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Blue light regulation of stomatal opening and the plasma membrane H^+-ATPase

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Light-induced stomatal responses were first reported by Francis Darwin (1898). Stomata open in response to light, including blue and red light (Shimazaki et al., 2007). Red light induces stomatal opening via photosynthesis in the mesophyll and guard cell chloroplasts (Mott et al., 2008; Suetsugu et al., 2014). In contrast, blue light as a signal induces stomatal opening. Phototropins expressed in guard cells act as major blue light receptors for stomatal opening (Kinoshita et al., 2001; Kinoshita et al., 2003; Inoue et al., 2008). Blue light-induced stomatal opening is mediated through activation of a plasma membrane (PM) H^+ pump, later identified as the PM H^+-ATPase, in guard cells (Assmann et al., 1985; Shimazaki et al., 1986; Kinoshita and Shimazaki, 1999). The blue light-activated pump provides driving force for stomatal opening concomitant with ion accumulation and cell volume increase in guard cells (Schroeder et al., 1987; Kinoshita and Hayashi, 2011). Note that stomatal opening in response to weak blue light as a signal requires background red light, indicating that red light has a synergistic effect on the blue light response in guard cells (Shimazaki et al., 2007).

Recent investigations of guard cells with respect to blue light-induced stomatal opening have greatly advanced our understanding. In this review, we focus on the recent progress of the blue light signaling pathway in guard cells and its regulation of the PM H^+-ATPase activity.

Blue light-signaling for stomatal opening

Stomata effectively open in response to blue light, especially under strong red light (Shimazaki et al., 2007; Marten et al., 2010). Our understanding of the signaling model for stomatal opening was mainly constructed from studies of blue light-induced stomatal opening (Fig. 1). A single guard cell possesses all signaling components, from blue light-perception to cell-volume increase, for stomatal opening. When guard cells are irradiated by blue light, blue light-photoreceptor protein kinases, phototropins, are activated through autophosphorylation and initiate signaling for stomatal opening (Kinoshita et al., 2001; Christie, 2007). Blue light induces autophosphorylation of two Ser residues in the kinase activation-loop of phototropin molecules, and phosphorylation is required for downstream signaling, probably through substrate recognition (Inoue et al., 2008; Inoue et al., 2010; Inoue et al., 2011). The activated phototropins directly phosphorylate another protein kinase BLUE LIGHT SIGNALING 1 (BLUS1), and phosphorylated BLUS1 indirectly transmits the signal to type 1 protein

Figure 1

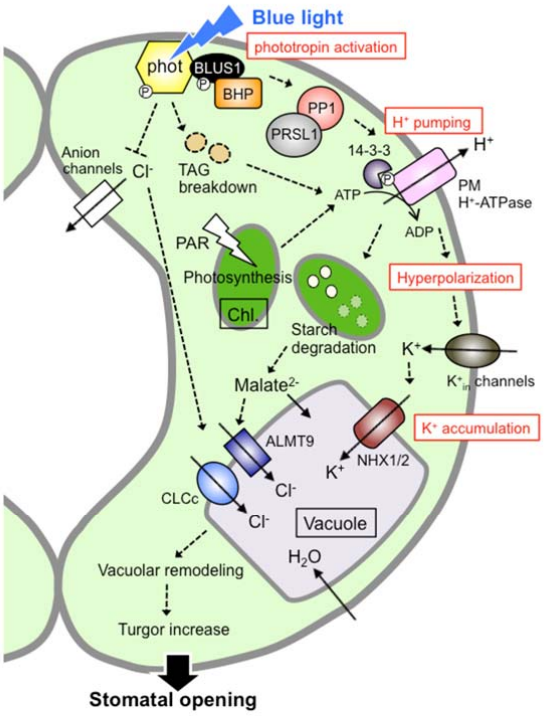

Figure 1. Blue light signaling pathway in stomatal guard cells.
Arrows and a T-bar represent positive and negative regulation, respectively. The P in the white circles indicates a phosphorylation of each protein. phot, phototropins; BLUS1, BLUE LIGHT SIGNALING1; BHP, BLUE LIGHT-DEPENDENT H^+-ATPASE PHOSPHORYLATION; PP1, Protein phosphatase 1; PRSL1, PP1 regulatory subunit2-like protein1; 14-3-3, 14-3-3 protein; K^+_{in} channel, inward rectifying K^+ channel; TAG, triacylglycerols; PAR, photosynthetically active radiation; Chl., Chloroplasts; NHX1/2, Na^+/H^+ EXCHANGER 1/2; ALMT9, aluminium-activated malate transporter 9; CLCc, chloride channel c. The time scale of each peak of the key signaling events for blue light-induced stomatal opening (approximately 2 h) is shown as follows: phototropin activation (within 1 min), H^+ pumping (approximately 2.5 min), Hyperpolarization (several min), K^+ accumulation (between 30 and 60 min). TAG breakdown, starch degradation, and vacuolar remodeling are observed within 1 to 2 h after the start of light illumination.

