PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2025.011 PHOTOSYNTHETICA 63 (2): 104-115, 2025

Special issue on Photosynthesis in extreme environments

REVIEW

Potential mechanisms for the rapid post-drought reversal of ABA-induced stomatal closure by melatonin, 5-aminolevulinic acid, and brassinosteroids

M. WASEEM[*,+], M.M. HASAN[**], Y. HAZZAZI[***], B.M. ALHARBI[#], M.U. GHANI[##], P. AHMAD[###], and M. CARRIQUÍ[†,+]

Guangdong Provincial Key Laboratory of Applied Botany, and Key Laboratory of National Forestry and Grassland Administration on Plant Conservation and Utilization in Southern China, South China Botanical Garden, Chinese Academy of Sciences, 510640 Guangzhou, China[*]
Independent Researcher, Green Model Town, 1214 Dhaka, Bangladesh[**]
Biology Department, Faculty of Science, 45142 Jazan University, Jazan, Saudi Arabia[***]
Biology Department, Faculty of Science, University of Tabuk, 71491 Tabuk, Saudi Arabia[#]
Institute of Agricultural Resources and Environment, Guangdong Academy of Agricultural Sciences, 510640 Guangzhou, China[##]
Department of Botany, GDC, 192301 Pulwama, Jammu and Kashmir, India[###]
Research Group on Plant Biology under Mediterranean conditions, Department of Biology, University of the Balearic Islands/Institute of Agro-Environmental Research and Water Economy – INAGEA, Carretera de Valldemossa, 07122 Palma, Spain[†]

Abstract

The regulation of stomatal movements is crucial for plants to optimize gas exchange and water balance. The plant hormone abscisic acid (ABA) triggers stomatal closure in response to drought, effectively minimizing water loss to prevent hydraulic failure. However, it significantly constrains photosynthesis, restricting plant growth and productivity. Therefore, rapid post-drought stomatal opening is crucial for earlier photosynthetic recovery. This review explores how phytohormones or plant growth regulators reverse ABA-induced stomatal closure. Phytomelatonin, 5-aminolevulinic acid, and brassinosteroids promote stomatal reopening by either ABA degradation or suppressing its biosynthesis through the downregulation of corresponding genes. This results in less ABA-induced H_2O_2 accumulation in guard cells, which lowers H_2O_2-triggered Ca^{2+} levels in guard cells, and promotes the opening of KAT1 (K^+_{in} channels). Insights from this review highlight the potential mechanisms of stomatal reopening for earlier post-drought gas exchange recovery, offering potential avenues to enhance plant productivity under changing environmental conditions.

Keywords: 5-aminolevulinic acid; abscisic acid; brassinosteroids; drought stress; photosynthesis; phytomelatonin; stomata.

Highlights

- ABA-induced stomatal closure minimizes water loss but constrains photosynthesis
- Rapid post-drought stomatal opening is crucial for earlier photosynthetic recovery
- Melatonin, ALA, and BRs have the potential to reverse ABA-induced stomatal closure

Received 27 June 2024
Accepted 25 March 2025

[+]Corresponding author
e-mail: waseem25@scbg.ac.cn
m.carriqui@uib.cat

Abbreviations: ABA – abscisic acid; ALA – 5-aminolevulinic acid; BRs – brassinosteroids; GHR1 – guard cell hydrogen peroxide-resistant1; NCED – 9-cis-epoxycarotenoid dioxygenase; PP2C – clade A type-2C protein phosphatases; PYL – pyrabactin resistance-like; PYR – pyrabactin resistance; RCAR – regulatory components of the abscisic acid receptor; ROS – reactive oxygen species; SLAC1 – Slow Anion Channel-Associated 1; SLAH3 – SLAC1 homolog 3; SnRK2 – SNF1-related protein kinases 2.

Acknowledgments: Marc Carriquí was supported by a Vicenç Mut 2022 postdoctoral fellowship (PD-047-2022) funded by Ministry of European Funds, University and Culture of the Government of the Balearic Islands.

Conflict of interest: The authors declare that they have no conflict of interest.

Introduction

Plants in nature consistently encounter environmental stresses (Sharma *et al.* 2022, Zhang *et al.* 2022). Drought is a major environmental stressor that negatively impacts plant physiology (Abid *et al.* 2018), considerably diminishing crop yield and presenting a significant challenge to agricultural production (Zhang *et al.* 2024). Plants have evolved integrated physiological, molecular, and defense mechanisms to mitigate the harmful consequences of drought stress, allowing them to detect and respond promptly to unfavorable environmental changes (Huber *et al.* 2019, Hasan *et al.* 2021a, Waseem *et al.* 2021, 2024). Among these, stomatal closure is a prevalent adaptive response vital for reducing transpiration, thus maintaining water status and preventing xylem hydraulic dysfunction (Blackman *et al.* 2009, Pirasteh-Anosheh *et al.* 2016).

The plant hormone abscisic acid (ABA) regulates stomatal movements during water-deficient conditions (Long *et al.* 2019, Hsu *et al.* 2021, Hasan *et al.* 2022). ABA triggers the activation of guard cell membrane channels and transporters, reducing turgor pressure and inducing stomatal closure (Brodribb and McAdam 2013). This strategy allows plants to minimize water loss, thereby sustaining cellular functions and delaying hydraulic dysfunction and, therefore, plant death (Brodribb *et al.* 2021). However, excessive accumulation of ABA may result in the overproduction of reactive oxygen species (ROS) (Li *et al.* 2015), causing oxidative damage such as lipid peroxidation, electrolyte leakage, and chlorophyll degradation (Demidchik *et al.* 2014, Sachdev *et al.* 2021). Prolonged stomatal closure also implies a sustained decline in photosynthetic activity, leading to stunted growth and lower crop yields, adversely affecting the overall plant health and productivity (Damour *et al.* 2009). Stomatal closure for an extended period can also result in leaf overheating (Marchin *et al.* 2022). Thus, controlling stomatal opening is equally critical as closure, and plants need to optimize stomatal behavior to balance water conservation with carbon fixation (Zhang *et al.* 2024).

