Phytohormone-Mediated Stomatal Response, Escape and Quiescence Strategies in Plants under Flooding Stress

Kazi Khayrul Bashar [1,*] [iD]**, Md. Zablul Tareq** [2]**, Md. Ruhul Amin** [1] [iD]**, Ummay Honi** [1] [iD]**, Md. Tahjib-Ul-Arif** [3] [iD]**, Md. Abu Sadat** [1] [iD] **and Quazi Md. Mosaddeque Hossen** [1] [iD]

[1] Bangladesh Jute Research Institute, Manik Mia Avenue, Dhaka 1207, Bangladesh; shironbge03@gmail.com (M.R.A.); lethe_0000@yahoo.com (U.H.); sadat@snu.ac.kr (M.A.S.); mosaddequebjri@gmail.com (Q.M.M.H.)
[2] Bangladesh Jute Research Institute, Jagir, Manikganj 1800, Bangladesh; zablulbarj@gmail.com
[3] Department of Biochemistry and Molecular Biology, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh; arif1002215@gmail.com
[*] Correspondence: kazi.khayrulbashar@gmail.com

Abstract: Generally, flooding causes waterlogging or submergence stress which is considered as one of the most important abiotic factors that severely hinders plant growth and development. Plants might not complete their life cycle even in short duration of flooding. As biologically intelligent organisms, plants always try to resist or survive under such adverse circumstances by adapting a wide array of mechanisms including hormonal homeostasis. Under this mechanism, plants try to adapt through diverse morphological, physiological and molecular changes, including the closing of stomata, elongating of petioles, hollow stems or internodes, or maintaining minimum physiological activity to store energy to combat post-flooding stress and to continue normal growth and development. Mainly, ethylene, gibberellins (GA) and abscisic acid (ABA) are directly and/or indirectly involved in hormonal homeostasis mechanisms. Responses of specific genes or transcription factors or reactive oxygen species (ROS) maintain the equilibrium between stomatal opening and closing, which is one of the fastest responses in plants when encountering flooding stress conditions. In this review paper, the sequential steps of some of the hormone-dependent survival mechanisms of plants under flooding stress conditions have been critically discussed.

Keywords: flood; plants; hormonal homeostasis; physiological activity

1. Introduction

Several oxygen limiting factors, such as flooding, waterlogging, and partial or full submergence are detrimental for normal growth and development of plants [1]. Sea, river belt and low land areas experience limited or reduced crop production due to the flooding stress. Plants try to adapt to these adverse conditions by applying several strategies, like the storage of energy, elongation of the petiole or internodes, maintenance of water level by regulating stomatal movements, the formation of adventitious roots, development of aerenchyma etc. [2–5]. Crop plants simultaneously activate various biochemical reactions, molecular and signaling pathways, and physiological processes to cope with this oxygen-limiting condition [1,6].

Phytohormone plays a central role in all morphological, anatomical, biochemical, molecular and signaling mechanisms for plant survival under oxygen-limiting stress conditions. Predominantly, ethylene, gibberellins (GA) and abscisic acid (ABA) play the most crucial roles during submergence stress conditions in plants [7]. Ethylene directly and/or indirectly induces GA expression that aids

plants in carrying out the escape and/or quiescence strategy. Petiole/internode elongation and storage of carbohydrates results from the escape and quiescence strategy, respectively in plants under submergence stress [8]. GAs are directly involved in escaping submergence stress in both DELLA (N-terminal D-E-L-L-A amino acid sequence) dependent and independent pathways [9]. Furthermore, ethylene and ABA are directly responsible for the stomatal closure under waterlogging or post-waterlogging stress [10]. On the other hand, GAs are responsible for the stomatal opening under the same stress conditions [11]. So, balanced expression of these three hormones is highly indispensable to maintain the ratio of stomatal opening and closing in plants under excess water stress conditions.

Based on the above facts, this review paper proposes flowcharts of sequential steps for stomatal closing and escaping and quiescencing strategies to offer the best possible explanations. This might help plant scientists to consider several factors during the development of waterlogging-tolerant plant varieties.