phosphatase (PP1) and its regulatory subunit PRSL1 (Takemiya et al., 2006; Takemiya et al., 2013a; Takemiya et al., 2013b; Takemiya et al., 2016). Note that BLUS1 expression is specific to guard cells and is not involved in the other

phototropin-mediated responses, such as phototropism, chloroplasts movements, and leaf flattening (Takemiya et al., 2013a), suggesting that BLUS1 defines signaling specificity of stomatal opening among the photoropin-mediated responses. The signal generated by BLUS1 finally activates the PM H^+-ATPase, mainly isoform AHA1, in guard cells through phosphorylation of a penultimate threonine in the C-terminus with subsequent binding of a 14-3-3 protein (Shimazaki et al., 2007; Hayashi et al., 2011; Yamauchi et al., 2016).

Very recently, a Raf-like protein kinase, BLUE LIGHT-DEPENDENT H^+-ATPASE PHOSPHORYLATION (BHP), was reported as the novel signaling component in blue light-dependent stomatal opening (Hayashi et al., 2017). BHP was identified through a screening of protein kinase inhibitors that suppress blue light-dependent PM H^+-ATPase phosphorylation in guard cells and similarities to the mammalian targets of the inhibitors. BHP does not bind to the PM H^+-ATPase but to BLUS1 and forms an early signaling complex with phototropins to mediate phosphorylation of a penultimate threonine of the PM H^+-ATPase (Hayashi et al., 2017). Guard cells in *bhp* mutant exhibited normal phosphorylation of the PM H^+-ATPase in response to the PM H^+-ATPase activator fusicoccin, suggesting that BHP is not likely to directly phosphorylate the penultimate threonine of PM H^+-ATPase. There may be an unidentified protein kinase that directly phosphorylates the PM H^+-ATPase in stomatal opening. In addition, whether BLUS1 phosphorylates and activates BHP is unknown at the present time. Further analyses are needed to clarify the early signaling for stomatal opening from photoropins to the PM H^+-ATPase activation and to identify the endogenous substrates of BLUS1, BHP, and PP1 in guard cells.

The blue light-activated PM H^+-ATPase drives H^+ transport across the PM and hyperpolarizes of the membrane (Shimazaki et al., 2007; Marten et al., 2010). This membrane hyperpolarization activates inward-rectifying K^+ (K^+_{in}) channels and induces an influx of K^+ (Lebaudy et al., 2008; Kim et al., 2010), resulting in the accumulation of K^+, and the counter anions Cl^-, nitrate, and malate^{2-}.K^+ and Cl^- are immediately transported into the vacuole via the tonoplast-localized K^+/H^+ exchangers NHX1 and NHX2 and vacuolar chloride channels ALMT9 and CLCc, respectively (Jossier et al., 2010; Chen et al., 2012; De Angeli et al., 2013; Andrés et al., 2014), and K^+ accumulation into the vacuole involves dynamic remodeling of vacuolar structure for stomatal opening (Andrés et al., 2014). Accumulation of these ions decreases the water

potential of guard cells, which leads to water uptake into the vacuole and turgor increase, leading to stomatal opening (Inoue et al., 2010; Marten et al., 2010). The details of ion transports in guard cells are reviewed in this Focus Issue (Eisenacha and De Angeli, 2017; Jezek and Blatt, 2017). Recently, Santelia and colleagues demonstrated that starch in guard cell chloroplasts is degraded by phototropin-mediated signaling downstream of PM H^+-ATPase activity and the degradation contributes to stomatal opening (Horrer et al., 2016), probably through malate synthesis (Shimazaki et al. 2007). It remains an interesting and important question on how the activity of the PM H^+-ATPase is linked to the starch degradation pathway in chloroplasts (Santelia and Lunn, 2017).