During the post-drought period, plants must efficiently reopen their stomata to resume photosynthesis, allowing them to accumulate additional assimilates to endure subsequent water scarcities (Trifilò *et al.* 2017, Tomasella *et al.* 2019). While plant water potential can fully recover within hours to days after re-watering (Hasan *et al.* 2021b), stomatal conductance can remain suppressed (Lovisolo *et al.* 2008, Ruehr *et al.* 2019). For short-term recovery, elevated ABA or ethylene levels may restrict stomatal re-opening (Duan *et al.* 2020, Hasan *et al.* 2024). Over the longer term, the extent of stomatal recovery is increasingly thought to correlate with the level of hydraulic damage in the xylem, such that persistent embolism formation limits or delays stomatal conductance restoration (Rehschuh *et al.* 2020, Wagner *et al.* 2023, Flor *et al.* 2025).

Several studies have examined whether high ABA contents persistently inhibit stomatal recovery after drought. In the grapevine, for example, stomatal closure can be triggered by hydraulic signals and subsequently maintained by ABA (Tombesi *et al.* 2015). Similarly, in poplar, a sustained post-drought elevation in ABA content was associated with carbohydrate mobilization and hydraulic recovery (Brunetti *et al.* 2020), suggesting that ABA accumulation can modulate stomatal conductance well beyond the immediate stress period. However, other research highlights potential species-specific differences. In Scots pine saplings, stomatal behavior during rewatering was largely independent of variations in ABA or cytokinins (Zlobin *et al.* 2023). Likewise, Liu *et al.* (2024) observed that in maize leaves, factors such as drought severity thresholds and hydraulic constraints can override the inhibitory effects of ABA on gas exchange during recovery. These contrasting findings indicate that the role of ABA in inhibiting long-term stomatal reopening may vary with species.

Therefore, comprehending the mechanisms underlying rapid post-drought stomatal reopening and photosynthetic recovery is essential for promoting the development of drought-resilient crops. To date, much research has focused on elucidating the mechanisms underlying stomatal closure in response to drought, with comparatively less attention given to post-drought stomatal recovery. This review summarizes the signaling pathways involved in ABA-induced stomatal closure and explores the interactions of melatonin, 5-aminolevulinic acid, and brassinosteroids with ABA signaling pathways, with a particular focus on possible mechanisms for post-drought reversal of ABA-mediated stomatal closure by these bioactive compounds. In addition, we elucidate the physiological significance of reversing ABA-induced stomatal closure in the context of plant recovery and stress resilience.

Signaling mechanisms of ABA-induced stomatal closure

Abscisic acid (ABA), a plant hormone, is pivotal in regulating stomatal movements and enhancing plant resilience to water-deficit conditions (Fig. 1). During restricted water supply, ABA accumulates in the leaves, aided by the enzyme 9-cis-epoxycarotenoid dioxygenase (NCED), which drives ABA biosynthesis (Li *et al.* 2015, Long *et al.* 2019). This accumulation results in decreased turgor pressure, narrowing the stomatal pore aperture, and ultimately leading to stomatal closure (Brodribb and McAdam 2013). ABA significantly enhances the activity of NADPH oxidase, resulting in increased H_2O_2 synthesis (Jiang and Zhang 2002, Postiglione and Muday 2023), a reactive oxygen species (ROS) that directly facilitates ABA-induced stomatal closure. It also activates Ca^{2+} channels in the plasma membrane, leading to elevated cytoplasmic Ca^{2+} contents in the guard cells (Neill *et al.* 2002). H_2O_2-induced stomatal closure has been documented in various vascular plant groups, encompassing woody plants (Deuner *et al.* 2011) and herbs (Zhang *et al.* 2001). Consequently, both ABA and H_2O_2 are pivotal in stomatal closure.

The buildup of ABA in plant tissues is governed by the interplay between its biosynthesis and breakdown