2. Ethylene, GA and ABA Interactions in Plants under Submergence Stress

Under submergence stress, ethylene, GA and ABA play influential roles in the survivability of the submerged plants, where ABA biosynthesis is reduced and GA signaling is induced for shoot elongation, especially in rice plants (variety: C9285) [12,13].

Plants have evolved two types of strategies, i.e., escape strategy and quiescence strategy, to survive under flooding stress. In the escape strategy, the rice plant elongates its internodes under slow progressive flooding conditions. On the other hand, rice plants reserve energy under deep transient flash flooding conditions to escape the unfavorable conditions, which is termed the quiescence strategy [14,15]. It is quite interesting that two different functions of two distinct gene families under the same subgroup of a transcription factor are involved in submergence tolerance in plants. This is a complex process, but one that is interesting to study, and required to unveil this mechanism by functional genomics. Under the *AP2/ERF* (*Apelata2/Ethylene response factor*) transcription factor (TF) subgroup, the *Snorkel (SK)* gene is responsible for internode elongation, whereas *Sub1A* (*Submergence 1A*) is related to shoot elongation restriction [16].

In low land rice varieties, the *ERF* transcription factor, *Sub1*, is considered as a major player in submergence tolerance [17,18]. As a quiescence strategy in rice genotypes, ethylene directly enhances *Sub1A* expression. *Sub1A* induces the over accumulation of GA signaling repressors, *Slender Rice-1* (*SLR1*) and *SLR1 Like-1* (*SLRL1*). *Sub1A,* a group under VII *AP2/ERF* transcription factor, restricts shoot elongation by suppressing the *SLR1* and *SLRL2* for saving energy that is necessary for growth and development under desubmergence conditions. Therefore, ethylene is indirectly responsible for the induction of these GA signaling repressors and the reduction of GA responsive gene expression under submergence stress through the *Sub1A*-dependent pathway. *Sub1A* may also play an important role in limiting ethylene production during submergence stress conditions, resulting in the restriction of ethylene-induced enhancement of GA responsiveness in submergence tolerant varieties [17]. The function of *Sub1A1* is also regulated by MPK3 (Mitogen-activated protein kinase3). MPK3-dependent phosphorylated *Sub1A1* binds to the G-box of the MPK3 promoter to regulate its activity [19].

On the other hand, ethylene can directly enhance GA responsive shoot elongation in rice genotypes as an escape strategy of submergence stress, which is not only a highly energy-consuming process, but also requires the continuous production of energy. Due to the lack of *Sub1A* in submergence-susceptible genotypes, plants' survivability in the desubmergence stage is very low or limited [20]. Thus, *Sub1A* acts as a limiting factor for ethylene-promoted GA responsive shoot elongation in tolerant genotypes during submergence conditions to store or save the energy required for normal physiological and biochemical activities [21].

Moreover, in rice, *Sub1A* actively participates in maintaining chlorophyll contents and carbohydrate reserves in photosynthetic tissues [22]. *Sub1A* increases brassinosteroid (BR) levels

