by *hen1* mutants is also linked to miR319. As a result of its actions, it promotes TCP-mRNAs cleavage and exhibit repression of hypocotyl elongation in plants [20]. Using a mutant showing longer hypocotyls than WT under RL, it has been established that miR319 plays a role in photomorphogenesis [18]. In addition to miR160, miR167 and miR848, three additional miRNAs affect *Arabidopsis* hypocotyl elongation under RL (Table 1) [18].

Apart from photomorphogenesis, hypocotyl elongation is an important process during adulthood. Having been isolated from one another, during their life cycle, plants may undergo high red to far red (HR:FR) light ratio. Ballaré and Pierik [78] found that when plants were grown in a close proximity to eachother, the HR:FR ratio plummets and these changes cause diverse physiological and morphological changes in them, allowing them to cope with a lower light level. An end of day, pulse of far-RL stimulated *Arabidopsis* plants grown under light/dark cycles (EOD-P-FR) to blossom earlier, extend their petioles, in plants growing under normal WL and dark cycles, the number of rosette branches was reduced [79]. In response to EOD-P-FR, several *miR156* genes were downregulated, resulting in a decrease in miR156. As a result, several miR156-targeted *SPL* genes were upregulated in plants treated with EOD-P-FR. Moreover, plants with reduced miR156 activity show constitutive EOD-P-FR responses when grown under WL [79].

PIFs are the mediators of PHY-dependent light responses. Under low R:FR light conditions, PIF abundance increased. PIFs also influenced EOD-P-FR responses in the opposite direction of miR156 [79]. Five *miR156* genes, including miR156e, contain PIF-binding sites that directly bind PIFs, inhibiting transcription of these genes. The results support the conclusion that miR156e targets the *PIF5* gene directly. miR156 levels are thus reduced, which results in an increased abundance of miR156-targeted *SPL* transcripts. In addition, miR156 appears to interact with PIF5 via a genetic analysis [79]. In summary, these findings suggest that miR156 responds to EOD-P-FR treatments and that miR156 may mediate at least some of the negative responses to low R:FR light through downregulation of *SPL* genes. In an attempt to reproduce these findings under the more closely proximity conditions, we will need to examine low R:FR conditions [79].

2.4.5. miRNAs mediated photoperiod regulations

Photosynthetic processes, development, and metabolism are profoundly affected by photoperiod. In addition to controlling the levels of some miRNAs, it also affects mRNA levels [80]. Photoperiod influences the expression of miR156 in potato [81] and soybean [37], but not in *Arabidopsis* [16]. miR172 levels under LD are higher than those under SD and this difference is not associated with transcription, as some miR172 primary transcripts are less abundant under SD than under LD [82]. As a result of reduced photoperiod responses and expression of two miRNA processing genes, *DCL1* and *SE*, the gigantea (*gi*) mutant has lower mature miR172 levels, than the WT. Considering that miR172 is still potently regulated by photoperiod in the *gi* mutant, it is likely that additional factors are involved in photoperiodic control [82]. It has also been observed that soybean and potato miR172 levels differ under LD and SD conditions [37,81], explaining that this modulation is likely evolutionarily conserved.

Interestingly, cryptochrome 1 and 2 and PHYA, and PHYB, the four major photoreceptors, regulate miR172 levels [83]. *Arabidopsis* downregulates miR172 when RL is present and upregulates it when BL is present, indicating that these changes are related to both light quality and duration. Maturation of miR172 is slowed by TOC1, a component of the CC. Even so, *Arabidopsis* does not experience daily variations in miR172 levels despite this reduction [82]. LD causes plants to flower earlier in *Arabidopsis* than SD, since photoperiod controls flowering. On the other hand, SD induces the flowering of soybeans and the formation of potato tubers [37,81]. *Arabidopsis* flowering and tuberization are both promoted by overexpression of miR172; and photoperiodic tuberization is reduced in potato [81], thus supporting miR172's involvement in photoperiodic processes. AP2 itself, which is also targeted by miR172, is partially redundantly repress flowering [84]. *Arabidopsis*, and soybeans showed reduced floral development responses to photoperiod when miR172-target genes were altered [83]. Several photoreceptors influence *Arabidopsis* to activate the miR172 transcript, which negatively regulates several genes involved in floral development, including *FLOWERING LOCUST (FT),* and promotes expression of others. Under LD conditions, miR172 targets are downregulated, thereby accelerating flowering [83].

It appears that miR156 is involved in photoperiodic flowering in several plant species (Table 1), and controls flowering in potatoes and soybeans, by negatively regulating miR172 [37,81]. Similarly, a variety of species showed their response to light via modulating miR170/171 family (Table 1). Additionally, the rice Os-miR171c promoter may be light responsive [85]. It is in agreement with this observation that Os-miR171c transcript levels oscillate during the day with an early morning peak, similar to that found for mature miR171 in *Arabidopsis* [85]. During dark and light hours, rice miR171 targets *OsHAM1 (ARABIDOPSIS THALIANA HAIRY MERISTEM 1)* to *OsHAM4*, exhibiting an increase in transcript expression. Although the nature of these rice oscillation patterns has not been determined, miR171c levels have been found to be higher under LD than SD even though the cause of the pattern is not known [85]. As the delayed heading (*dh*) mutant has an insertion of T-DNA into the Os-miR171c promoter, miR171c expression is upregulated, which suggests miR171c regulates heading process [85]. A second factor upregulating miR171c is LD, which promotes rice flowering under non-inductive conditions, and could hence influence rice flowering. The regulation of rice flowering by miR171 remains unclear, however, the data suggests that miR171c and *OsHAMs* are involved in regulating floral emergence in WT plants based on their expression patterns at the apex of their shoots. By comparing the expression levels of WT and mutant cells, there was also an evidence for downregulating the three key flowering regulators {*EHD1 (Early heading date 1), Hd3a (Heading date 3a)*, and *RFT1 (RICE FLOWERING LOCUS T 1)*} [85]. Furthermore, the mutant also expressed a greater amount of miR156, which inhibits flowering in several plant species [64,86], and of *OsPHYC*, which is also known to delay flowering in rice [85]. As a result, miR171 may in part, regulate *OsPHYC*-mediated light responses.