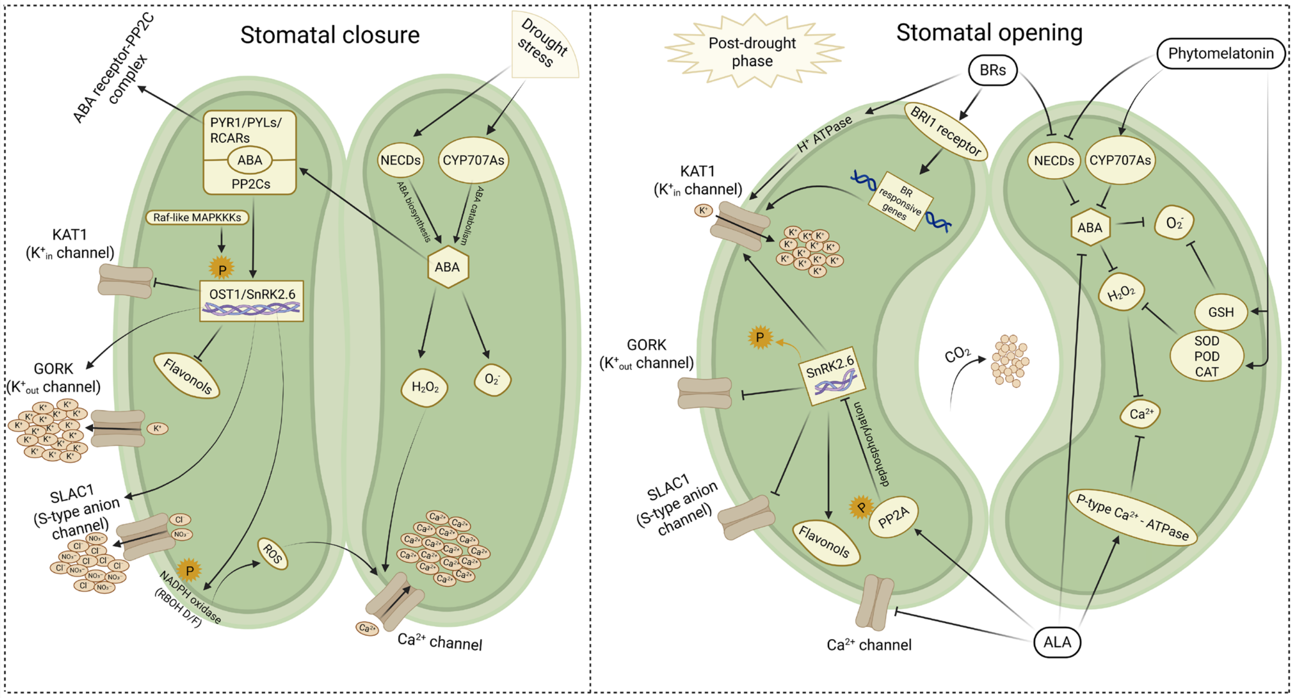


Fig. 1. Proposed schematic diagram illustrating the ABA-induced stomatal closure and possible mechanisms by which phytomelatonin, 5-aminolevulinic acid (ALA), and brassinosteroids (BRs) may reverse ABA-induced stomatal closure during the post-drought phase. → represents a positive effect, and —| represents a negative effect. ABA – absicisic acid; ALA – 5-aminolevulinic acid; BRs – brassinosteroids; SOD – superoxide dismutase; POD – peroxidase; CAT – catalase; GSH – glutathione; P – phosphorylation; NCEDs – 9-cis-epoxycarotenoid dioxygenase; CYP707A – ABA 8'-hydroxylase; H_2O_2 – hydrogen peroxide; AKSs – ABA-responsive kinase substrates; PYR1/PYLs/RCARs – PYRABACTIN RESISTANCE/PYRABACTIN RESISTANCE-LIKE/REGULATORY COMPONENTS OF THE ABSCISIC ACID RECEPTOR; SnRK2.6 – SNF1-regulated protein kinase 2.6; OST1 – OPEN STOMATA 1; PP2C – protein phosphatase 2C; Ca^{2+} – calcium ions; KAT1 – potassium channel protein; GORK – guard cell outward-rectifying K^+ channel, PP2A – protein phosphatase 2A; SLAC1 – Slow Anion Channel-Associated 1.

(Kushiro *et al.* 2004). The NCED enzyme catalyzes the cleavage of the 11, 12 double bonds of a C40 carotenoid (Car), resulting in the production of xanthoxin (Qin and Zeevaart 1999). Among *Arabidopsis*'s five NCED family members, AtNCED3 is essential for ABA production in response to drought (Iuchi *et al.* 2001). ABA undergoes catabolism to produce 8'-hydroxy ABA *via* hydroxylation by ABA 8'-hydroxylase (Nambara and Marion-Poll 2005). The hydroxylation occurring at the 8'-position appears to be the crucial step in the breakdown of ABA. This is facilitated by CYP707A, an ABA 8'-hydroxylase from the class of cytochrome P450 monooxygenase (Saito *et al.* 2004). Research indicates that MdCYP707A1 and MdCYP707A2 are responsible for the regulation of ABA metabolism in apple under drought conditions (Kondo *et al.* 2012). Overall, these enzymes help plants withstand water stress by regulating ABA contents. ABA-induced stomatal closure typically involves the ion efflux from guard cells. This movement of ions subsequently induces osmotic water efflux, leading to decreased turgor pressure of the guard cells, ultimately causing stomatal closure. The activation of S-type (slow) and R-type (rapid) anion channels is crucial during this process (Keller *et al.* 1989, Schroeder and Hagiwara 1989), facilitating the efflux of anions from guard cells and contributing to plasma membrane depolarization. This subsequently triggers the activation of potassium efflux channels. The sustained activation of both S-type anion channels and potassium efflux channels for extended periods allows efficient solute release from guard cells and causes stomatal closing (Schroeder and Hagiwara 1989).

The key elements involved in ABA signaling during stomatal movement include clade A type-2C protein phosphatases (PP2Cs) (Park *et al.* 2009), SNF1-related protein kinases 2 (SnRK2s), specifically SnRK2.2, SnRK2.3, and SnRK2.6/OST1 (Takahashi *et al.* 2020), and the Pyrabactin Resistance, Pyrabactin Resistance-Like, and Regulatory Components of the Abscisic Acid Receptor (PYR/PYL/RCAR) (Raghavendra *et al.* 2010). Additionally, ion channels such as Slow Anion Channel-Associated 1 (SLAC1) (Geiger *et al.* 2009) and SLAC1 homolog 3 (SLAH3) (Hedrich and Geiger 2017) are integral to the process. Various factors modulate the activity of these signaling components (Chen *et al.* 2020). Under non-stress conditions (*i.e.*, without ABA), clade A PP2C phosphatases inhibit protein kinases such as SnRK2s (Park *et al.* 2009, Raghavendra *et al.* 2010) and Guard Cell Hydrogen Peroxide-Resistant1 (GHR1) (Hua *et al.* 2012) by directly interacting with them. During drought stress, however, ABA receptors from the PYR1/PYLs/RCAR family bind to ABA, creating a complex with PP2Cs that suppresses their activity

(Park *et al*. 2009). This suppression allows other kinases, such as Raf-like MAPKKKs (Saruhashi *et al*. 2015), to phosphorylate and activate SnRK2s, triggering downstream ABA signaling pathways. The activation of SnRK2s is a pivotal step in this process (Mustilli *et al*. 2002, Takahashi *et al*. 2017). Of the ten *SnRK2* genes in *Arabidopsis*, *SnRK2.2*, *SnRK2.3*, and *OST1/SnRK2.6*, are strongly activated by ABA (Boudsocq *et al*. 2004; Fig. 1).