in rice plants under submergence stress. BR induces GA catabolic *SLR1* proteins which restrict shoot elongation under oxygen-limiting conditions. In addition, BR enhances the expression of *GA2ox7* (*GA 2 oxidase7*) as an early response (within 1 d after submergence), which is responsible for catabolic GA degradation of endogenous GA_4 [23] (Figure 1). *OsAP2-39*, an *Apelata 2* (*AP2*) transcription factor, directly regulates the ABA biosynthetic gene *OsNCED1* (*9-cis-epoxycarotenoid dioxygenase 1*) and the GA repressing *EUI* (*Elongation of uppermost internode I*) gene. Over-expression of *OsAP2-39* has been shown to enhance drought resistance in rice by producing more ABA and degrading GA [24], which supports the antagonistic crosstalk between ABA and GA as a crucial mechanism to control plant growth and development under abiotic stress conditions [25]. From the above discussion, it can be said that *OsAP2-39* might have great scope to restrict GA signaling in plants under waterlogging or submergence conditions, and stomatal control through ABA signaling pathways under desubmergence conditions.
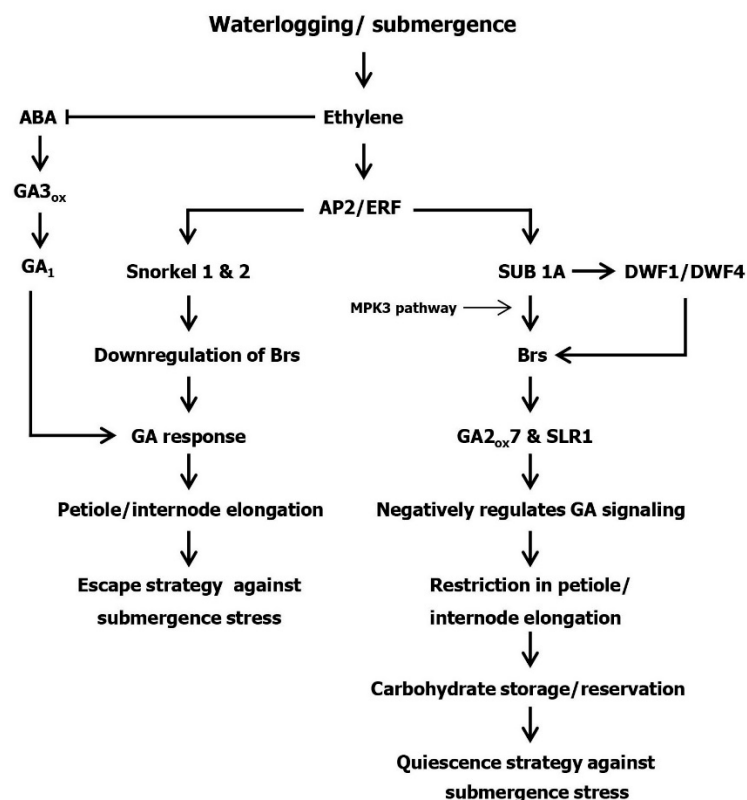

Figure 1. Ethylene-mediated escape and quiescence strategies in plants against submergence stress. Enhanced ethylene expression under submergence stress induces *Snorkel* and *Sub1A* genes for escape and quiescence strategies respectively. Ethylene suppresses ABA expression, which triggers GA_1 expression for escape strategy in plants. ABA: Abscisic acid; AP2/ERF: Apelata2/Ethylene response factor; Brs: Brassinosteroids; DWF1/4: Dwarf 1/4; GA_1: Gibberellins 1; GA2ox7: GA 2 oxidase7; GA3ox: GA 3 oxidase; Sub1A: Submergence1A; SLRL1: SLR1 Like-1.

In deep water rice, ethylene enhances the expression of *Snorkel1* (*SK1*) and *Snorkel2* (*SK2*) which are responsible for significant internode elongation via GA signaling pathways [26]. *Snorkel* genes are only present in lowland deepwater rice accessions for their internode elongation through downregulation of BR biosynthesis as an escape mechanism under submergence stress [1] (Figure 2).
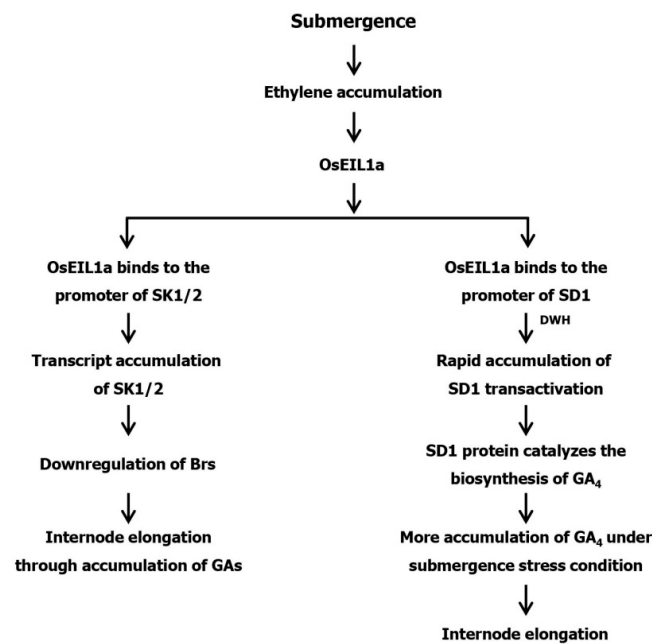
Figure 2. Proposed model for rice internode elongation under submergence stress conditions. Modified figure [13]. *EIL1a* binds with the both promoters of *SK1/2* and *SD1* in rice under submergence stress conditions. *SK1/2* downregulates Brs that induce internode elongation through the accumulation of GAs. On the other hand, *SD1* induces internode elongation through the accumulation of GA_4. Brs: brassinosteroids; EIL1a: Ethylene Insensitive 3-like 1a; GA: Gibberellins; SD1: Semidwarf1; SK1/2: Snorkel 1/2.