In addition to the pursuit of signaling components as described above, regulation of the expression and localization of key signaling factors that determines stomatal aperture indirectly have also been investigated recently. For example, the bHLH family transcription factors of ABA-RESPONSIVE KINASE SUBSTRATEs (AKSs) and GARP transcription factors of GOLDEN 2-LIKE 1 and 2 (GLK1 and 2) bind to the promoter of the K^+_{in} channel *KAT1* gene and increase the K^+_{in} channel expression in guard cells (Takahashi et al., 2013; Nagatoshi et al., 2016). GLKs also positively regulate *BLUS1* expression (Nagatoshi et al., 2016). These transcriptional regulations contribute to enhance stomatal opening. Moreover, the signaling components for photoperiodic flowering including cryptochromes, GIGANTEA, CONSTANS, EARLY FLOWERING 3, FLOWERING LOCUS T (FT), TWIN SISTER OF FT, and SUPPRESSOR OF OVEREXPRESSION OF CO 1, are expressed in guard cells and also affect light-induced stomatal opening probably via transcriptional regulations in guard cells, but details of the regulatory targets are unknown (Kinoshita et al., 2011; Ando et al., 2013; Kimura et al., 2015). In addition, the Munc13-like protein PATROL1 may be involved in the enhancement of light-induced stomatal opening by promoting the recruitment of AHA1 to the PM of guard cells (Hashimoto-Sugimoto et al., 2013). Both aminophospholipid ATPase (ALA10) flippase and phospholipase $A_2\beta$ (PL $A_2\beta$) are involved in light-induced stomatal opening through lysophospholipid generation (Seo et al., 2008; Poulsen et al., 2015). ALA10 promotes phospholipid uptake into guard cells and PL $A_2\beta$ generates lysophospholipids using phospholipids as a substrate. One of the products, lysophosphatidylcholine functions as a specific activator of the PM H^+-ATPase (Palmgren, 2001), because both ALA10 and PL $A_2\beta$ may have a positive effect on the stomatal opening through enhance the PM H^+-ATPase activity.

Furthermore, photosynthetic processes in guard cell chloroplasts provide fuel (ATP and/or reducing equivalents) for blue light-dependent H^+ pumping of the PM H^+-ATPase and contribute to stomatal opening (Suetsugu et al., 2014). Correspondingly, guard cells lacking chloroplasts in the *crumpled leaf* mutant displayed attenuation of both guard cell ATP levels and stomatal opening in response to light (Wang et al., 2014). Stored triacylglycerols in guard cells are broken down in response to light and the catabolic process is also thought to supply ATP for PM H^+-ATPase activity in stomatal opening (McLachlan et al., 2016).

Crosstalk between blue light- and ABA-signaling in light-induced stomatal opening

The plant hormone ABA synthesized in response to drought stress conditions drastically reduces stomatal aperture to prevent water loss in the presence of light (Bauer et al., 2013; Waadt et al., 2014; Kim et al., 2010; Osakabe et al., 2014). ABA induces stomatal closure in already open stomata, called "stomatal closure" and simultaneously inhibits light-induced stomatal opening, called "inhibition of stomatal opening", and both physiological regulatory mechanisms are required to close stomata efficiently under sunlight. It is known that ABA-signaling in guard cells effectively suppresses blue light-signaling in inhibition of stomatal opening with various ways. First, ABA accelerates the release of ions from guard cells by activating S- and R-type anion channels, outward-rectifying K^+ channels, and K^+ uptake transporters (KUPs) in stomatal closure (Negi et al., 2008; Vahisalu et al., 2008; Kim et al., 2010; Osakabe et al., 2013). ABA suppresses these processes via ABA-receptor components PYR/PYL/RCAR-PP2Cs-SnRK2s in guard cells. (Fujii et al., 2009; Ma et al., 2009; Park et al., 2009; Umezawa et al., 2009; Vlad et al., 2009; Jezek and Blatt, 2017) with subsequent second messengers H_2O_2, H_2S, NO, phosphatidic acid (PA), and cytosolic Ca^{2+} (Inoue et al., 2010; Scuffi et al., 2014). It has been reported that H_2S also functions in parallel to ABA signaling events (Papanatsiou et al., 2015). Simultaneously, in the inhibition of stomatal opening, ABA suppresses blue light-signaling of the activation of PM H^+-ATPase via ABA-receptor components and H_2O_2, NO, PA, and Ca^{2+} (Shimazaki et al., 2007; Zhang et al., 2007; Inoue et al., 2010; Kim et al., 2010; Takemiya and Shimazaki, 2010; Hayashi et al., 2011; Hayashi and Kinoshita, 2011). PA directly inhibits PP1 catalytic activity and blocks blue light-signaling between phototropins and the PM H^+-ATPase (Takemiya and Shimazaki, 2010). In addition, ABA inhibits K^+_{in}