Among kinases, OST1 stands out as a key activator of NADPH oxidase, significantly increasing ROS levels in guard cells (Bharath *et al*. 2021). This kinase promotes the activation of Respiratory Burst Oxidase Homolog D and F (RBOH D/F), resulting in elevated levels of ROS, nitric oxide (NO), and calcium (Ca^{2+}). The subsequent rise in Ca^{2+} triggers the activation of Ca^{2+}-dependent protein kinases (CDPKs), which, in turn, stimulate slow anion channel 1 (SLAC1), S-type anion channel 3 (SLAH3), and outward-rectifying potassium channels (K^+_{out}). This coordinated ion efflux from guard cells causes stomatal closure (Montillet *et al*. 2013, Ye *et al*. 2015). Additionally, SnRK2.2 and SnRK2.3 are thought to contribute to longer-term drought responses in guard cells (Virlouvet and Fromm 2015).

Phytomelatonin triggers the reopening of stomata through ABA degradation and scavenging of ROS

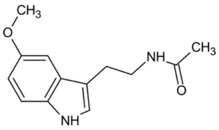
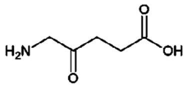
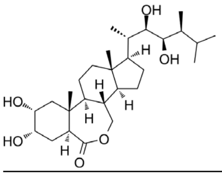
Phytomelatonin, chemically identified as N-acetyl-5-methoxytryptamine, is an indole hormone that was first reported independently by Dubbels *et al.* (1995) and Hattori *et al.* (1995). Research has revealed substantial concentrations of endogenous phytomelatonin in various plant organs (Posmyk and Janas 2009, Stege *et al.* 2010, Korkmaz *et al.* 2014), and multiple functional roles of phytomelatonin have been reported (Back 2021, Wang *et al.* 2022; Table 1). In plants, tryptophan serves as the precursor for melatonin biosynthesis and tryptamine is formed through the catalytic activity of tryptophan decarboxylase (TDC) in cytoplasm. Subsequently, tryptamine undergoes hydroxylation mediated by tryptamine 5-hydroxylase (T5H) to produce serotonin in endoplasmic reticulum. Serotonin is then transformed into N-acetylserotonin through the enzymatic activity of serotonin N-acetyletransferase (SNAT) in chloroplasts or into 5-methoxytryptamine *via* the action of N-acetylserotonin methyltransferase (ASMT)/caffeic acid O-methyltransferase (COMT) in cytoplasm. Consequently, both N-acetylserotonin and 5-methoxytryptamine are converted into melatonin through enzymatic reactions catalyzed by ASMT/COMT and SNAT, respectively (Tan *et al.* 2015, Back *et al*. 2016, Liu *et al.* 2022; Fig. 1*A*).

Phytomelatonin acts as a primary defensive molecule against oxidative stress by directly scavenging harmful free radicals and enhancing the activity of genes responsible for producing antioxidant enzymes (Tan *et al.* 2012, Khan *et al.* 2020). Recent studies have reported its remarkable antioxidant properties compared to other molecules, as one molecule of melatonin can neutralize approximately ten free radicals (Ressmeyer *et al.* 2003), providing robust protection against abiotic stresses (Zhang *et al.* 2013). Moreover, phytomelatonin interacts with other plant hormones, such as ABA, to facilitate the reversal of ABA-induced stomatal closure (Li *et al.* 2015). Under drought stress, increased expression of the *NCED* gene, involved in ABA biosynthesis (Qin and Zeevaart 1999, Kondo *et al.* 2012), results in elevated ABA contents in guard cells, triggering stomatal closure (Iuchi *et al.* 2001). However, pretreatment with exogenous melatonin upregulates melatonin synthetic genes such as tryptophan decarboxylase (*TDC*), tryptamine 5-hydroxylase (*T5H*), arylalkylamine N-acetyltransferase (*AANAT*), and N-acetylserotonin methyltransferase (*ASMT*), leading to a significant increase in endogenous melatonin contents (Zheng *et al.* 2017, Erland *et al.* 2019). Then, this melatonin suppresses the upregulation of the *NCED* gene (ABA biosynthesis) while promoting the upregulation of *CYP707A* (ABA catabolism). Consequently, it reduces ABA accumulation in guard cells and induces reopening of stomata (Li *et al.* 2015, 2021; Table 1). These findings suggest that melatonin application during the post-drought phase could promote stomatal reopening and facilitate earlier recovery of gas exchange by inhibiting ABA biosynthesis genes and promoting those involved in ABA catabolism.

Pretreatment with melatonin also preserves chlorophyll contents by scavenging H_2O_2 and O_2^- molecules (Li *et al.* 2021), suggesting that melatonin acts as an antioxidant. Melatonin enhances the activity of antioxidant enzymes, particularly catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) (Dai *et al.* 2020), as well as nonenzymatic antioxidants like glutathione (GSH) (Hasanuzzaman *et al.* 2017), which are effective in degrading H_2O_2 (Li *et al.* 2012, Park *et al.* 2013) and scavenges H_2O_2 molecules (Tan *et al.* 2000, 2007; Reiter *et al.* 2007). Consequently, the decreased contents of both ABA and H_2O_2 synergistically promote stomata reopening under drought conditions (Fig. 2). The antioxidant effects of melatonin have been reported in apple (Wang *et al.* 2012), grapes (Vitalini *et al.* 2013), rice (Park *et al.* 2013), and maize (Jiang *et al.* 2016), where it facilitates the reversal of stomatal closure. In apple leaves, exogenously applied melatonin helps maintain high turgor pressure in the guard cells and keeps stomata open (Li *et al.* 2015).