In rice, *Snorkel* dependent (variety: C9285) and independent (variety: T65) internode elongation for escaping the submergence stress conditions was discovered by [13]. In this escaping strategy the accumulated ethylene enhances *OsEIL1a* (*Ethylene Insensitive 3-like 1a*) in rice plants. In the *Snorkel* dependent escaping strategy, *OsEIL1a* binds to the promoter of *Snorkel1/2* to accumulate the transcript of *Snorkel1/2* [27]. This leads to the downregulation of BR to induce GA-mediated (mainly GA_1) internode elongation [22,25]. GA response enhances the expression of cyclins transcription factor, which leads to rapid cell division in lotus (*Nelumbo nucifera*) under submergence stress conditions [28]. However, as a *Snorkel* independent escaping strategy, *OsEIL1a* binds to the promoter of *SD1 (Semidwarf1)* for DWH (deepwater rice-specific haplotype) mediated rapid amplification of *SD1* transactivation. The SD1 protein catalyzes the biosynthesis of bioactive GA species, GA_4 that increases GA_4 level in addition to GA_1 after submergence. GA_4 is more capable of internode elongation than GA_1 [13]. So, *Snorkel* independent *SD1* mediated internode elongation in rice is comparatively faster than that of the *Snorkel* dependent pathway (Figure 2).

Rumex plants showed *Snorkel* independent petiole elongation. In flood-tolerant *Rumex palustris*, ethylene reduces *RpNCED* expression which inhibits ABA biosynthesis. Thus, *R. palustris* elongates its petiole by degrading ABA into phaseic acid and enhancing GA_1 mediated gene expression in an ethylene-mediated pathway under oxygen-limited condition [29]. *R. palustris* maintains gas exchange between the submerged tissues and the atmosphere by elongating shoots under long-term flooding stress condition [29,30]. In this stress condition, the accumulation of ethylene not only breaks down ABA into phaseic acid, but also downregulates ABA expression by inhibiting 9-cis-epoxycarotenoid dioxygenase expression. Elevated content of ethylene independently degrades ABA through ABA 8' hydroxylase pathway under submergence stress conditions [31]. Inhibition of ABA stimulates GA 3-oxidase to produce bioactive GA (GA_1). The downstream function of GA is to mobilize food materials by the breakdown of starch and cell wall loosening, which ultimately elongates internode or leaf sheath to escape submergence or waterlogging stress conditions [30]. In rice, a similar type of ABA-dependent GA expression was also reported [32]. Both the quiescence strategy and escape

strategy are considered as the survival mechanisms of plants under submergence stress, but escape strategy is considered as a yield limiting factor in rice plants under de-submergence stress [33].