In addition to controlling photoperiodic flowering, miR5200 controls flower emergence by responding to the length of the day. The plant blooms much more rapidly under SD in comparison to LD, and mature miR5200 and its precursors, pri-miR5200a and pri-miR5200b, are found at levels that are much higher than those under SD [87,88]. Under SD and LD, miR5200a and miR5200b are positively correlated to active histone markers and negatively correlated to repressive histone marks. The *miR5200* gene expression is conserved in five more Pooideae species under SD than LD [87,88]. Two *FT-like* genes, *FTL1* and *FTL2*, are targeted by miR5200 in *B. distachyon* under long photoperiods whereas they are not under short photoperiods. Under LD, plants overexpressing miR5200 flower later than WT. Reduced miR5200 activity leads to earlier flowering on plants compared to WT showing the same patterns of response to photoperiod as the WT. Plants with reduced miR5200 levels produce *FTL1* and *FTL2* mRNA at higher levels under SD as opposed to LD conditions [87,88].

2.4.6. miRNA mediated photo-control of auxiliary bud growth

There are not much studies available about the involvement of miRNAs in light mediated control of axillary bud growth (ABG) in plants. However, very recently Mallet et al. [89] utilized the Rosa bush model and carried out a bioinformatics analysis of miRNAs from the previously available Rosa genomes. The authors explained that there were nine genes involved in photo-control of ABG in Rosa, which were the predicted targets of seven conserved miRNA families. Previous studies had already mentioned about the involvement of two miRNA families (miR156, miR164) in ABG via targeting *SPLs* and *NACs {NAM (no apical meristem, Petunia), ATAF1–2 (Arabidopsis thaliana activating factor), CUC2 (cup-shaped cotyledon, Arabidopsis)}, EXPA3 (Expansin 3)* and *APX1 (Ascorbate peroxidase 1)* [89–92], however, other five miRNAs (miR159, miR166, miR399, miR477, miR8175) were not discovered for their role in ABG. Authors hypothesized that due to the presence of other dominant miRNAs, the function of these five miRNAs may be masked in photo-control of ABG in Rosa. Although, the above-mentioned five miRNAs targeting *CKX (CYTOKININ OXIDASE/DEHYDROGENASE 1), 6PFK (6-Phosphofructokinase), RBOHB1 (RESPIRATORY BURST OXIDASE PROTEIEN 1), CYCD3 (Cyclin C-domain 3) and CYCD2, SUSY1 (SUCROSE SYNTHASE 1),* have been demonstrated for their considerable role in plant development, pathogen immunity and light intensity [93–98], however, in-depth studies are required to characterize them specifically for ABG.

3. Conclusions and future prospects

In certain plant organs and tissues, certain miRNAs are associated with specific biological processes occurring during certain developmental stages. Light is an essential environmental cue for plants. Changing climatic conditions significantly influence the wavelength of light particularly UV fluxes that play vital role in terrestrial ecosystems. Moreover, different altitude levels have a considerable impact on light as well due to variations in plant canopy coverage and clouds. Therefore, it is pertinent to dig deeper into the environment-mediated changes in light wavelengths and patterns followed by understanding the molecular mechanisms involved in these aspects. As light considerable impacts on various plant physiological and molecular mechanisms, therefore, the modulation of miRNAs by light is not surprising. Although, plant miRNA mediated response to diverse light wavelengths is hot topic to research, still a few light-responsive miRNAs have been uncovered and validated. Moreover, the functional roles of these particular miRNAs and their corresponding regulatory pathways should be confirmed urgently, so that they can be effectively utilized to engineer the plants to survive against the light mediated tissue and cell damage. Similarly, it is well understood that a single miRNA can target many genes thus engaging it in multiple roles at a same time as some target genes may be pleiotropic. Based on the accumulation of certain miRNA families, a correlation pattern of various miRNA families with distinct light conditions occurs

in different plant species. The regulation of light and photoperiod signaling by miRNAs appears to be two-dimensional, since miRNAs also have the ability to target these factors and are thus necessary for their proper function. Artificial miRNAs, target mimics, and overexpression of miRNA-resistant targets are examples of miRNA-based transgenic methods to improve agricultural and agronomic features. Even though so much research has been done related to miRNAs response during different light wavelengths and phytochrome mediated AS [99-102], still some key questions related to light responsive miRNAs and related elements should addressed. For example, how miRNAs coordinate with phytochromes when UV stresses plants? How miRNAs participate in crosstalk between light regulated phytohormone signaling and photoreceptors? What are the miRNA related contributions to photosynthesis and pigment screening during plant exposure to different light wavelengths? How do miRNAs contribute to plant fitness during tissues exposure to UV radiations? To uncover these questions, several approaches that can provide more insights such as transcriptomic, epigenetics, and functional assays. Additionally, the clustered regularly interspaced short palindromic repeats (CRISPR)-Cas9 technology that is a vital tool for a non-transgenic RNA-guided genome editing and targeted gene knockdown, can be used to exploit light-responsive miRNAs in a better way via editing their genetic targets to engineer economically important crops to ensure future food security.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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