Several studies have shown that the expression levels of melatonin synthesis genes are higher in drought-sensitive species, *e.g.*, *Malus hupehensis*, compared to drought-tolerant species, *e.g.*, *Malus prunifolia*, indicating that melatonin expression is stress-inducible (Tan *et al.* 2012, Arnao and Hernández-Ruiz 2013). However, Li *et al.* (2015) showed that drought-sensitive species (*Malus hupehensis*) may be less efficient in melatonin biosynthesis due to genetic mutations affecting key biosynthetic enzymes. Despite this, exogenous melatonin application has been shown to enhance the expression of melatonin biosynthetic genes, potentially compensating for enzymatic inefficiencies and leading to increased endogenous melatonin production. This endogenous melatonin also increases the expression of specific stress-responsive genes, indicating their potential role in enhancing drought

Table 1. Summary of studies investigating the effects of exogenous melatonin, 5-aminolevulinic acid (ALA), and brassinosteroids (BRs) on stomatal opening in various plant species.

Plant hormone	Plant name	Mechanism of action	References
Phytomelatonin 	Apple (*Malus hupehensis*) (*Malus prunifolia*)	Downregulates ABA synthetic gene (*MdNECD3*), upregulates ABA catabolic genes (*MdCYP707A1*, *MdCYP707A2*), and upregulates the expression of melatonin synthetic genes (*MdTDC1*, *MdAANAT2*, *MdT5H4*, and *MdASMT1*), causing opening of stomata	Li *et al.* (2015)
	Maize (*Zea mays*)	Inhibits upregulation of ABA synthesis-related gene (*NECD1*), promotes upregulation of ABA catabolic genes (*ABA8ox1* and *ABA8ox3*) and increases endogenous melatonin levels, thus opening stomata	Li *et al.* (2020)
5-aminolevulinic acid (ALA) 	*Arabidopsis thaliana*	Decreases ABA-induced H_2O_2 and cytosolic Ca^{2+} accumulation in guard cells to inhibit the stomatal closure	An *et al.* (2016)
	Melon (*Cucumis melo*)	Increases stomatal conductance and photosynthetic rate as well as apparent quantum yield and carboxylation efficiency	Wang *et al.* (2004)
	Apple (*Malus domestica*)	Flavonols induced by ALA inhibit ABA-induced stomatal closure *via* decreasing ROS accumulation in guard cells	Liu *et al.* (2016)
	Pepper (*Capsicum annuum*)	Increases relative water content, stomatal conductance, and superoxide dismutase (SOD) activity, thus improves plant growth	Korkmaz *et al.* (2010)
	Oilseed rape (*Brassica napus*)	Improves plant growth, photosynthetic gaseous exchange capacity, water potential, and chlorophyll content	Naeem *et al.* (2010)
	Apple (*Malus domestica*)	Promotes *Malus domestica* protein phosphatases 2A catalytic subunit (MdPP2AC) enzyme activity that enhances stomatal opening by reducing Ca^{2+} and H_2O_2 levels but increasing flavonol levels in guard cells	Chen *et al.* (2023)
Brassinosteroids (BRs) 	*Arabidopsis thaliana*	Mediates sufficient K^+ uptake *via* K^+_{in} channel expression in guard cells that results in inhibition of ABA-induced stomatal closure	Inoue *et al.* (2017)
	Arabidopsis thaliana	Downregulates ABA biosynthetic genes that reduces ABA accumulation in guard cells, leading to the inhibition of ABA-induced stomatal closure	Ha *et al.* (2018)

tolerance (Supriya *et al.* 2022). Enhanced stress tolerance reduces electrolyte leakage, preserves photosynthetic pigments, and improves photosynthesis efficiency by facilitating stomatal reopening (Jones 1998, Yang *et al.* 2022), highlighting its potential agricultural applications for improving crop performance.

5-aminolevulinic acid reverses ABA-induced stomatal closure *via* reducing H_2O_2 and Ca^{2+} contents

5-aminolevulinic acid (ALA) is a critical precursor in tetrapyrrole biosynthesis, producing essential compounds such as chlorophyll and heme in plants (An *et al.* 2016). Since its discovery by Bindu and Vivekanandan (1998), ALA has been recognized for its hormonal activities in plant tissue culture. Over the past two decades, extensive research has highlighted ALA's significance as a pivotal intermediate in biological metabolism and a vital plant growth regulator (Wu *et al.* 2019). It modulates various key physiological processes, including promoting plant growth and enhancing plant stress tolerance (Akram and Ashraf 2013).

For the biosynthesis of ALA, the C5-pathway serves as the predominant process among higher plants (Jiang *et al.* 2022; Fig. 2*B*). L-glutamate serves as the precursor for ALA synthesis in the C5-pathway, where it undergoes ligation with $tRNA^{Glu}$ to form L-glutamyl-tRNA, mediated by glutamyl-tRNA synthetase (GluTS) enzyme (Czarnecki and Grimm 2012). Subsequently, GluTR catalyzes the conversion of the carboxyl group of Glu-tRNA into a formyl group, leading to the formation of L-glutamic acid 1-semialdehyde (GSA) (Tanaka and Tanaka 2007). Finally, ALA is synthesized *via* transamination catalyzed by glutamate-1-semialdehyde aminotransferase (GSAT) (Akram and Ashraf 2013, Wu *et al.* 2019; Fig 1*B*). All these enzymatic reactions take place within the chloroplast stroma (Wang and Grimm 2015). GluTR plays a crucial role in the ALA synthesis pathway, regulating ALA contents and acting as a rate-limiting factor in its synthesis (Zhao *et al.* 2014). In higher plants, this reductase is encoded by the *HEMA1* gene (Nagahatenna *et al.* 2015).