3. DELLA-Dependent GA Expression under Submergence Stress

Gibberellin-insensitive dwarf 1 (GID1), a soluble receptor for GA signaling, is involved in GA-mediated signaling pathways in plants under stress conditions, especially during abiotic stress conditions [34,35]. GA binds to GID1 and generates a GID1-GA complex which has the ability to interact with different growth repressors like DELLA or SLENDER1 (SLR1), a DELLA ortholog in rice [33]. Five types of DELLA are present in the model plant *Arabidopsis thaliana*, namely Gibberellin-insensitive (GAI), Repressor of GA1-3 (RGA), RGA-like1 (RGL1), RGL2 and RGL3 [36]. GID1-GA complex facilitates GA-mediated interaction between GID1 and DELLA protein, which is responsible for conformational changes in DELLA proteins. The *Sleepy1* (*SLY1*) gene contain the F-box domain, which is a positive regulator of GA signaling in *Arabidopsis*. *Sleepy1* (*SLY1*) in *Arabidopsis* and GID2 in rice are capable of recognizing this change of DELLA proteins where *SCF* (*SLY1*) (Skp1, Cullin, F-box), E3 ubiquitin ligase ubiquitinates DELLA protein, targeting DELLA for degradation through proteolysis by the 26S proteasome [34,35,37]. Thus GA expression is continued in plants by suppressing the expression of DELLA protein (Figure 3A).
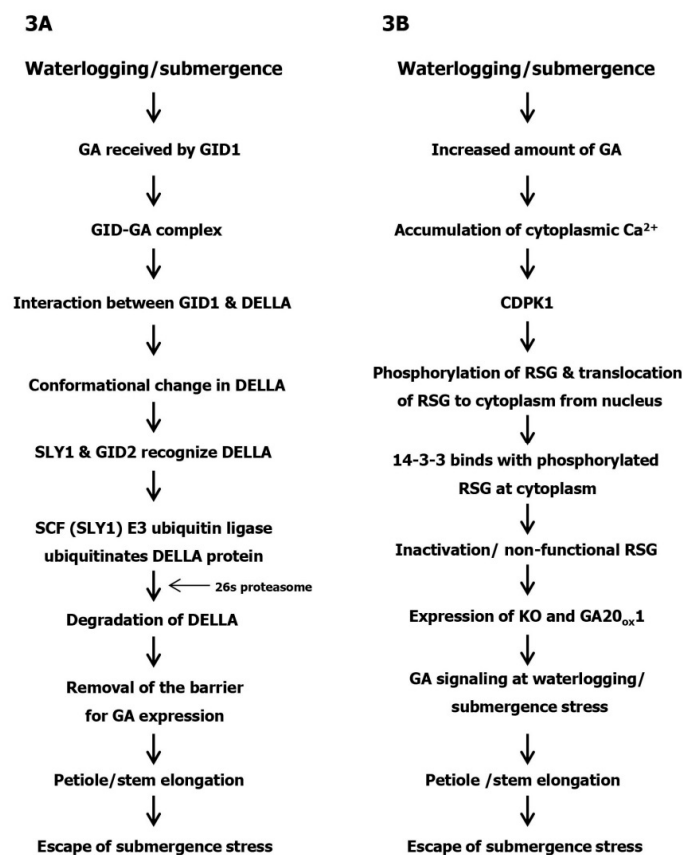

Figure 3. DELLA-dependent and -independent GA signaling in plants under submergence stress conditions. (**3A**) DELLA-dependent escape strategy in plants; GID-GA complex makes conformational change in DELLA. After that SCF ubiquitinates DELLA protein which induces GA expression for petiole/stem elongation. (**3B**) DELLA-independent escape strategy in plants; Ca^{2+} accumulation enhances CDPK1 production for the phosphorylation of RSG to translocate it into the cytoplasm from nucleus. 14-3-3 inactivates RSG as a GA-mediated submergence escaping strategy. CDPK1: Ca2+-dependent protein kinase 1; DELLA: N-terminal D-E-L-L-A amino acid sequence; GA: Gibberellins; GA20ox1: GA 20 oxidase1; GID1: Gibberellin-insensitive dwarf 1; GID2: Gibberellin-insensitive dwarf 2; RSG: Repression of shoot growth; SCF: Skp1, Cullin, F-box; SLY1: Sleepy1.

4. DELLA Independent GA Expression under Submergence Stress

GAs can increase cytoplasmic Ca^{2+} very rapidly during various cellular processes occurring inside the cell. However, the mechanism of increasing GA-mediated cytoplasmic Ca^{2+} in a DELLA-independent manner is still unknown. The GA-mediated increase of Ca^{2+} and degradation of DELLAs are completely independent processes [38]. An elevated level of cytoplasmic Ca^{2+} activates Ca^{2+}-dependent protein kinase (NtCDPK1) via a DELLA-independent GA pathway in tobacco [39]. NtCDPK1 is responsible for the translocation of Repression of shoot growth (RSG) from the nucleus to the cytoplasm [40,41]. RSG represses the expression of two important GA biosynthetic genes, *NtKO* and *NtGA20ox1*, which are considered as GA enhancing genes [42,43]. RSG binds to the promoter region of *NtGA20ox1* through GA-mediated approach while RSG binds to *NtKO* promoter in the independent manner of GA concentrations [43]. NtCDPK1 acts as a RSG kinase and phosphorylates RSG, which promotes 14-3-3 to bind with RSG at cytoplasm [40,44,45]. In rice plants, CDPK is induced under low oxygen stress for survivability under anaerobic conditions [46]. 14-3-3 proteins directly bind to the RSG in the cytoplasm and regulate RSG function negatively, making non-functional RSG [41,47]. So, inactivation of RSG by 14-3-3 proteins indirectly helps to express both *NtKO* and *NtGA20ox1* to continue GA biosynthesis for different cellular processes (Figure 3B).