channel activity and many ABA-signaling components affect this inhibition (Kim et al., 2010; Jezek and Blatt, 2017). OPEN STOMATA 1 (OST1), an ABA-activated protein kinase that operates downstream of the ABA-receptor components, suppresses K^+_{in} channel KAT1 activity through direct phosphorylation (Sato et al., 2009). The second messengers, such as Ca^{2+}, and G-proteins Gα and Gβ are also involved in ABA-induced K^+_{in} channel inhibition (Fan et al., 2008; Kim et al., 2010). Moreover, the S-type anion channels SLAC1 and SLAH3, which drive stomatal closure, are strongly upregulated by drought stress in guard cells and inhibit KAT1 activity by direct binding (Zhang et al., 2016). Second, ABA decreases the expression of K^+_{in} channel genes via inactivation of AKS transcription factors through phosphorylation by OST1 in guard cells (Takahashi et al., 2013; Takahashi et al., 2016). Third, ABA promotes internalization of KAT1 from the PM into endomembrane compartments by endocytosis, thereby reducing the amount of K^+_{in} channels functioning at the PM (Sutter et al., 2007).

Conversely, when plants are grown under well-watered conditions, blue light suppresses signaling of ABA-induced stomatal closure to promote stomatal opening. Blue light-receptor cryptochromes reduce ABA content in the plant body, and this process is thought to affect ABA-signaling in guard cells (Boccalandro et al., 2012). More directly, blue light also stimulates stomatal opening by suppressing anion release from guard cells. This process involves light-dependent inhibition of S-type anion channels in a phototropin-dependent manner (Marten et al., 2007). It was also reported that light-produced phosphatidylinositol 4,5-bisphosphate inhibits anion channel activity in guard cells (Lee et al., 2007). Consistent with these results, stomata in the *slac1-1* mutant are slightly open under dark-adapted conditions and open larger than those in wild type in response to light (Wang et al., 2012).

Involvement of PM H^+-ATPase in stomatal opening

PM H^+-ATPases, a family of P-type ATPases, consist of a functional polypeptide with 10 transmembrane domains and three cytosolic domains, including the N-terminal domain, catalytic domain, and C-terminal autoinhibitory domain (Fig. 2). In *Arabidopsis*, eleven genes encode PM H^+-ATPases (*AHA1–AHA11*), and a double-knockout mutant of *AHA1* and *AHA2*, which are predominantly expressed in all cell types, displays an embryonic lethal phenotype (Haruta et al., 2010). The membrane potential and proton gradient created by PM H^+-ATPases energize multiple ion channels