ALA has been proven to enhance plant photosynthesis by increasing chlorophyll biosynthesis (Wu *et al.*

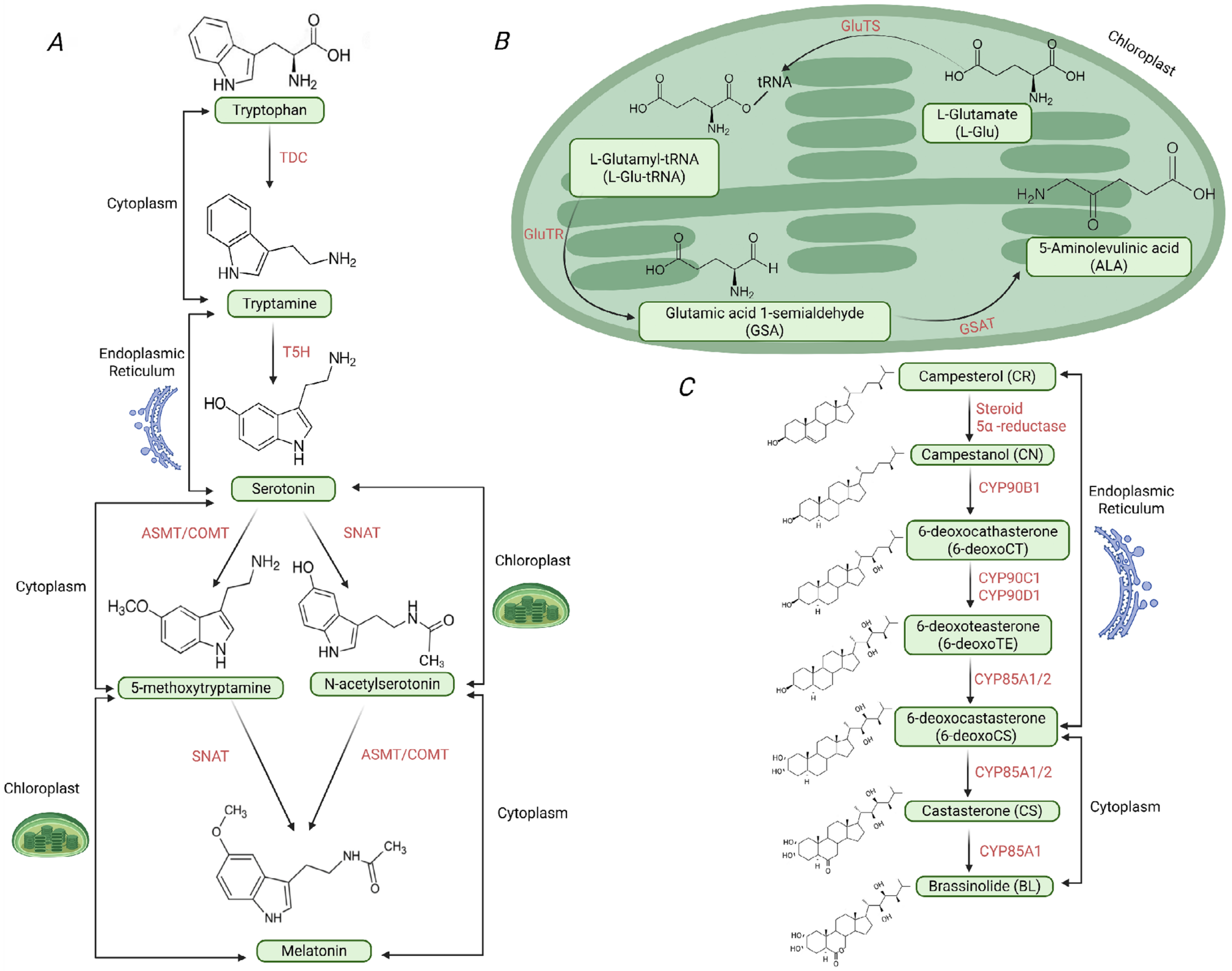


Fig. 2. Simplified biosynthetic pathways of (*A*) melatonin, (*B*) 5-aminolevulinic acid (ALA), and (*C*) brassinosteroids (BRs) in plants, highlighting enzymatic reactions and subcellular localizations. The enzymes involved in melatonin biosynthesis are: TDC (tryptophan decarboxylase), T5H (tryptamine 5-hydroxylase), ASMT (N-acetylserotonin methyltransferase), COMT (caffeic acid O-methyltransferase), and SNAT (serotonin N-acetyle transferase). The enzymes responsible for ALA biosynthesis are GluTS (glutamyl-tRNA synthetase), GluTR (glutamyl-tRNA reductase), and GSAT (glutamate-1-semialdehyde aminotransferase). The enzymes and cytochrome P450s (CYP450s) responsible for the biosynthesis of brassinolide are steroid 5α-reductase, CYP90B1, CYP90C1, CYP90D1, CYP85A1, and CYP85A2.

2019) and by increasing stomatal conductance in both non-stressed and stressful environments, thereby promoting plant growth and development (Liu *et al.* 2011, Akram and Ashraf 2013, An *et al.* 2016). H_2O_2 and Ca^{2+} are important signaling molecules in guard cells for ABA-induced stomatal closure, which limits plant photosynthesis and growth (Pei *et al.* 2000, Wang *et al.* 2014). Interestingly, in many species (Wang *et al.* 2004, Youssef and Awad 2008, Korkmaz *et al.* 2010), the exogenous application of ALA eliminates H_2O_2 molecules through its antioxidant defense system and reduces Ca^{2+} in guard cells. Thus, the elimination of H_2O_2 reduces the stomatal limitation and significantly promotes stomatal reopening, suggesting that ALA has significant potential for use in agriculture and forestry production.