5. ABA in Plants under Waterlogging Stress

Imbalanced conditions between leaf transpiration and root water uptake creates dehydration (physiological drought) stress in plants, that is noticed in plants under waterlogging stress with partially or fully damaged root tissues. The plant hormone ABA has the ability to modify root hydraulic properties [48]. For example, ABA downregulation and upregulation in tomato plants expresses lower and higher hydraulic conductance, respectively [49,50]. Depending on both the flooding duration and plant species, ABA differentially responds in leaves and in the roots of plants. *Malus sieversii* is considered as less tolerant to hypoxia than *Malus hupehensis,* showing a larger increase in ABA in both the leaf and root tissues [51]. In *Gerbera jamesonii,* ABA levels were increased in both leaf and root, where a transient increase in root follows a sharp decrease in the recovery period [52]. ABA is also increased in roots and leaves of *Triticum aestivum* L., but gradually decreases after reaching certain levels [53].

6. Stomatal Regulation at Waterlogging Stress

Stomata is a specialized epidermal pore-like structure consisting of two guard cells through which plants exchange both CO_2 and O_2 with the environment [54,55]. Stomatal conductance was insignificantly affected by flooding stress despite a significant reduction of photosynthesis in both flood-tolerant and flood-sensitive poplar genotypes [56]. A similar finding was also reported in maize plants where flooding resulted in a significant decrease in photosynthesis and ribulose-1,5-bisphosphate carboxylase activity without a noticeable reduction in the rates of stomatal conductance [57]. In GID1 mutated rice plant, increased chlorophyll content has been found, which is subsequently responsible for the increase of carbohydrate production and decrease of reactive oxygen species (ROS) accumulation under submergence stress [58]. Reduction in leaf transpiration is a common phenomenon of flooding stress, which affects the lowered stomatal aperture [59–61]. It is difficult to believe that flooding paradoxically causes leaf dehydration in plants [62–64]. Stomatal closing is operated by the turgor pressure and volume of guard cells. ABA-dependent signaling effluxes of anions, potassium ions and conversion of malate into starch trigger the reduction of turgor pressure, as well as changing the volume of guard cells close the stomata [65]. Under hypoxic stress, *hypoxia responsive universal stress protein 1* (*HRU1*) activates *AtrbohD* (*Respiratory burst oxidase homolog protein D*), following interaction between *ROP2* (*Rho of plants 2*) and *AtrbohD* in *Arabidopsis* under low oxygen stress conditions. NADPH oxidase *AtrbohD* is responsible for alcoholic fermentation and ABA-dependent stomatal closure in plants under abundant water conditions [66,67]. It has been

reported that barley plants swiftly close the stomata after flooding stress imposition [68]. A similar phenomenon was also observed in pea plants under flooding conditions, where a prompt closure of stomata from older leaves was recorded. Wilting of younger leaves was protected by older pea leaves by increasing ABA-dependent stomatal closure [69]. Unwilted younger pea leaves might result from the ABA transportation from older to younger leaves or de novo biosynthesis of ABA in the younger leaves [70]. Though *Populus deltoides* is considered as a waterlogging tolerant plant species, it showed a significant reduction in stomatal conductance at both waterlogging and de-waterlogging stress, with an exception at recovery period after 90 days of waterlogging stress [71].