Figure 2

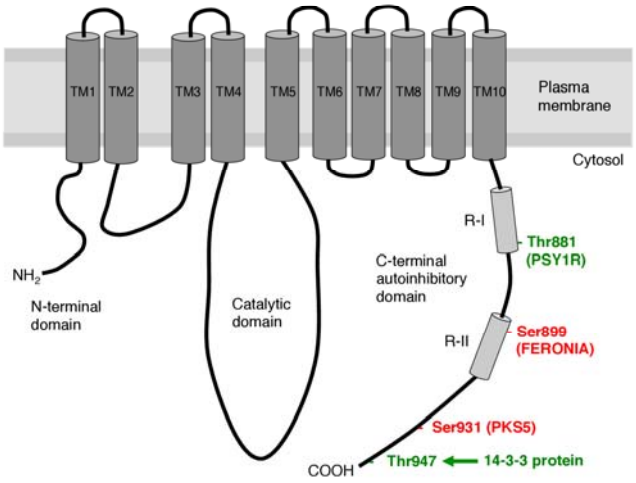

Figure 2. Schematic structure of PM H$^+$-ATPases.
PM H$^+$-ATPases possess 10 transmembrane domains (TM1-10) and three cytosolic domains, including the N-terminal domain, catalytic domain, and C-terminal autoinhibitory domain containing the R-I and R-II regions (Palmgren, 2001). There are several phosphorylation sites in the C-terminal domain (Thr881, Ser899, Ser931, and Thr947). Thr881, Ser899, and Ser931 are phosphorylated by PSY1R, FERONIA, and PKS5, respectively. 14-3-3 protein binds to the phosphorylated penultimate threonine (Thr947). Phosphorylations of Thr881 and Thr947 lead to activation of PM H$^+$-ATPase (Green). Phosphorylations of Ser899 and Ser931 lead to inactivation of PM H$^+$-ATPase (Red). The numbering of the amino acid residues corresponds to *Arabidopsis* H$^+$-ATPase2 (AHA2).

191 and various H$^+$-coupled transporters in the PM for diverse physiological responses
192 including stomatal movement, phloem loading and unloading, xylem loading and
193 unloading, seed germination, solute uptake in roots, leaf movement, tip growth, and cell

194 expansion (Haruta et al., 2015; Wang et al., 2014b; Takahashi and Kinoshita, 2016). In
195 addition, proton transport through PM H^+-ATPases controls cytosolic pH homeostasis
196 and apoplastic pH (Falhof et al., 2016). It is worthy of note that modeling analyses of
197 ion transport in the stomatal guard cells reveal importance of PM H^+-ATPase activity
198 not only in proton gradient formation and pH control, but also in driving K^+ Ca^{2+}, anion
199 transport and metabolism in guard cells (Chen et al. 2012; Hills et al. 2012;
200 Minguet-Parramona et al. 2016), demonstrating that PM H^+-ATPase plays a pivotal role
201 in guard cells physiology.
202 Since the 1970s, it has been known that light induces proton extrusion from stomatal
203 guard cells, K^+ uptake, and swelling of guard cells. Physiological and
204 electro-physiological analyses revealed the properties of blue light-activated proton
205 pump using *Vicia* guard cell protoplasts (Assmann et al. 1985; Shimazaki et al., 1986).
206 Later, conclusive evidence was obtained by biochemical analysis. PM H^+-ATPase is
207 activated and phosphorylated in response to blue light on a penultimate threonine
208 residue in the C-terminus and 14-3-3 protein binds to the phosphorylated C-terminus
209 region (Kinoshita and Shimazaki, 1999; Kinoshita and Shimazaki, 2002).
210 In addition to biochemical evidence, genetic evidence has also been obtained.
211 Dominant mutants of *AHA1*, a major H^+-ATPase isoform in *Arabidopsis*, *ost2-1D* and
212 *ost2-2D*, displayed constitutively open stomatal phenotypes, since dominant mutations
213 cause constitutive activity of H^+-ATPase (Merlot et al., 2007). More recently, it was
214 reported that loss of function mutants of *AHA1* showed reduced blue light-induced
215 stomatal opening (Yamauchi et al., 2016) and a closed stomatal phenotype (Osakabe et
216 al., 2016). Furthermore, a loss of function mutant of OSA7, a major PM H^+-ATPase
217 isoform in rice, also showed reduced blue light-induced increase of stomatal
218 conductance (Toda et al., 2016). Overexpression of *AHA2* using a strong guard cell
219 promoter enhanced light-induced stomatal opening, leading to increased photosynthetic
220 activity and plant biomass (Yang et al., 2008; Wang et al., 2014a). These biochemical
221 and genetic findings clearly demonstrate that the PM H^+-ATPases act as H^+ pumps in
222 the PM and are vital for stomatal opening.
223
224 **Regulation of PM H^+-ATPase by reversible phosphorylation**
225 It has been demonstrated that PM H^+-ATPase activity is regulated by phosphorylation of
226 several sites (Haruta et al. 2015; Falhof et al. 2016). The first reported and most studied

phosphorylation site is the penultimate threonine in the C-terminus (Palmgren, 2001; Wang et al., 2014b). Blue light activates PM H^+-ATPase via the guard cell-specific signaling pathway, leading to phosphorylation of the penultimate threonine in guard cells (Shimazaki et al. 2007). In addition, recent investigations revealed that phosphorylation level of the penultimate threonine in PM H^+-ATPase were modulated in response to physiological and environmental signals, such as light, salt, sucrose, auxin, gibberellin, and ABA in several tissues and cell types besides guard cells (Niittylä et al., 2007; Chen et al., 2010; Okumura et al., 2012; Takahashi et al., 2012; Hayashi et al., 2014; Inoue et al., 2016; Okumura et al., 2016). These results indicate that there are several unique signaling pathways in each tissue and cell type, but a final regulatory mechanism, that is, phosphorylation of the penultimate threonine at the C-terminus of the H^+-ATPase, is common in these responses.