Exogenous application of ALA reduces ABA-induced H_2O_2 accumulation through the degradation of ABA or by disrupting ABA signaling (An *et al.* 2016; Table 1). Furthermore, it has been shown that ALA reduces cytoplasmic Ca^{2+} in guard cells by suppressing Ca^{2+} channel activity. This effect is similar to that of ethylene glycol tetraacetic acid (EGTA), a Ca-chelating agent, and $AlCl_3$, a blocker of Ca^{2+} channels. As a result, ALA significantly inhibits the closure of stomata by decreasing cytoplasmic Ca^{2+} contents (Schwartz 1985, Zhao *et al.* 2007). ALA also employs some H_2O_2-independent signal pathways for decreasing cytoplasmic Ca^{2+}, such as P-type Ca^{2+}-ATPase, which reduces Ca^{2+} contents by removing cytosolic Ca^{2+} and hence reducing Ca^{2+} content (Fig. 2) (Kollist *et al.* 2014).

The SNF1-regulated protein kinase 2s (SnRK2s) is known to be a key component in the signaling pathways of ABA-induced stomatal closure (Tajdel *et al.* 2016, Li *et al.* 2021, Hasan *et al.* 2022). The SnRK2.6, after being phosphorylated, activates the subsequent elements of ABA signaling (Pei *et al.* 2000, Fujii and Zhu 2009). In contrast, serine/threonine protein phosphatase 2A (PP2A) acts as an inhibitory factor in ABA-mediated signal transduction. PP2A plays a critical role in the dephosphorylation of SnRK2.6, thereby affecting its kinase activity and ABA signal transduction pathways. In apple (Xiong *et al.* 2018) and *Arabidopsis* (An *et al.* 2020), ALA enhances the PP2A enzyme activity and simultaneously suppresses SnRK2.6 activity (Table 1; Chen *et al.* 2023). Furthermore, PP2A interacts with SnRK2.6 for its dephosphorylation and subsequent inhibition of ABA signaling, which ultimately leads to the reopening of stomata (Fig. 2; Chen *et al.* 2023). Xiong *et al.* (2018) showed that treatment with the PP2A inhibitor okadaic acid enhances ABA-induced stomatal closure. This suggests that ALA may facilitate stomatal reopening by activating PP2A. Based on these findings, ALA promotes the re-opening of stomata by inhibiting SnRK2.6 kinase activity through its dephosphorylation *via* activated PP2A.

The enhancement of stomatal opening by ALA also depends on the formation of flavonols in guard cells (Liu *et al.* 2016). It has been demonstrated that PP2A overexpression reduces Ca^{2+} and H_2O_2 contents, whereas it significantly increases flavonol contents. In an experiment by Chen *et al.* (2023), when the expression of PP2A was partially silenced, it resulted in the overexpression of SnRK2.6 and showed opposite effects by increasing Ca^{2+} and H_2O_2 contents in guard cells and reducing flavonol contents. Flavonols act as negative regulators of ABA-induced stomatal closure by modulating ROS contents in guard cells, thereby promoting stomatal opening (Watkins *et al.* 2014). In addition, during ABA-mediated signaling of stomatal closure, the expression of SnRK2.6 blocks KAT1 (K^+_{in} channel), whereas promotes the opening of SLAC1 and GORK (K^+_{out} channel), thus reducing K^+ in guard cells. ALA causes the opening of KAT1 (K^+_{in} channel) and the closing of SLAC1 and GORK, leading to reduced cytoplasmic Ca^{2+}, H_2O_2, and increased flavonols and K^+ into guard cells to open stomata (An *et al.* 2016; Fig. 2).

Brassinosteroids (BR) inhibit stomatal closure through opening of K^+_{in} channels and repression of ABA-biosynthetic genes

Brassinosteroids (BRs) are important plant steroidal hormones that control various physiological processes in plants, including growth, development, and stress resistance (Nolan *et al.* 2020). Mitchell *et al.* (1970) isolated brassinolide, the first identified BR, from *Brassica napus* pollen. The biosynthetic pathway of BRs in plants begins with campesterol, a sterol precursor, which is synthesized from squalene through a series of enzymatic reactions in the cytosol and endoplasmic reticulum. Campesterol is converted to campestanol through the action of the steroid 5α-reductase enzyme, which is encoded by the *DET2* gene. Campestanol (CN) undergoes a series of modifications, including hydroxylation and oxidation reactions catalyzed by cytochrome P450 enzymes, leading to the sequential formation of 6-deoxocathasterone (6-deoxoCT), 6-deoxoteasterone (6-deoxoTE), 6-deoxocastasterone (6-deoxoCS), castasterone (CS), and ultimately brassinolide (BL), one of the most biologically active brassinosteroids in plants. In addition to brassinolide, various other brassinosteroids are synthesized through similar enzymatic steps (Fujioka and Yokota 2003, Chung and Choe 2013, Oh *et al.* 2015; Fig. 1*C*).

Recent studies have uncovered that BRs have the potential to reverse ABA-induced stomatal closure by repressing ABA biosynthetic genes or promoting the activity of K^+_{in} channels (Table 1; Inoue *et al.* 2017, Ha *et al.* 2018). For example, BR treatment downregulates the expression of ABA-biosynthetic genes, such as *NECDs* and *AAO3*, that leads to reduced ABA accumulation, thereby promoting stomatal reopening (Ha *et al.* 2018). Some studies have shown that phytohormone BR is perceived by the extracellular domain of the BRASSINOSTEROID INSENSITIVE 1 (BRI1) receptor located on the cell surface (He *et al.* 2000, Wang *et al.* 2001). Upon activation of the BRI1 receptor, subsequent components start intracellular signaling, which regulates the expression of BR-responsive genes (Belkhadir and Chory 2006, Clouse 2011). This regulation results in the opening of K^+_{in} channels, triggering an influx of K^+ ions (Kwak *et al.* 2001, Lebaudy *et al.* 2008). BRs also have been shown to enhance plasma membrane H^+-ATPase activation, leading to an increase in the hyperpolarization of the guard cell plasma membrane (Assmann *et al.* 1985, Shimazaki *et al.* 1986). The hyperpolarization of guard cells facilitates the uptake of potassium ions through K^+_{in} channels (Dietrich *et al.* 2001, Marten *et al.* 2010). As a result, potassium ions reduce the water potential of guard cells, leading to the absorption of water and the subsequent opening of stomata (Inoue *et al.* 2010). Thus, BRs may regulate the stomatal aperture by modulating the K^+_{in} channels (Fig. 2).