Hormonal Regulation in Stomatal Closing of Plants under Waterlogging Stress

Several waterlogging related experiments showed a positive correlation between ABA accumulation and increase in ROS, in soybean roots [72], barley roots and leaves [73], maize leaves [74], bread wheat roots [75]. The enzymatic mechanisms responsible for ABA-triggered ROS generation in guard cells at the molecular level are little known at present. ABA initiates H_2O_2 generation by using the plasma membrane NADPH oxidase [76]. H_2O_2 activates plasma membrane Ca^{2+} channels, resulting in an increase in Ca^{2+} level in guard cells. [77]. Inhibition of inward K^+ channels in guard cells is the result of increased Ca^{2+} level in the cytoplasm of guard cells [78,79]. This results in reduced solute accumulation following a reduced amount of water entrance in the guard cells and ultimately leading to stomata closure [80]. In *Arabidopsis*, H_2O_2 can also stimulate NO (nitric oxide) production to induce stomatal closure [81]. Ethylene and ABA activate CuAO (copper amine oxidase) in *Vicia faba* [82,83]. Oxidation of putrescine by CuAO produces H_2O_2, follows stomatal closure in *V. faba* [82] (Figure 4). ABA is also responsible for stomatal closing in plants as a survival mechanism under post-waterlogging stress [84].

Moreover, H_2O_2 is also produced by extracellular calmodulin (ExtCaM) which is activated by heterotrophic G protein [85]. In rice, accumulated ethylene induces G protein for aerenchyma formation under flooding stress [86]. G protein induces H_2O_2 production for epidermal cell death in rice under submergence stress [87]. Inactivation of CTR1 (Constitutive triple response 1) is induced by the binding of ethylene to ETR1 (Ethylene receptor 1), ERS1 (Ethylene response sensor 1) and EIN4 (Ethylene insensitive 4), resulting in the activation of G_{alpha} (G protein alpha subunit). G_{alpha} promotes H_2O_2 production in plants via NADPH oxidases. ETR1 and ERS1 translocate the signals of H_2O_2 to EIN2, EIN3 and ARR2 (2-component response regulator), which are essential for stomatal closure functioning [88]. Activated G proteins may inhibit inward K^+ channels via an elevated level of cytoplasmic Ca^{2+} in the guard cells [78,79]. From the above discussion, a proposed signaling pathway may work for stomatal closure in plants under waterlogging stress (Figure 4).

In *Arabidopsis thaliana*, flooding stress operates H_2O_2-mediated stomatal closure followed by an increase in antioxidant enzyme activities [89]. Improvement of anoxia tolerance was confirmed by applying exogenous ABA in different plants including maize, citrus, lettuce and *Arabidopsis* [90–94]. Waterlogged pea plant restricted its leaf ABA to translocate in shoot, while in non-waterlogged plants, ABA moves readily from shoots to roots [95,96]. This extra ABA in pea leaves was responsible for reducing leaf transpiration by the closing of stomata [96].