The protein kinase responsible for the phosphorylation of the penultimate threonine in PM H^+-ATPase has not been identified, despite strenuous efforts, although *in vitro* protein kinase activity for the penultimate threonine of PM H^+-ATPase was found in the plasma membrane isolated from spinach leaves, the microsomes from guard cell protoplasts of *Vicia*, and the plasma membrane from etiolated seedlings of *Arabidopsis* (Kinoshita and Hayashi 2011). On the other hand, it was suggested that dephosphorylation of the phosphorylated penultimate threonine of PM H^+-ATPases is mediated by the membrane-localized Mg^{2+}/Mn^{2+}-dependent protein phosphatase 2C (PP2C)-like activity in *Vicia* guard cells and *Arabidopsis* etiolated seedlings (Hayashi et al., 2010). Eventually, D-clade PP2Cs were shown to be involved in the dephosphorylation of PM H^+-ATPase in etiolated seedlings (Schweighofer et al. 2004; Spartz et al., 2014; Ren and Gray, 2015). In addition, *SMALL AUXIN-UP RNAs* (*SAURs*), a large multigene family of early-auxin-responsive genes, inhibit D-clade PP2C activity through physical interaction (Spartz et al., 2014; Sun et al. 2016). It is noteworthy that SAUR19-overexpressing plants displayed enhanced water loss in detached leaves, wilted faster than wild type upon cessation of watering, and exhibited delayed stomatal closure (Spartz et al., 2014; Spartz et al., 2017), and that many *SAUR* genes are repressed by ABA, which certainly reduces stomatal aperture (Nemhauser et al. 2006; Kodaira et al. 2011). Taken together these biochemical and genetic data strongly suggest that clade D of PP2C and SAURs are involved in the regulation of PM H^+-ATPase in stomatal guard cells. However, it is still unknown that how SAURs are

regulated in response to blue light in guard cells.

In addition to the penultimate threonine, three residues were demonstrated to regulate PM H^+-ATPase activity using non-guard cells (Haruta et al., 2015; Rudashevskaya et al., 2012) (Fig. 2). A receptor kinase, FERONIA, phosphorylates a serine residue (Ser899 in AHA2) in the C-terminal autoinhibitory domain of PM H^+-ATPase and this phosphorylation suppresses proton efflux by PM H^+-ATPase (Haruta et al., 2014). Moreover, the phosphorylation of a threonine residue (Thr881 in AHA2) in the C-terminal autoinhibitory domain of PM H^+-ATPase is induced by a receptor kinase, PSY1R, and application of the ligand peptide for PSY1R, PSY1, increased proton efflux, suggesting that phosphorylation of Thr881 activates PM H^+-ATPase activity (Fuglsang et al., 2014). In addition, the serine residue (Ser931 in AHA2) in the C-terminal autoinhibitory domain of the PM H^+-ATPase is phosphorylated by PKS5, a Ser/Thr protein kinase. Phosphorylation of Ser931 inhibits interaction of the PM H^+-ATPase with 14-3-3 protein and decreases PM H^+-ATPase activity (Fuglsang et al., 2007). The physical interaction of chaperone J3 with PKS5 induces the activation of PM H^+-ATPase by repressing PKS5 activity (Yang et al., 2010). In addition, it has been reported that type 2A protein phosphatase scaffolding subunit A interacts with the C-terminus region of PM H^+-ATPase (Fuglsang et al., 2006), and that a negative regulator of plant immunity RIN4 activates PM H^+-ATPase activity and the *rin4* mutant shows reduced stomatal aperture (Liu et al., 2009). Thus, post-translational modifications, such as phosphorylation of multiple sites in the C-terminal domain and/or protein-protein interactions, regulate PM H^+-ATPase activity. Blue light induces phosphorylation on multiple serine and threonine residues in the C-terminus of the PM H^+-ATPase in *Vicia* guard cells (Kinoshita and Shimazaki, 1999). However, it is still unclear whether other phosphorylation sites, such as Thr881, Ser899, and Ser931, are involved in the regulation of PM H^+-ATPase in guard cells in response to blue light. Further investigations will be needed to clarify this.