Physiological role of reversal of ABA-induced stomatal closure

Stomatal resistance is a major limiting factor to photosynthesis and plant growth under non-stressed and drought conditions (Yang *et al*. 2012, Wang *et al*. 2014, Gago *et al*. 2019). However, few attempts have been made to stimulate stomatal opening to improve photosynthesis, likely because of the challenge of balancing CO_2 absorption and water loss (Inoue *et al.* 2017, Chen *et al.* 2023), especially in the face of xylem hydraulic dysfunction by cavitation under drought stress (Choat *et al*. 2018). For example, although the *SLAC1* mutant in rice possesses stomata that remain open for extended periods, facilitating increased CO_2 absorption for photosynthesis under well-watered conditions, the mutation did not ultimately impact plant growth, as plants experienced increased water loss due to open stomata, making them more susceptible to drought (Kusumi *et al*. 2012).

Earlier stomatal reopening and subsequent recovery of gas exchange after the drought period can significantly benefit plants by (*1*) enabling them to continue photosynthesis and recover their productivity (Gago *et al.* 2020), (*2*) establishing a transpiration stream that enables the absorption of mineral nutrients by roots and their distribution across various plant tissues, vital for growth (Shimazaki *et al.* 2007), (*3*) assisting plants in regulating leaf temperature *via* evaporative cooling (Urban *et al.* 2017, Marchin *et al.* 2022), (*4*) mitigating the risks of carbon starvation and enabling plants to allocate resources for repairing drought-induced cellular damage while restoring physiological functions (Peltier *et al.* 2023). An early reopening of stomata also enhances CO_2 fixation, hence diminishing photorespiration and avoiding oxidative damage caused by ROS (Sierla *et al.* 2016). Plants that can rapidly reverse stomatal closure can quickly take advantage of favorable conditions, such as increased soil moisture and atmospheric CO_2 availability. Thus, crops engineered for accelerated reversal of ABA-induced stomatal closure could achieve high yields by resuming photosynthesis and biomass accumulation sooner.

Nevertheless, forcibly inducing stomatal opening in plants with severe hydraulic damage can exacerbate water deficits within the leaf if xylem embolism is widespread (Rehschuh *et al.* 2020, Wagner *et al.* 2023). In such scenarios, leaf water consumption may surpass the capacity of xylem water supply, intensifying further hydraulic damage and potentially jeopardizing survival (Brodribb *et al.* 2021). Therefore, the net benefit of promoting stomatal reopening hinges on both the plant's capacity to recover its hydraulic functions and the extent of drought-induced xylem embolism. Facilitating earlier post-drought stomatal recovery requires an understanding that hydraulic recovery capacity varies among species, and even among different varieties within the same species, depending on their structural and physiological traits (Duan *et al.* 2022). In species capable of efficient development of new conductive tissues, promoting stomatal reopening after drought can accelerate photosynthetic recovery; however, in species with limited hydraulic recovery capacity, early stomatal opening is not advisable as it may increase the risk of hydraulic failure. As such, these traits should be carefully considered in breeding programs aimed at optimizing post-drought recovery.

Effective methods for post-drought rapid stomatal recovery and stress tolerance are crucial in the face of global climate change and food insecurity. Recently, upregulation of stomatal opening by application of phytohormones or plant growth regulators to improve drought tolerance has been demonstrated, indicating promising potential in agriculture and forestry (Li *et al.* 2015, Chen *et al.* 2023). Thus, it is possible to enhance plant photosynthesis as well as resilience to many abiotic stressors by applying melatonin, ALA, and BRs during a post-drought recovery phase. The application of these bioactive compounds can restore stomatal function and facilitate the transition from stomatal closing to opening. However, to optimize their effectiveness, it is essential to select the appropriate timing of application, ensuring that stomatal opening is promoted without causing excessive water loss, which could compromise xylem hydraulic integrity (Brodribb *et al.* 2021) and therefore plant survival.

Concluding remarks and future perspectives

This review sheds light on the potential mechanisms underlying the post-drought reversal of ABA-induced stomatal closure, highlighting its role in enhancing photosynthesis after drought stress in plants. We have provided insights into the molecular aspects of these physiological processes. The application of phytomelatonin, ALA, and BRs can effectively inhibit or reverse ABA-induced stomatal closure by reducing the contents of H_2O_2 and Ca^{2+}, opening K^+_{in} channels, and repressing ABA biosynthetic genes. Furthermore, their application increases the endogenous concentration of phytomelatonin, ALA, and BRs through respective biosynthetic gene activation. Therefore, we anticipate that applying these phytohormones or genetically modifying the biosynthesis of these phytohormones has the potential to enhance plant photosynthesis and growth. Understanding the precise mechanisms controlling stomatal opening is crucial to ensure the correct application of substances that induce this process. This knowledge will help maximize their benefits for plant growth and photosynthesis while minimizing the potential negative effects of prolonged stomatal closure. Future research should focus on optimizing these treatments under field conditions to enhance their practical applicability in improving drought resilience. This information can then be utilized for breeding programs aimed at developing crop varieties with enhanced drought resilience by early opening of stomata during the post-drought phase.

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