Stomata closing may occur in an ABA-independent manner. As for example, ABA was increased in citrus after 3 weeks of flooding, indicating that closing of stomata and increase of ABA are independent in citrus plants upon flooding stress, and not only that ABA was transported to younger leaves from older leaves, rather than, as expected, being transportated from roots to shoots [97].
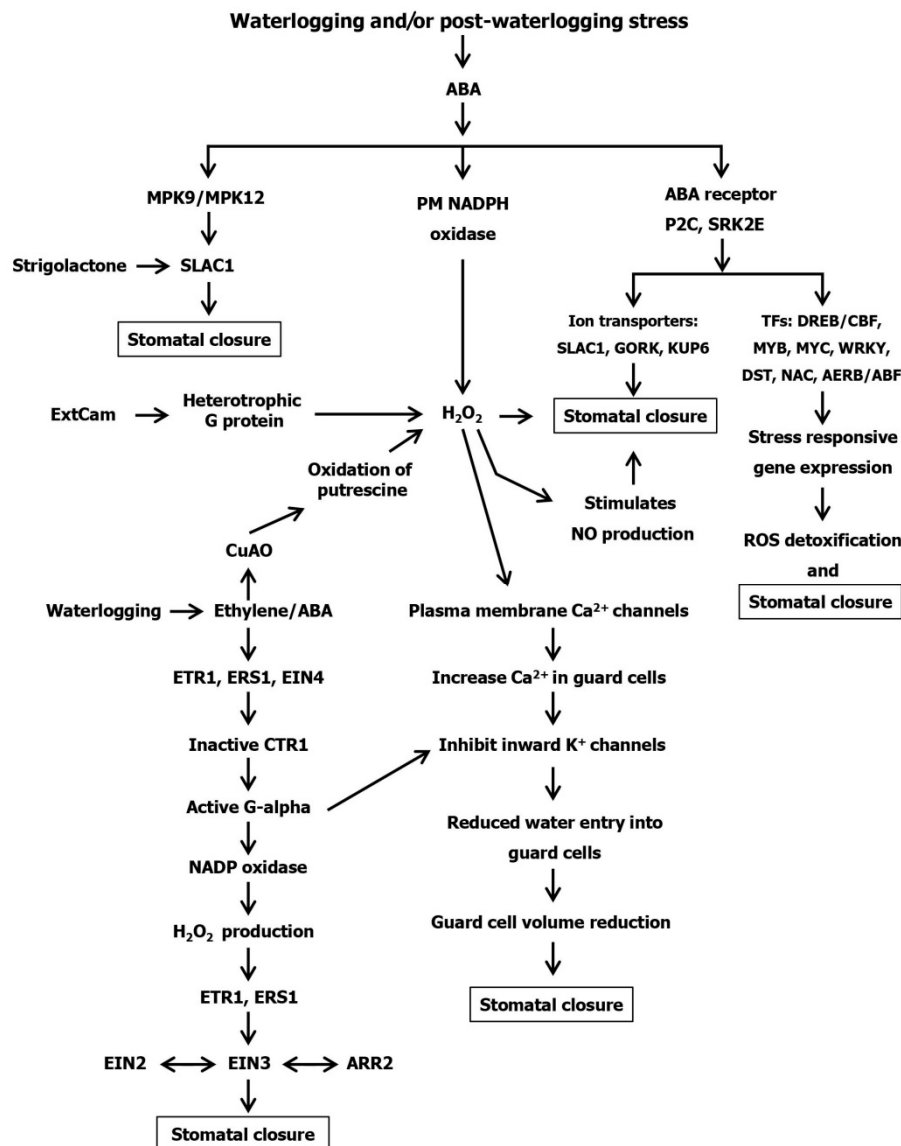
Figure 4. Proposed model for hormone mediated stomatal closure under waterlogging and/or post-waterlogging stress conditions. Modified figure [84]. Ethylene and/or ABA are directly or indirectly enhance H_2O_2 production under waterlogging and/or post-waterlogging stress conditions. H_2O_2 is directly responsible for closing of stomata or indirectly increasing Ca^{2+} in the guard cell for stomatal closure by reducing the volume of the guard cell. ABA: Abscisic acid; AREB/ABF: (ABA)-responsive element binding proteins/ABRE(ABA-responsive element)-binding factors; ARR2: 2-component response regulator; CTR1: Constitutive triple response 1; CuAO: Copper amine oxisase; DREB/CBF: Dehydration-responsive element-binding/C-repeat binding factor; DST: Drought and salt tolerance; EIN: Ethylene Insensitive; ERS1: Ethylene response sensor 1; ETR1: Ethylene receptor 1; ExtCaM: Extracellular Calmodulin; GORK: Guard cell outward-rectifying K+; KUP6: K+ uptake transporter 6; MPK3/9: Mitogen-activated protein kinase3/9; MYB: **My**elo**b**lastosis; MYC2: **My**elo**c**ytomatosis; NAC: NAM (No apical meristem), ATAF (Arabidopsis transcription activation factor) and CUC (Cup-shaped cotyledon) transcription factor; P2C: Protein phosphatase 2C; ROS: Reactive oxygen species; SLAC1: Slow anion channel-associated 1; SRK2E: SNF1 (Sucrose nonfermenting 1)-related protein kinase 2; WRKY: W-tryptophan, R-arginine, K-lysine, Y-tyrosine.

7. Conclusions

From this above discussion, it can be concluded that ethylene directly or indirectly regulates the expression of gibberellins (GAs) and abscisic acid (ABA) in plants under flooding stress conditions. However, ABA plays a major role in stomatal closing, whereas escape and quiescence strategies are controlled by the expression of GA. Finally, it can be concluded that plants maintain their internal homeostasis by balancing hormonal cross talk under excess water stress.

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