Conclusion and perspective

In this review, we described recent advances in the blue light signaling pathway in stomatal guard cells and the regulatory mechanisms of PM H^+-ATPase. Stomata open in response to blue light to facilitate gas exchange between the plant and the atmosphere. This response is key to terrestrial plant life, as gas exchange is necessary not only for

293 photosynthesis but also for water uptake from the roots. So far, major signaling
294 components involved in the blue light signaling pathway in stomatal guard cells have
295 been identified, such as phototropin, BLUS1, BHP, PP1, and PM H^+-ATPase; however,
296 the signaling mechanism is not fully understood. For example, how do blue light signals
297 induce phosphorylation of the penultimate threonine of PM H^+-ATPase, which is a key
298 enzyme for stomatal opening? Whether blue light signal induces the phosphorylation of
299 PM H^+-ATPase or suppresses dephosphorylation of PM H^+-ATPase, or both, is still
300 unknown. Elucidation of this mechanism and identification of the kinase and
301 phosphatase for PM H^+-ATPase in guard cells will provide novel insights into both the
302 blue light signaling pathway through phototropins and the regulation of H^+-ATPase in
303 plant cells. Given the importance of stomatal regulation, future investigations will not
304 only improve our understanding of the molecular mechanisms of signaling pathways in
305 plants, but also provide important clues for agricultural strategies to improve
306 photosynthetic or water use efficiency, leading to an increase in the biomass and harvest
307 of crops.
308
309
310 **Figure legends**
311
312 Figure 1. Blue light signaling pathway in stomatal guard cells.
313 Arrows and a T-bar represent positive and negative regulation, respectively. The P in the
314 white circles indicates a phosphorylation of each protein. phot, phototropins; BLUS1,
315 BLUE LIGHT SIGNALING1; BHP, BLUE LIGHT-DEPENDENT H^+-ATPASE
316 PHOSPHORYLATION; PP1, Protein phosphatase 1; PRSL1, PP1 regulatory
317 subunit2-like protein1; 14-3-3, 14-3-3 protein; K^+_{in} channel, inward rectifying K^+
318 channel; TAG, triacylglycerols; PAR, photosynthetically active radiation; Chl.,
319 Chloroplasts; NHX1/2, Na^+/H^+ EXCHANGER 1/2; ALMT9, aluminium-activated
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337

338

ADVANCES

- Phototropin kinases activate the plasma membrane (PM) H^+-ATPase in guard cells, which provides driving force for the accumulation of K^+ through K^+_{in} channels in the PM.
- ABA suppresses blue light-induced activation of PM H^+-ATPase and K^+_{in} channel via ABA receptor components PYR/PYL/RCAR-PP2Cs-SnRK2s in guard cells.
- The novel protein kinase BLUS1 acts as a phototropin substrate and transduces blue light signal to the PM H^+-ATPase via the type 1 protein phosphatase and its regulatory subunit PRSL1.
- A Raf-like kinase BHP interacts with BLUS1 and mediates blue light signaling between BLUS1 and PM H^+-ATPase.
- Degradation of starch in guard cell chloroplasts is required for phototropin-mediated signaling downstream of PM H^+-ATPase activity and contributes to stomatal opening through malate synthesis.
- PP2C-Ds directly dephosphorylate the penultimate threonine of PM H^+-ATPase in etiolated seedlings and are potentially involved in dephosphorylation of PM H^+-ATPase in guard cells.

OUTSTANDING QUESTIONS

- How does the blue light signal induce phosphorylation of the penultimate threonine in PM H^+-ATPase in guard cells? How do phototropin-BLUS1, BHP, PP1, and H^+-ATPase connect in this signaling pathway?
- What are substrates of BLUS1, BHP, and PP1 in guard cells?
- What protein kinase is involved in direct phosphorylation of the penultimate threonine of PM H^+-ATPase in guard cells and other cell types?
- Are PP2C-Ds involved in direct dephosphorylation of PM H^+-ATPase in guard cells?
- How does PM H^+-ATPase activation induce degradation of starch in guard cell chloroplasts?
- What is a next game-changing technique, following patch-clamp, gas-exchange, and thermal imaging, in stomatal research? Are live-cell imaging, chemical biology, and comprehensive proteomics in guard cells powerful approaches for future studies?

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